Fachbereich Erziehungswissenschaft und Psychologie
der Freien Universität Berlin

Prosocial Behaviour in Captive Sumatran Orangutans (*Pongo abelii*)

Dissertation

zur Erlangung des akademischen Grades

Doktorin der Philosophie (Dr. phil.)

Doctor of Philosophy (Ph.D.)

vorgelegt von

Magistra Artium

Kathrin Susanne Kopp, geb. Werner

Berlin, 2016

Tag der Disputation: 10.01.2017

Erstgutachterin

Prof. Dr. Katja Liebal
Freie Universität Berlin

Zweitgutachterin

PD Dr. Judith Maria Burkart
Universität Zürich

Gemeinsame Promotionsordnung zum Dr. phil/Ph.D. der Freien Universität Berlin vom 2. Dez. 2008 (FU-Mitteilungen 60/2008)

TABLE OF CONTENTS

1 GENERAL INTRODUCTION

The objective of this doctoral thesis is to provide the first systematic investigation on prosociality, a trait that characterises a broad range of behaviours in humans, in our close, yet still not well-known great ape relatives – the orangutans. I will start this general introductory chapter by defining the central concepts. In a second step, I will argue why we need to widen our focus towards a comparative perspective when we study human behaviour and its underlying psychological mechanisms. After introducing the comparative approach, I will suggest general social contexts in which prosocial behaviours are to be expected and briefly review research on particular types of prosocial behaviour in primates. In the third part, I will introduce Sumatran orangutans (*Pongo abelii*) and their particular species characteristics that make them an extraordinary species to study with regard to prosocial behaviour. At the end of this chapter, I will formulate the research questions guiding the line of thoughts throughout this thesis.

1.1 A COMPARATIVE PERSPECTIVE ON PROSOCIAL BEHAVIOUR

1.1.1 A definition of prosocial behaviour

Before starting to consider the phenomenon of prosociality, it is necessary to provide a definition, since *prosocial behaviour* is not a common concept in everyday life. Moreover, since there is no scientific consensus how to define prosocial behaviour, neither within psychology nor across disciplines (Dovidio, Piliavin, Schroeder, & Penner, 2006, p. 21), a consistent and explicit operational definition is even more essential.

To define prosocial behaviour, I follow Eisenberg and Mussen (1989, p. 3): A particular intentional behaviour is defined as *prosocial*, if it results in benefits for an individual or individuals other than the actor. By this rather broad definition, which does not presume a particular motivation underlying the action of a person performing a prosocial act, a wide range of behaviours in different contexts can be subsumed into the category *prosocial behaviour*: e.g. sharing resources, cooperating, helping, intervening in case of conflict, consoling or reconciling.

To emphasise, the criterion that prosocial behaviour benefits another individual does not exclude forms of behaviour from being prosocial, which additionally benefit the actor as well. Nor does it claim that prosocial behaviour has to be motivated by altruism, i.e. solely by genuine concerns for the welfare of the other individual(s) in question. Following Batson and Powell (2003, p. 463), the concepts *altruistic* and *prosocial*, which are often used synonymously, have to be thoroughly kept apart: While *prosocial* specifies a particular *behaviour*, *altruistic* is a specification of a *motivation* underlying a particular behaviour.

1.1.2 Why we need a comparative perspective on human behaviour

In his seminal article *On aims and methods of Ethology* from 1963, Nikolaas Tinbergen outlines that the single question "Why do these animals behave as they do?" actually covers four "Why-questions", each addressing a different level of explanation:

1. *Causation*: What previous events contributed to the occurrence of an actual behaviour? What factors and mechanisms cause the observed behaviour?
2. *Survival value*: What fitness-related, adaptive function(s) does or did the behaviour have? Why has this behaviour been established in the course of the evolution of the species?
3. *Ontogeny*: How has this behaviour developed during the ontogeny of an individual? To which degree is it fix and to which changeable or adjustable depending on the environment?
4. *Evolution*: How did the behaviour evolve? Is it a uniquely species-specific behaviour, or does it occur in other species as well? If it is known for more than one species, did it evolve once or several times in different phylogenetic lineages?

Prosocial behaviour has been a research topic for psychologists for about a century, even if the term *prosocial* first came into use in the early 1960s. Social psychologists mainly focus on possible determinants of prosocial decisions and behaviour (Baldassarri & Grossman, 2013; Batson & Shaw, 1991; Dovidio et al., 2006; Penner & Finkelstein, 1998). Developmental psychologists, on the other hand, are generally interested in when prosocial behaviour and its underlying psychological mechanisms emerge, how they develop over a person's lifespan, and which factors shape their ontogenetic development (Baillargeon et al., 2011; Eisenberg, Fabes, & Spinrad, 2007; Eisenberg & Mussen, 1989; Hay, 1994; A. Martin & Olson, 2015; Zahn-Waxler, Radke-Yarrow, & King, 1979; Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992). Acknowledging Tinbergen's analysis, it becomes obvious that classic developmental and social psychology primarily address the first and third level, i.e. focus on proximate questions, when asking: "Why do people act prosocially?"

To gain a comprehensive understanding of human prosociality, however, it is necessary to also analyse prosocial behaviour at the second and fourth levels, which obviously require an evolutionary but also a comparative perspective on behaviour (Liebal & Haun, 2012). Questions on the survival or – as it is put today – on the adaptive value of prosocial behaviour build the natural issue tackled by evolutionary biologists, behavioural ecologists and biological anthropologists.

The comparative approach, at which I want to focus here, provides an additional method to address ultimate questions on the fourth level. This method has been successfully applied by biologists, especially ethologists, for more than 50 years (Tinbergen, 1963). Since the 1990s, it has become attractive to psychologists as well (e.g. Johnson-Pynn, Fragaszy, & Cummins-Sebree, 2003; Tomasello & Call, 1997), who started to address psychological mechanisms and developmental aspects of prosocial behaviour from a genuinely comparative perspective. In the following section, I want to outline the basic ideas of this approach and its application in comparative behavioural research and psychology, since this approach is both the motivation for and methodological underpinning of my studies on prosociality in captive orangutans.

1.1.3 The comparative approach

The very central idea of the comparative approach in behavioural and psychological research is the assumption that not only anatomical or physiological features, but also animal behaviour and psychological mechanisms have – at least to some degree – a biological basis and are, consequently, a target of natural selection. Since *Homo sapiens* is a mammal species, more specifically a great ape or hominid species (Groves, 2001), this assumption regards human behaviour and psychological mechanisms as well.

However, non-physical features generally provide a certain problem for anyone who aims to study their evolutionary history and adaptive functions, because they do not leave any physical record, or if so, only one that is indirect. Thus, building an evolutionary history on fossils alone would not be an appropriate method in the case of a behavioural trait.

A more promising alternative makes use of some essential assumptions about evolution (Darwin, 1859):

If we assume,

(i) that in the course of evolution, species evolve from other species due to processes as e.g. natural selection, and
(ii) that new features seldom emerge *de novo*, thus instead develop from already existing features or parts of features, and
(iii) that a feature which is successful (or at least neutral) with regard to its adaptive value and therefore spread throughout a species will generally endure in many subsequent species as long as it does not become maladaptive in a changing environment,

it then follows:

(i) that for each two extant species there had been a species that was their last common ancestor, and
(ii) that closely related species share many features that have already evolved during their common evolutionary history.

When we find a particular feature in two or more closely related species, but not in phylogenetically more distant species, then it is very probable that this feature is an evolutionary heritage of a common ancestor. Of course, there is still a probability that the feature evolved twice or more often in the evolutionary history of these species after the splitting of the common phylogenetic lineage. However, for reasons of scientific parsimony it is reasonable to regard those features as homologous, i.e. as features with the same evolutionary origin.

Based on these assumptions, a comparative approach on human behaviour and psychology has two research directions: First, in order to ensure that the behavioural or psychological trait in question is universal for humans, a comparison across different cultures is necessary (Henrich, Heine, & Norenzayan, 2010). If this trait can be found in many, very dissimilar cultures, then, using Ockham's razor, it is very probable that it is a cross-cultural, universal human feature. Second, in order to investigate whether this trait is exclusively human-specific, it is necessary to look for it systematically in as many closely and more distantly related species as possible. For instance, if this trait can also be found in the other great apes, but not in lesser apes or monkeys, then it has probably evolved in a common ancestor of all recent hominids after the divergence of the common lineage of lesser and great apes.

1.1.4 Prosocial behaviours across species

A comparative approach to prosocial behaviour has two major challenges: The first challenge is to find an appropriate definition of prosocial behaviour which is, on the one hand, specific enough to cover human prosociality and, on the other, broad enough to avoid assumptions that would exclude non-human species *a priori* (section cf. 1.1, p. 1). The second challenge is to establish methods that allow for a valid comparison both across cultures and species. To fulfil the latter requirement, a variety of methods has been developed ranging from standardised recording and sampling methods for observational studies (Altmann, 1974), to methods on studying social relationships (Silk, Cheney, & Seyfarth, 2013), post-conflict behaviour (de Waal & Yoshihara, 1983; Veenema, Das, & Aureli, 1994) and food sharing (de Waal, 1989a), and up to experimental paradigms, e.g. variants of the prosocial choice task (Burkart, Fehr, Efferson, & van Schaik, 2007; Colman, Liebold, & Boren, 1969; Horner, Carter, Suchak, & de Waal, 2011; Silk et al., 2005) or the ultimatum game (Hill & Gurven, 2004; Jensen, Call, & Tomasello, 2007; Marlowe et al., 2011; Proctor, Williamson, de Waal, & Brosnan, 2013), as well as tasks on cooperative problem solving (Crawford, 1937; Cronin, Kurian, & Snowdon, 2005; Drea & Carter, 2009) or on instrumental helping (Melis et al., 2011; Warneken, Hare, Melis, Hanus, & Tomasello, 2007).

Over the past three decades, intra- and interspecies comparisons of prosociality and its underlying psychological mechanisms has already deepened our insight into its evolutionary origins (Silk & House, 2011). I will outline some of these findings in the following subsections.

1.1.4.1 Prosocial behaviour and the benefits and costs of group life

Prosociality requires sociality, i.e. group life. Living in groups is one possibility for mastering life that is realised in many species, especially the vast majority of extant diurnal primates including humans. In doing so, primates exhibit a great diversity with regard to group size, mating systems and social structure (Kappeler & van Schaik, 2002).

Group life can be extremely beneficial for an individual, for instance due to better possibilities to detect and protect against predators, enhanced opportunities to mate, greater success to find, exploit, and maintain resources and a reduction of the risk of infanticide (Dunbar, 1988; Sterck, Watts, & van Schaik, 1997; van Schaik & Kappeler, 1997). Furthermore and especially important for primates, sociality is an essential precondition for the transmission of information and the acquisition of skills by social learning (Silk, 2007a; van Schaik & Burkart, 2011).

Advantages of group living arise not only from the mere presence of conspecifics, but also from cooperative interactions in several contexts (Aureli & de Waal, 2000a). Such interactions, which are prosocial behaviours as defined earlier (cf. section 1.1, p. 1), include e.g. alarm calls (Seyfarth, Cheney, & Marler, 1980), allogrooming (Schino & Aureli, 2008), allomaternal care and cooperative breeding (Buchan, Alberts, Silk, & Altmann, 2003; Burkart & van Schaik, 2010; Hill & Hurtado, 2009; Kramer, 2011; Stanford, 1992), cooperative hunting (Boesch, 1994; Packer & Pusey, 1982; Wiessner, 2002), reciprocal exchange of benefits (Bliege Bird, Bird, Smith, & Kushnick, 2002; Carter & Wilkinson, 2013; de Waal, 1997a; Gomes & Boesch, 2009; Romero & Aureli, 2008; Seyfarth & Cheney, 1984) and coalitionary support (Koyama, Caws, & Aureli, 2006; Newton-Fisher, 2006; Schino, Tiddi, & di Sorrentino, 2007). Early studies have investigated these behaviours mainly with regard to their ultimate mechanisms and functional aspects of the interacting individuals' relationships. However, since providing benefits to others often proved to be selective with regard to particular partners, more recent research increasingly takes psychological mechanisms, social as well as contextual factors for behavioural decisions on an individual level into account (Burkart et al., 2007; Cronin, 2012; de Waal & Suchak, 2010; Penner, Dovidio, Piliavin, & Schroeder, 2005).

Particularly in primates, but also in some non-primate species, prosocial interactions predominantly take place among individuals with close long-term relationships, e.g. between mothers and offspring, pair-bonded mating partners, and even between kin or non-kin of the same sex or of different sex outside of a direct mating context, such as allies or friends[1] (Carter & Wilkinson, 2013; Connor, 2007). This comparably recent scientific acknowledgement of interindividual bonds in non-human primates and other mammals (Silk, 2007a) may provide a solution to the controversially debated problem of long-term contingent cooperation (Carter, 2014; Schino & Aureli, 2009, 2010). Several socio-cognitive and affective psychological mechanisms of different complexity have been suggested to promote reciprocity and social bonding (de Waal & Brosnan, 2006; Dunbar & Shultz, 2010; Jaeggi & Gurven, 2013a; Schino & Aureli, 2016; Yamamoto & Takimoto, 2012) that need to be further investigated (Freidin, Carballo, & Bentosela, 2015). Although more research is still needed, there is evidence of a fitness-increasing effect of sociality and social bonds in several primate species and other mammals (Silk, 2007b).

Despite its benefits, group life also means costs for an individual, e.g. due to the higher risk of disease transmission (Côté & Poulinb, 1995) or interindividual conflicts of interest, because of age- or sex-specific needs (van Schaik & van Noordwijk, 1986) or competition over limited resources such as food or mating partners (Janson, 1988; Robbins, 2008). Competition over resources may potentially result in direct costs including injuries or even death due to aggressive interactions, but also in indirect costs by violating and destabilising valuable social relationships (Aureli & de Waal, 2000a; Kummer, 1978). Since social bonds play a central role for the exchange of benefits within primate groups, violating long-term relationships might have even more damaging consequences for an individual than the immediate costs. However, following a broad definition, *conflicts of interest* indicate interindividual conflicts that "[...]arises when individuals express incompatible goals, interests, or actions" (Cords & Killen, 1998) which do not necessarily have to result in aggression (Judge, 2003).

With the *Relational Model*, de Waal and colleagues (de Waal, 1996; de Waal & Aureli, 1997) suggest that an interindividual conflict of interest may result either in avoiding a confrontation, in tolerant behaviour such as sharing, or in aggression. In the latter case, the quality of the relationship influences whether post-conflict affiliative interactions between the opponents take place to minimise the damage for their relationship. Group living species have developed several conflict management mechanisms including various prosocial behaviours to prevent or end conflicts or to minimise their costs. The spectrum of these mechanisms ranges from ritualised greetings (Colmenares, Hofer, & East, 2000; de Waal, 1986), dominance relationships (Preuschoft & van Schaik, 2000), appeasement (Palagi, Paoli, & Borgognini Tarli, 2006), tolerated transfer of food

---

[1] The usage of the terms *friends* or *friendship* with regard to non-human primates is controversial within the literature. While some authors consequently avoid them for non-human social relationships and use e.g. *close associates* instead, others use them set in quotation marks or italics to emphasise both the similarity and a possible qualitative difference from human social relationships. Still, others use them for human and non-human primates alike (Seyfarth & Cheney, 2012; Silk, 2002c).

(Stevens, 2004), third party intervention (Flack, Girvan, de Waal, & Krakauer, 2006) to reconciliation and consolation (de Waal & van Roosmalen, 1979) and right on up to proto and – at least in humans – explicit social norms (Rudolf von Rohr, Burkart, & van Schaik, 2011).

Given the benefits and challenges of group life, prosocial behaviour can generally serve two functions which may be interdependent: increasing benefits and decreasing costs. From this perspective, prosocial behaviour can be expected in three general social contexts: (i) in the context of problem solving so as to increase the benefits of group life, and in (ii) potential or (iii) actual conflict situations so as to reduce the costs of group life. Helping and cooperating are typical prosocial behaviours expected when assistance is needed to solve a problem. Sharing food is appropriate prosocial behaviour in potential conflict situations due to the unequal distribution of resources, while third party intervention and affiliative post-conflict behaviours are those in actual conflicts (Fig. 1).

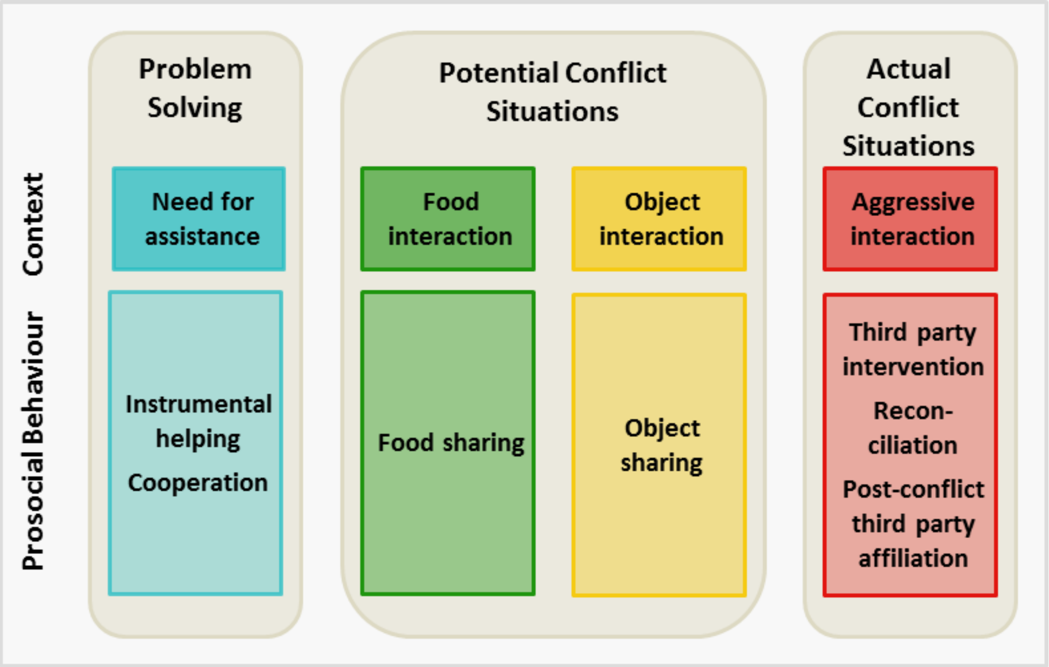

Fig. 1 Situations in which prosocial behaviour might be expected as a means to cope with group life

It has to be emphasised that the proposed categorisation of sharing as prosocial behaviour to mitigate potential conflict situations is only one possible and probably unusual perspective on sharing. However, understanding sharing in terms of managing potential conflicts of interest only means to look at the same phenomenon that is more commonly described as cooperative behaviour from a different angle. This perspective is a functional one and does not make any assumptions about the actual motivation for an individual to share in a particular situation. Sharing, which is motivated by the genuine desire to benefit another individual, is as much captured by this conception as sharing motivated by the intention of avoiding harassment or by the expectation of reciprocated benefits.

My empirical studies, which form the central part of this doctoral thesis (cf. Chapter 2), focus on prosocial behaviours in potential and actual conflict situations. Although my present work does not investigate instrumental helping and cooperation, I will include these items in the following overview about the research on prosociality, since they constitute an essential part of scientific effort to investigate prosocial behaviour in primates.

1.1.4.2 Helping and cooperation

Being confronted with an individual being in need of help or assistance to solve a problem of some sort is a classic context of psychological research on prosocial behaviour (Batson & Powell, 2003). On a more abstract level, two general types of prosocial behaviour can be distinguished with regard to assisted problem solving: cooperation and helping. Cooperation can generally be defined as coordinated interactions of “two or more individuals [...] to achieve a common goal” (Boesch & Boesch, 1989, p. 550). The benefit of these interactions is usually a shared one. Helping, on the other hand, is a unidirectional action: an individual in need is assisted by another one to achieve her individual goal, and the outcome of this interaction usually directly benefits the helped individual (Warneken & Tomasello, 2007). It is worth noting that applying these specifications only refers to direct, immediate benefits, regardless of whether benefits may also result indirectly, e.g. in terms of inclusive fitness (Hamilton, 1964), or in the long run, e.g. by contingent reciprocation (Trivers, 1971). These rather broad definitions of cooperation and helping do not assume specific motivations to underlie the respective prosocial behaviour.

However, researchers often distinguish different levels or types of cooperation and helping. Depending on their scientific discipline, the criteria determining these levels or types may differ. For example, researchers with a biological background have suggested discriminating levels of cooperation with respect to whether cooperative interactions are coordinated in time and/or space and whether coordinated actions complement each other to achieve a common goal (Boesch & Boesch, 1989). Comparative psychologists, on the other hand, differentiate between types of cooperation with regard to their underlying motivations and required socio-cognitive skills, e.g. whether interacting individuals use each other as a social tool to achieve their individual goals or whether they have joint intentions and interact to achieve a common goal (Tomasello & Vaish, 2013). Although *common goal* is included as a defining criterion in both approaches, the latter presupposes particular socio-cognitive abilities, while the former makes no assumptions in this respect but rather refers to a shared beneficial outcome of the interaction (Chalmeau & Gallo, 1995).

Cooperation is an essential and multifaceted feature of human groups and societies at all levels. A well investigated and fundamental example of cooperation is cooperative hunting, occurring both in early and recent human hunter-gatherer societies (Bliege Bird & Power, 2015; Gurven & Hill, 2009; Hawkes, 1991; Stiner, Gopher, & Barkai, 2011). However, cooperation is not limited to the human species (Packer & Ruttan, 1988). For example, group hunting has been found across different taxa, e.g. in invertebrates (Ward & Enders, 1985), fish (Strubin, Steinegger, & Bshary, 2011), raptors (Hector, 1986), social carnivores (Lamprecht, 1978; Mills, 1985; Schaller, 1972), marine mammals (Hoelzel, 1991), and primates (Boesch & Boesch, 1989; Hausfater, 1976; Rose, 1997). The most elaborated group hunting – followed by sharing of prey – in non-human primates occurs in populations of wild chimpanzees, especially in the Taï Forest, Côte d'Ivoire, where they hunt red colobus monkeys (*Procolobus* spp.) while acting in teams with coordinated roles (Boesch, 2002).

Other examples of cooperation and helping in non-human primates are allomaternal care and communal group defence in cooperative breeding callitrichids (Burkart, Hrdy, & van Schaik, 2009), territorial boundary control by male chimpanzees (Watts & Mitani, 2001), and coalitionary support (Harcourt & de Waal, 1992), both among males (Mitani, 2009a; van Hooff & van Schaik, 1994) and females (Newton-Fisher, 2006; Sterck et al., 1997). Furthermore, there are several reports on adoptions of orphans by adult females and males and also juveniles, both related and unrelated (Boesch, Bole, Eckhardt, & Boesch, 2010; Thierry & Anderson, 1986).

Prosocial behaviours in general, though helping and sharing in particular, have been characterised as either *reactive*, i.e. in response to extern stimuli, or *proactive*, i.e. due to an intrinsic motivation without being confronted with an extern stimulus (Burkart et al., 2009; Jaeggi, Burkart, et al., 2010). It has been suggested that particular motivations and socio-cognitive abilities such as *other-regarding preferences* and *shared intentionality* being present or absent indicate quantitative and/or qualitative differences between human prosociality on the one hand and prosociality in non-human primates on the other (Fletcher, Warneken, & Tomasello, 2012; Melis & Semmann, 2010; Rekers, Haun, & Tomasello, 2011; Rudolf von Rohr et al., 2011; Tomasello, Carpenter, Call, Behne, & Moll, 2005).

Meanwhile, there is a large body of experimental studies aimed at identifying motivations that underlie prosocial acts in humans and other animals, mainly following one of those paradigms: the prosocial choice task (Burkart et al., 2007; Horner et al., 2011; Massen, Luyten, Spruijt, & Sterck, 2011; Silk et al., 2005; Takimoto, Kuroshima, & Fujita, 2010; Vonk et al., 2008), instrumental helping tasks (Melis et al., 2011; Skerry, Sheskin, & Santos, 2011; Warneken, Chen, & Tomasello, 2006; Yamamoto, Humle, & Tanaka, 2009, 2012), variants of the ultimatum game (Fehr, Bernhard, &

Rockenbach, 2008; Jensen et al., 2007; Proctor et al., 2013; Rochat et al., 2009) or food sharing tests (Lakshminarayanan & Santos, 2008; Tan & Hare, 2013). The results are heterogeneous, sometimes even contradictory, which might be – at least partly – due to methodological inconsistencies or shortcomings (Baumard & Sperber, 2010; Cronin, 2012; Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016). A more fundamental critique addresses generalisations of results in experiments with humans belonging to overwhelming extent to western, educated, industrialized, rich and democratic societies (Henrich et al., 2010) to account for human behaviour in general. This improper generalised human behaviour is then often used to be contrasted with e.g. *the* chimpanzee behaviour, the latter likewise resulting from generalisations of results of experiments, mostly conducted with chimpanzees in captivity, ignoring possible population differences as well (Boesch, 2010). Both aspects of this critique are justified since they emphasize the very core of comparative research: to be consequently comparable both in cross-species and in intra-species research. So, the question whether human prosociality differs fundamentally or gradually from non-human prosociality is still in debate.

Within this extensive work on cooperation and helping in primates, experimental studies on orangutans are highly underrepresented – especially compared to the large number of studies on chimpanzees. Due to their semi-solitary lifestyle (Delgado & van Schaik, 2000), wild orangutans are expected to barely have any opportunities to cooperate (cf. section 1.2.2). As far as we currently know, orangutans neither hunt cooperatively nor do they engage in cooperative territory defence. Until very recently, there was also no evidence for any coalition formation in wild orangutans. The only report on a coalitionary, coordinated action considered a dyadic, lethal attack by a young female and an unflanged male, who were in consortship with each other, against another female who on her part received protection from a flanged male (Marzec et al., 2016). However, orangutan mothers regularly help their offspring when traveling through the canopy: either by bridging two trees with their body to let the infant climb along or by swaying one tree closer to the other to enable the infant to get to the other side (van Noordwijk et al., 2009).

Only but a few experiments on cooperation or helping in orangutans have been published to date. Nevertheless, their findings were interesting, since they demonstrated both the ability to cooperate in a problem solving task (Chalmeau, Lardeux, Brandibas, & Gallo, 1997) and to reciprocate in an exchange task (Dufour, Pele, Neumann, Thierry, & Call, 2009). A comparison across four great ape species with regard to the behaviour during a token-exchange test revealed that only orangutans frequently engaged in directed gifts and begging gestures (Pelé, Dufour, Thierry, & Call, 2009). Liebal and colleagues found that orangutans, but not chimpanzees, were ready to help conspecifics in need and – in doing so – were possibly motivated by sympathy (Liebal, Vaish, Haun, & Tomasello, 2014). A recently conducted prosocial choice task, however, did not reveal any concerns for others (Kim, Martinez, Choe, Lee, & Tomonaga, 2015). There are some factors which might account for the contrasting results of the two latter studies. For example, the opportunity for the helper to get food in the second, but not in the first task might have had an influence on their prosocial performance (Cronin, 2012). Another possible reason might be that the results of the prosocial choice task reflect the behaviour of only two individuals, which hardly allows for concluding a general lack of concern for others in orangutans.

After this overview on helping and cooperation in primates, in the next section, I will introduce research areas and findings on food sharing, which is the topic of the first two studies I will present in this thesis.

1.1.4.3 Food sharing

Food sharing, i.e. the tolerated transfer of defensible food items between food-interested individuals (Feistner & McGrew, 1989), is a fundamental type of prosocial behaviour. Despite being influenced and shaped by culture (Gurven, 2004; Rao & Stewart, 1999; Stewart & McBride-Chang, 2000), sharing food and other resources is universal in humans (Gurven, 2004; Gurven & Jaeggi, 2015).

Sharing food is not limited to *Homo sapiens*, but occurs in many non-human primates as well as non-primate species (e.g. Boesch & Boesch, 1989; Burkart et al., 2007; Carter & Wilkinson, 2013; de Kort, Emery, & Clayton, 2003; de Waal, 1989a; Fruth & Hohmann, 2002; Jaeggi & Gurven, 2013a; Rapaport, 2001). Nevertheless, human food sharing reveals some extraordinary characteristics: (i) In contrast to most other mammals – with exception of other great apes –, humans continue to regularly provision their offspring after weaning, often until adulthood (H. Kaplan & Gurven, 2005). (ii) In human forager families, food sharing occurs among three generations: offspring, parents, and grandparents both from parents to children, grandparents to grandchildren and *vice versa* (H. S. Kaplan, Hooper, & Gurven, 2009). (iii) Food sharing emerges very early in human ontogeny (Tomasello & Vaish, 2013; Zahn-Waxler et al., 1992). (iv) Food sharing in humans is not restricted to kin, but occurs frequently und extensively also with unrelated adults (Gurven & Jaeggi, 2015).

Sharing with immature offspring is a regular behaviour in at least 38 non-human primate species (Jaeggi & van Schaik, 2011). Sharing among unrelated adults, however, is currently known for less than half of these species. Since there is no primate species in which sharing occurs among adults, but not between adults and their offspring, sharing with offspring has been suggested to be an evolutionary predecessor for sharing in other contexts (Jaeggi & van Schaik, 2011).

In terms of its ultimate function, food sharing with offspring potentially increases inclusive fitness (Hamilton, 1964) due to nutritional and/or informational benefits (Brown, Almond, & van

Bergen, 2004). Kin selection (Maynard Smith, 1964) is therefore a widely accepted explanation for its evolution (Jaeggi & van Schaik, 2011).

Sharing with non-kin, on the other hand, could have evolved through different mechanisms, e.g. avoiding costs of harassment (Brown, 2004; Gilby, 2006; Stevens & Stephens, 2002), reciprocity (Bliege Bird & Bird, 1997; de Waal, 1997a; Gurven, 2006; Trivers, 1971) or costly signalling (Hockings et al., 2007; Nolin, 2012; Zahavi, 1995). According to the first explanation, food sharing increases the possessor's fitness immediately, when the costs of defending a food source are higher than the benefit of consuming all the food. Corresponding to the latter explanations, food sharing increases the individual fitness of the possessor in the long run (Jaeggi & Gurven, 2013b). Both the time range within which food sharing yields benefits and the actual "currency" of these benefits, e.g. food (de Waal, 1997b), grooming (de Waal, 1997a; Jaeggi, de Groot, Stevens, & van Schaik, 2013), coalitionary support (Mitani & Watts, 2001) or sexual access (Gomes & Boesch, 2009), vary across species and also within species depending on the particular sharing partner. The underlying mechanisms here are not necessarily mutually exclusive (Jaeggi & van Schaik, 2011; Mitani, 2006; Stevens & Gilby, 2004).

Given heterogeneous empirical evidence for particular sharing patterns among unrelated adults, it seems most likely that there is more than one single ultimate as well as more than one proximate function when it comes to food sharing in primates, even within one species (Silk et al. 2013). Although there is still an unsettled controversy on different concepts of reciprocity, its cognitive preconditions and its applicability to non-human species (e.g. Clutton-Brock 2009; Schino and Aureli 2009), recent research has accumulated convincing evidence for a correlation between enduring, close relationships (social bonds) and long-term reciprocity and cooperation in primates (Carter 2014; Freidin et al. 2015).

Food transfer types can be differentiated with regard to the extent of the active contribution by the food possessing individual (Jaeggi & Gurven, 2013a). In *passive* sharing, a non-possessor is allowed to take food without resistance or assistance by the possessor, which requires social tolerance and inhibitory control. In contrast, *active* sharing involves an action by the possessor that facilitates or performs the transfer and can either be *reactive*, i.e. upon request, or *proactive*, i.e. possessor-initiated (Jaeggi, Burkart, et al., 2010). Passive sharing additionally presupposes inhibitory control and a high level of social tolerance by the possessor (Burkart et al., 2009). The prerequisites of reactive sharing include furthermore the possessor's ability to recognise and respond to signs of need (Jaeggi & Gurven, 2013a), in addition to this, a motivation to share (spontaneous prosociality: Burkart et al., 2009) is essential for proactive sharing (Jaeggi, Burkart, et al., 2010).

Primate species considerably differ in their social tolerance indicated for instance by the extent to which – if at all – food sharing occurs in a species, as well as in their socio-cognitive and motivational abilities, reflected e.g. by the proportions of passive, re- and proactive sharing. In contrast to humans who frequently share re- and proactively, passive sharing is the most frequent sharing type in all non-human primate species, with callitrichids, great apes and capuchins revealing the highest frequencies (Jaeggi & Gurven, 2013a). Great apes, especially chimpanzees and bonobos, and also capuchin monkeys have been found to share actively among adults upon request, but to a much less extent. While proactive sharing is extremely rare in great apes, in cooperative breeding callitrichids provisioning of immatures is frequently initiated by the food possessor (Feistner & McGrew, 1989; Jaeggi, Burkart, et al., 2010), suggesting a link between cooperative breeding and the evolution of spontaneous prosociality (Burkart et al., 2009).

Interactions over food (hereafter: food interactions) occur in several ways and result either in food transfer or not. Table 1 provides a summary of the different transfer types I consider in this thesis. For each type an operational definition and a categorisation regarding tolerance and the possessor’s active involvement are provided, accomplished by references to analogous concepts from previous studies on food transfer.

Food sharing is heavily investigated in several primate species, especially in chimpanzees. However, only little is known about food sharing behaviour and its possible functions in orangutans in the wild and even less in captivity, where orangutans – contrary to their natural social organisation (cf. subsection 1.2) – live in permanent groups. With the first two studies presented in Chapter 2, I aim to fill this gap: While the first study focuses on the occurrence and behavioural variety of sharing as a means for orangutans to cope with permanent group life, the main objectives of the second study on the one hand are to investigate the potential impact of social bonds on food sharing in captive orangutans and, on the other hand, probable differences in the sharing behaviour across the great ape species.

Table 1 Operational definitions: Transfer types with assigned tolerance and active involvement of the possessor and analogous concepts used by other authors (This table was already included – in a slightly adapted form – in the prior publication of Study 2 (Kopp & Liebal, 2016, Electronic Supplementary Material ESM1, ST3))

Due to copyright reasons, this table is not available in the online version of this dissertation. Please see the original article at http://dx.doi.org/10.1007/s00265-016-2130-2. You may also contact the author for a copy of the manuscript at kathrin.kopp@fu-berlin.de.

1.1.4.4 Prosocial behaviours in conflict management

Although various mechanisms that prevent potential conflict situations from becoming open conflicts have evolved across species, their actual occurrence and/or effectiveness may depend on several factors, such as (i) species characteristics, e.g. social structure (Kappeler & van Schaik, 2002; Pereira & Kappeler, 2000; Thierry et al., 2008); (ii) socio-ecological factors, e.g. food abundance or social density (Judge, 2000); (iii) the particular context, e.g. rank or food competition, sexual or parent-offspring conflict (Clarke, Henzi, & Barrett, 2009; Heesen, Rogahn, Macdonald, Ostner, & Schuelke, 2014; Maestripieri, 2002; Watts, 2004); (iv) characteristics of the respective individuals and their relationship, e.g. personality traits like sociability (Capitanio, 1999), kin-, sex- or rank-relation, and relationship quality (Palagi & Norscia, 2013; Silk, Brosnan, et al., 2013; Stumpf, Martinez-Mota, Milich, Righini, & Shattuck, 2011); or (v) socio-cultural aspects, at least – but not necessarily uniquely – in humans (Fry, 2000; Günsoy, Cross, Uskul, Adams, & Gercek-Swing, 2015; Ohbuchi, Fukushima, & Tedeschi, 1999).

Therefore, open conflicts are not always preventable. They are potentially costly for the involved individuals, both directly, e.g. because of physical injuries, and indirectly, e.g. due to the loss of status or weakening social relationships with valuable partners (de Waal & Aureli, 1997). Conflicts may also violate the stability of the whole group, when social networks are affected (Flack et al., 2006).

However, while early behavioural research on interindividual conflicts had mainly focused on aggression as an antisocial and/or maladaptive force, which needed to be modified or inhibited (Lorenz, 1963); starting in the late 1970ies, the perspective on conflicts has changed (de Waal, 2000). Studying post-conflict behaviour in non-human primates (e.g. de Waal & van Roosmalen, 1979), researchers extended their focus and considered conflicts in a much broader sense (cf. definition on page 6). This perspective shift allowed for acknowledging conflicts and conflict management as essential and integral elements of social life, which play a crucial role in negotiating and stabilising social relationships, in distress alleviation and in maintaining group cohesion (Aureli, 1997; de Waal, 1986, 1996; de Waal & Aureli, 1997; Silk, 2002a).

Across human cultures, anthropologists have identified a multitude of conflict resolution procedures aiming at ceasing ongoing conflicts and mending relationships that have been disturbed by interindividual conflicts. Depending on the particular culture, these strategies revealed to be more or less elaborated and ritualised (Fry, 2000). However, despite all cultural variability, humans share some of these strategies which other species, especially with other primates (Cords & Killen, 1998). In the following, I will introduce two general prosocial strategies: third party interventions and post-conflict affiliations.

Third party interventions, that cease ongoing aggressive interactions, can, on the one hand, minimise direct costs for the opponents and, on the other hand, may reduce social tension and thereby prevent the conflict from affecting the whole group (Watts, Colmenares, & Arnold, 2000). Affiliative post-conflict behaviours, in turn, can minimise indirect costs for one or both of the opponents and/or the whole group by reducing anxiety (Aureli, 1997) and uncertainty (Silk, 2000) and restoring disturbed relationships (Cords & Aureli, 2000). Furthermore, both interventions and post-conflict affiliations by third parties may provide benefits for bystanders and opponents by promoting social bonding between a bystander and one of the former opponents (de Waal & Aureli, 1996; Petit & Thierry, 2000).

Third party interventions

Prosocial third party interventions in open conflicts can be either *partial* or *impartial* (Boehm, 1994).

Partial interventions in order to cease conflicts can be defined as selective agonistic actions of a bystander against the aggressor, which can be interpreted either as protecting the victim or as punishing the aggressor, respectively (Clutton-Brock & Parker, 1995a), depending on the assumed motivations of the bystander (Hall & Brosnan, 2016). It has to be mentioned that third party's interferences that directly support the aggressor are – per definition – prosocial as well. Nevertheless, I do not consider this kind of cooperative behaviour in the current context, because supporting the aggressor does not usually cease, but raise the aggression.

Partial interventions can be found across the primate order, for instance in baboons, humans, chimpanzees, langurs, macaques and gorillas (e.g. Buchan et al., 2003; Chaux, 2005; Goodall, 1986; Ren et al., 1991; Schino et al., 2007; Scott & Lockard, 2007; Verbeek, Hartup, & Collins, 2000), and beyond (Krueger, Schneider, Flauger, & Heinze, 2015). In humans, partial interventions are quite frequent. For example, Vuchinich, Emery, and Cassidy (1988) investigated third party interventions in conflicts that occurred during family meals. They found that in half of the cases the intervening individual had tried to form an alliance with one of the conflict parties. Furthermore, already at preschool age, children partially intervene in peer conflicts in order to support friends (Chaux, 2005; Grammer, 1992).

Several functions of partial interventions have been suggested, which are not necessarily mutually exclusive: e.g. protecting and/or supporting kin in rank acquisition and rank maintenance (Borries, Launhardt, Epplen, Epplen, & Winkler, 1999; Schino et al., 2007; Silk, 2002b), stabilising or reinforcing of the current hierarchy (Berman, Lonica, & Li, 2007; Chapais, 1992), reciprocating coalitionary support (Mitani, 2006, 2009b), helping friends and stabilising social bonds (Cords, 1997) or reducing the severity of regularly occurring male aggressions against females (Newton-Fisher, 2006). Correspondingly, different evolutionary mechanisms may account for partial third party interventions, especially kin selection (Hamilton, 1964; Silk, 2002b) and reciprocity (Schino & Aureli, 2009; Trivers, 1971).

Impartial interventions (also called policing; Flack et al., 2006), in contrast, do not involve aggressive behaviour against any of the opponents (Rudolf von Rohr et al., 2012). In humans, this type of third party intervention is very common and may be – depending on context and cultural aspects – highly elaborated, often even institutionalised (Fry, 2000). While there are forms of impartial third party intervention humans, such as breaking up a fight of men in a pub, being similar to those found in non-human primates; other forms, such as mediation, have been exclusively found in humans. Mediation consists in the attempt of a neutral third party or multiple third parties "[…]to assist antagonists in arriving at agreements" (Fry, 2000, p. 336). Mediators may e.g. be common friends or kin of the opponents, highly respected persons or persons specifically acting as judges in a community (Fry, 2000).

Although impartial intervention is less common across species than partial intervention (Petit & Thierry, 2000), its occurrence has been reported for a variety of non-human primates, such as chimpanzees (Boehm, 1994; Rudolf von Rohr et al., 2012), gorillas (Watts, 1997), orangutans (Marzec et al., 2016; Tajima & Kurotori, 2010; Zucker, 1987), langurs (Ren et al., 1991) and macaques (Petit & Thierry, 1994, 2000). Several functions of impartial interventions have been proposed. Some of these may contribute to benefit the intervener (or *arbitrator*, Rudolf von Rohr et al., 2012) directly, e.g. by maintaining dominance over group members or control over mating partners (Boehm, 1994; Petit & Thierry, 2000; Watts, 1991, 1997). Others may benefit the arbitrator indirectly by maintaining or increasing group stabilisation (Flack et al., 2006; Rudolf von Rohr et al., 2012).

Post-conflict affiliations

Starting with the first systematic investigation of conflict resolution in chimpanzees by de Waal and van Roosmalen (1979), affiliative post-conflict interactions both between former opponents (*reconciliation*) and between a former opponent and an uninvolved third party (*post-conflict third party affiliation*) have been intensely studied in primate and non-primate species.

Reconciliation occurs across the primate order (Silk, 2002a). In humans, reconciliation like other forms of conflict management is considerably shaped by the respective culture. There are implicit and explicit forms of human reconciliation (Fujisawa, Kutsukake, & Hasegawa, 2005; Verbeek, 2008). Implicit reconciliation consists in engaging in rather unspecific affiliative interactions in the immediate aftermath of a conflict, but without direct reference to the conflict. Implicit reconciliatory behavioural displays are, for instance, being friendly, initiating laughter, gentle touching, talking without apologies, or starting playing (Butovskaya & Kozintsev, 1999; Fujisawa et al., 2005). However, there are many explicit and often ritualised forms of reconciliation, which are culture-dependent. These interactions range from handshakes, embraces, verbal apologies, sharing, offering gifts, up to reconciliation celebrations including the families of the former opponents or even the whole community. Furthermore, explicit reconciliation strategies in humans often include uninvolved third parties whose function is to mediate the reconciliation between former opponents. Respective third parties might be socially bonded with one of the former opponents or might have an influential position in the particular community (Fry, 2000). Ljungberg and colleagues found that the type of reconciliatory strategies actually used by pre-school children clearly correlated to the conflict cause. For instance, explicit verbal apologies occurred almost exclusively to reconcile after physical harm, while conflicts over objects were typically reconciled by offering objects (Ljungberg, Horowitz, Jansson, Westlund, & Clarke, 2005).

Children reconcile more often with friends than with non-friends, suggesting that one important function of reconciliation in humans consists in repairing disturbed valuable relationships (Cords & Killen, 1998). Reconciliation events that additionally include a large proportion of community members or even the whole group (e.g. the trance dance by Ju/wasi hunter-gatherers, Thomas, 1994) suggest that a further function consists in protecting or re-establishing group stability and cohesion.

Friendly post-conflict reunions between former opponents are also present in the majority of the investigated non-human primate species. For instance, reconciliation has been found in baboons (Castles & Whiten, 1998b; Romero, Colmenares, & Aureli, 2008), bonobos (Palagi & Norscia, 2013), capuchins (Manson, Perry, & Stahl, 2005; Verbeek & de Waal, 1997), callitrichids (Penate, Pelaez, & Sanchez, 2009; Westlund, Ljungberg, Borefelt, & Abrahamsson, 2000), chimpanzees (Arnold & Whiten, 2001; Fraser & Aureli, 2008; Fraser, Stahl, & Aureli, 2008, 2010; Koski & Sterck, 2007, 2009; Palagi, Cordoni, & Borgognini Tarli, 2006; Watts, 2006; Wittig & Boesch, 2003), gorillas (Cordoni, Palagi, & Borgognini Tarli, 2006; Watts, 1995a), leaf monkeys (Arnold & Barton, 2001), and macaques (Aureli, 1992; Aureli, Das, Verleur, & van Hooff, 1994; Aureli & van Schaik, 1991; Aureli, Veenema, van Panthaleon van Eck, & van Hooff, 1993; Berman, Ionica, Dorner, & Li, 2006; Call, Aureli, & de Waal, 2002; Duboscq, Agil, Engelhardt, & Thierry, 2014; McFarland & Majolo, 2012; Romero et al., 2008; Thierry et al., 2008). Furthermore, it occurs also outside of the primate order, e.g. in wolves (Cordoni & Palagi, 2008) and corvids (Fraser & Bugnyar, 2011).

Although the term *reconciliation,* which has been introduced by de Waal and van Roosmalen (1979), implies a specific function, most authors use it descriptively as a synonym for *post-conflict affiliation between former opponents*, allowing for more functions than restoring the opponents' relationship (but see Silk, 1997). In this thesis, I follow this widely accepted descriptive application of *reconciliation*.

At least three functions of reconciliation have been suggested, which are not necessarily alternatives, but might be complementary or interdependent (Aureli, Cords, & van Schaik, 2002; but see Silk, 2002a): (i) restoring valuable social relationships which have been violated or disturbed by the conflict (Valuable Relationship Hypothesis: Aureli et al., 1989; de Waal & Aureli, 1997), (ii) reducing uncertainty and anxiety following a conflict (*Uncertainty-Reduction Hypothesis*: Aureli, 1997; Aureli & van Schaik, 1991), and (iii) honestly signalling non-aggressive or benign intent to enable the resumption of non-aggressive interactions (*Benign Intent Hypothesis*: Silk, 1996; Silk, 1997, 2000). Empirical evidence for these hypotheses is mixed (Aureli, 1997; Berman et al., 2006; Cooper, Aureli, & Singh, 2007; Das, Penke, & van Hooff, 1998; Duboscq et al., 2014; Koski, Koops, & Sterck, 2007; Kutsukake & Castles, 2004; Leone & Palagi, 2010), which might suggest that the function of reconciliation varies across primate species (Silk, 2002a). Moreover, it might also suggest that reconciliation might serve more than one function and might be directly and/or indirectly beneficial even within a single species (Aureli et al., 2002; Silk, 1998).

Post-conflict third party affiliation with the victim of a conflict is less common in non-human primates compared to reconciliation (Aureli et al., 1993; Castles & Whiten, 1998a; Cordoni et al., 2006; de Waal & Aureli, 1996; Palagi, Cordoni, et al., 2006; Palagi, Paoli, & Borgognini Tarli, 2004) and has been described for other primate species than great apes only 14 years ago (Call et al., 2002; McFarland & Majolo, 2012). However, the empirical evidence for its occurrence is discussed, even with regard to great apes (Arnold & Whiten, 2001; Cordoni et al., 2006; Watts, 1995b; Wittig & Boesch, 2003).

In their first systematic investigation of affiliative interactions in the aftermath of conflicts, de Waal and van Roosmalen (1979) referred to post-conflict affiliations between a victim and a bystander as *consolation*. Like reconciliation, the term *consolation* implies a specific function, in this case distress alleviation in the victim. In contrast to *reconciliation,* however, *consolation* is a frequently debated concept and its usage differs across authors and studies. While some researchers use it in a mere descriptive way and indicate – as originally defined – both solicited and spontaneous post-conflict third party affiliations with the victim as *consolation* (Castles & Whiten, 1998a; Watts, 1995b), others differentiate between *solicited* and *unsolicited consolation* (Fraser & Aureli, 2008; Verbeek & de Waal, 1997) and some authors refer only to unsolicited post-conflict third party affiliation as (proper) *consolation* (Palagi, Cordoni, et al., 2006). Other authors, finally, avoid this concept at all, because of its narrowing or even probably misleading functional connotation (Koski & Sterck, 2007; Silk, 1997). To avoid any semantic confusion, I follow the last mentioned authors and use *post-conflict third party affiliation* – or short *PCTA* – in order to refer to the respective interaction and use *consolation* only in a strict functional way.

As for the other types of prosocial conflict management, several possible functions have been suggested for PCTA: (i) calming and alleviating post-conflict stress in the victim (Aureli, 1997); (ii) protecting bystanders from redirected aggressions (Koski & Sterck, 2009); (iii) repairing the relationship between the opponents as a substitute for reconciliation (Fraser & Aureli, 2008); (iv) protecting the victim against further aggression (Palagi & Norscia, 2013); and (v) promoting social bonds between the bystander and the victim (Koski & Sterck, 2007). Again, empirical evidence for each hypothesis is heterogeneous. For instance, Wittig and Boesch (2010) found strong evidence for the *Relationship Repair Hypothesis*, moderate support for the *Consolation Hypothesis* and no evidence for the *Self-Protection Hypothesis*. Koski and Sterck (2007), on the other hand, provided contradicting results. The debate on the function(s) of PCTA is still ongoing. As for the case of reconciliation, there might be more than one function of post-conflict third party affiliations and therefore probably more than one evolutionary mechanism, which brought PCTA about in different species.

To sum up, prosocial conflict management strategies have been intensely investigated in many non-human primate species. However, apart from a few reports on third party interventions in wild and captive orangutans, no such investigation on conflict resolution in group-living orangutans has been published to date. With the third study of my thesis (subchapter 2.3), I provide the first systematic investigation of conflict patterns and prosocial conflict resolution in a group of captive Sumatran orangutans.

1.2 THE STUDY SPECIES: SUMATRAN ORANGUTAN (*PONGO ABELII*)

1.2.1 Phylogeny

Orangutans belong to the hominid genus *Pongo* that is most distantly related to humans. Their phylogenetic lineage diverged from the common lineage of all other modern great apes about 12-16 million years ago (Locke et al., 2011).

The recently completed sequencing of the orangutan genome shed new light onto the phylogeny of orangutans and the genetic proximity of modern great apes (Locke et al., 2011). Based on sequence identity, the divergence of the only two extant orangutan species, Bornean and Sumatran orangutan (*Pongo pygmaeus* and *Pongo abelii*, respectively; Brandon-Jones et al., 2004), has been estimated as having taken place between 0.6 and 6.4 million years ago, depending on the particular approach and used molecular markers (Goossens et al., 2009). A more recent study estimates that the split up of these lineages has taken place less than 1 million years ago, comparable to the divergence of chimpanzees and bonobos (*Pan troglodytes* and *Pan paniscus*, respectively) (Prüfer et al., 2012). Findings from a genetic comparison indicate that the evolution of the genetic structure proceeded much faster in *Pan* and *Homo* after the *Pongo* lineage split apart. This strongly supports the view that the modern orangutan genome resembles the genome of the common hominid ancestor more than any other extant great ape species' genome does (Locke et al., 2011), which alone means that orangutans should be of special interest for a comparative perspective on prosociality.

1.2.2 Ecology, characteristic features and social structure

Orangutans are the only non-human great apes that naturally occur outside of Africa. During the Pleistocene, orangutan populations spread across a range throughout southern Asia including the mainland (Delgado & van Schaik, 2000). Today, there are only fragmented populations left in the rain forests of the northern part of Sumatra and across Borneo (Husson et al., 2009; Marshall et al., 2009), forming the two species of Sumatran and Bornean orangutans (Brandon-Jones et al., 2004; Groves, 2001). Estimating orangutan densities is methodologically highly demanding (Spehar et al., 2010). The most recent estimation of Sumatran orangutans took place in 2015 (Wich et al., 2016) and of Bornean orangutans in 2003 (Ancrenaz et al., 2008). According to these latest estimations, the total number of Sumatran orangutans is about 14.600 individuals (conservation status: critically endangered; IUCN Red List of Threatened Species. Version 2016-2) and of Bornean orangutans between 45.000 and 69.000 individuals (conservation status recently re-assessed as: critically endangered; IUCN Red List. Version 2016-2). The population trend is still decreasing due to the rapidly ongoing deforestation and fragmentation of their habitat, mainly for the sake of oil palm plantations as well as for the claims of the timber and paper industry, but also due to poaching and the illegal trade of orangutan infants as pets after killing their mothers (Marshall et al., 2009; Wich et al., 2016). Therefore, there are probably even fewer orangutans left today.

Compared to the African great apes, both orangutan species reveal several unique physical and behavioural characteristics. Despite their heavy body mass and size (adult males can reach a body weight of 80 kg), they are truly arboreal and show several anatomical and behavioural adaptations to the life in the canopy of the tropical rainforests (MacKinnon, 1974; Thorpe & Crompton, 2006). Especially in Sumatra where large terrestrial predators like the Sumatran tiger (*Panthera tigris*) are present, orangutans barely leave the canopy. In Borneo, where tigers are absent, particularly male orangutans come down from the trees more often to travel terrestrially (Ancrenaz et al., 2014; Delgado & van Schaik, 2000; Rijksen, 1978; Thorpe & Crompton, 2009).

Orangutans show a strong sexual dimorphism, with adult males being twice the size of females. They also show a male bimaturism. Only fully developed (or *flanged*) males display specific secondary sexual characteristics, such as cheek pads (so called flanges), a large throat sac or a long coat of hair, and they are able to produce the characteristic long calls. *Unflanged* males on the other hand, though being fertile and sexually active, stay in an “arrested” condition which may last up to 20 years after reaching sexual maturity (E. A. Fox, 2002; MacKinnon, 1974; Rijksen, 1978; Utami, Goossens, Bruford, de Ruiter, & van Hooff, 2002). These two male morphs follow different, but successful mating strategies (Utami Atmoko, Mitra Setia, et al., 2009). While dominant flanged males usually prefer the “sitting, calling, waiting” strategy, which includes reproductive consortships and cooperative mating, the main strategy of unflanged males can be described as “going, searching, finding” often including coerced mating (Utami et al., 2002). Females often resist copulations with particular individuals, often unflanged males, while cooperatively associating and mating with others, suggesting there is a form of female partner choice (Utami Atmoko, Mitra Setia, et al., 2009).

Orangutans have a slower life history than African great apes. At about eight years of age, orangutans of both species have the largest interbirth interval of all modern non-human primates and weaning takes place around the seventh year of age, about two years later than in chimpanzees (Wich et al., 2009). Immature orangutans crucially depend on their mothers regarding feeding and protection, and in order to acquire dietary, foraging and other essential survival skills via social learning (Jaeggi, Dunkel, et al., 2010b; van Noordwijk et al., 2009; van Noordwijk & van Schaik, 2005).

The dependence of orangutan infants and juveniles on their mothers is especially strong due to the social organization of orangutans, which is unique among diurnal primates and can be described as an individual-based fission fusion society (van Schaik, 1999) with a mean party size of less than two individuals. This semi-solitary lifestyle of orangutans is probably an adaptive strategy to cope with feeding competition. Being large, primarily frugivorous animals (MacKinnon, 1974; Rijksen, 1978), orangutans need sizable amounts of fruits, which the South-Asian rainforests cannot provide continuously in such quantities that would allow orangutans to live in permanent groups (Delgado & van Schaik, 2000). However, orangutans are not as solitarily or even “anti-social” (Sugardjito & Nurhuda, 1981, p. 415) as assumed earlier; in periods of high fruit abundance they aggregate in large fruit trees and occasionally form travel bands. Furthermore, recent findings revealed that, in orangutans in contrast to other great apes, females are the philopatric sex (Arora et al., 2012; van Noordwijk et al., 2012), which means that mature males disperse, orangutan females tend to stay in their natal area (Mitra Setia, Delgado, Utami Atmoko, Singleton, & van Schaik, 2009). Adult females and their dependent offspring live in large, overlapping home ranges which overlap with the larger home range of a resident flanged male (Singleton, Knott, Morrogh-Bernard, Wich, & van Schaik, 2009; van Schaik, 1999). Females and males temporarily engage in consortships which are characterised by coordinated traveling, cooperative mating and other social interactions.

Comparative studies on Sumatran and Bornean study populations revealed considerable variations in the degree of social tolerance and party size between the two orangutan species and even between different populations of one species (Delgado & van Schaik, 2000; van Schaik, Marshall, & Wich, 2009). Sumatran orangutans are generally more sociable than Bornean orangutans; especially in Suaq Balimbing where reproductive synchrony results in large parties during the pre-birth period, featuring an almost stable composition for more than two weeks (van Schaik, 1999). After giving birth, females – joined by their infant and their older offspring – associate among each other and are unusually tolerant, exhibiting behaviours including feeding in close proximity and occasional food sharing among adult females (Singleton & van Schaik, 2002; van Schaik, 1999). In Bornean orangutans, maternally related females with dependent offspring also associate with each other. Though the females themselves usually do not engage in affiliative interactions, they tolerate and sometimes even enable social play among their offspring (van Noordwijk et al., 2012).

In summary, given these findings regarding social interactions among wild orangutans, the social potential of orangutans is probably more sophisticated than previously assumed suggesting that developing close social relationships might be relevant for orangutans, even outside of the mother-offspring context.

1.2.3 Orangutans in captivity

The circumstances for orangutans in captivity differ dramatically from natural conditions. In modern zoos, orangutans are usually kept in permanent groups, mostly comprising an adult male, several adult females and their offspring. Since the relationship between flanged males is always hostile (Utami Atmoko, Singleton, van Noordwijk, van Schaik, & Mitra Setia, 2009), adult males cannot be kept together in a single group. The usual group structure in zoos account for the natural dispersal strategy of male orangutans (Knott, 2009), and simultaneously precludes the occurrence of any interactions among adult males as well as any female partner choice.

Furthermore, in contrast to female clusters in the wild, which are formed by related individuals (Singleton et al., 2009), zoo-groups comprise also unrelated females. In their natural habitat, associated unrelated females show more aggressions among each other. These aggressions usually result in breaking up the association. In contrast, related females in the wild show more social tolerance, enable social play of their infants and sometimes even share food, (van Noordwijk et al., 2012).

Notwithstanding their social behaviour in the wild, captive orangutans generally seem to cope surprisingly well with group life. In zoos, they engage in affiliative interactions, such as social play, contact sitting, sometimes also grooming and even third party interventions to prevent or cease conflicts (Jantschke, 1972; Maple, 1980; Poole, 1987; Tajima & Kurotori, 2010; Zucker, 1987; Zucker, Dennon, Puleo, & Maple, 1986; Zucker, Mitchell, & Maple, 1978).

These seemingly contradicting observations from the wild and from captivity reflect an astonishing flexibility and the ability of orangutans to adapt their social behaviour to different social circumstances. This, however, raises the question, which role prosocial behaviours might play when captive orangutans have to deal with the challenges of group life.

1.3 RESEARCH QUESTIONS

Based on the considerations and findings outlined in this chapter concerning contexts and functions of prosocial behaviour in primates on the one hand, and behavioural characteristics of wild and captive orangutans on the other, my research questions for this thesis are as follows:

(i) Do socially housed Sumatran orangutans act prosocially; and if they do so, in which contexts?

(ii) Which prosocial behaviours do orangutans share with the other great apes, particularly with chimpanzees?

(iii) What are possible functions of prosocial behaviour in orangutans?

In order to answer these questions, I conducted three empirical studies, which are the topic of the next chapter.

2 STUDIES

This chapter presents three studies on prosocial behaviour in zoo-living orangutans, each addressing a specific hypothesis. The following three sections are each dedicated to a respective study and are subdivided into (i) an introduction providing an overview of the scientific background, my hypothesis and the derived predictions, (ii) a detailed description of the applied methods, (iii) a presentation of the results, and (iv) a discussion of the main findings with regard to the predictions and the hypothesis.

The first and the third study have an observational design, because they investigate prosocial behaviour of captive orangutans in potential and in actual conflict situations, respectively –

situations that occurred in their daily group life. The second study has a quasi-experimental design to investigate factors influencing food sharing under controlled conditions. This latter study has recently already been published (Kopp & Liebal, 2016), while the two observational studies have been neither published nor submitted for publication yet.

2.1 STUDY 1: SHARING FOOD AND OBJECTS AS A MEANS TO COPE WITH GROUP LIFE IN CAPTIVE SUMATRAN ORANGUTANS

2.1.1 Introduction

As already outlined in the General Introduction (section 1.1.4.3), sharing resources, especially food, is a particularly fundamental type of prosocial behaviour found in many non-human primates (Jaeggi & Gurven, 2013a). Food sharing with offspring occurs in all these species, and, additionally, sharing among adults takes place in about half of them, both between the sexes and within sex (Jaeggi & van Schaik, 2011). Besides the nutritional benefit, which is the most obvious one, especially with regard to sharing high-valued food that is difficult to obtain or to process, such as meat of prey, honey, nuts or fruits with hard peels, food sharing may provide informational benefits for the recipient as well as indirect social advantages for the individual who shares, both playing an essential role in primate societies (Brown et al., 2004; Hamburg, Finkenauer, & Schuengel, 2014; Jaeggi, van Noordwijk, & van Schaik, 2008; Mitani & Watts, 2001; Nishida, Hasegawa, Hayaki, Takahata, & Uehara, 1992).

Recent research on food sharing revealed that food sharing occurs selectively; furthermore, that selectivity is not only affected by functional traits of potential sharing partners, such as relatedness, social rank, sex, age or fertility status, but also by the interindividual relationship (Jaeggi et al., 2013; Jaeggi & Gurven, 2013b; Sabbatini, Vizioli, Visalberghi, & Schino, 2012; Silk, Brosnan, et al., 2013). In their meta-analysis including studies on 68 primate species, Jaeggi and van Schaik (2011) demonstrate, that the occurrence of intra- and/or inter-sex food sharing in a species is significantly correlated with the occurrence of coalitions among adults of the same and/or different sex. Food sharing and reciprocating favours are most probably crucial for establishing long-term interindividual relationships, i.e. social bonds (Freidin et al., 2015; Schino & Aureli, 2009).

This interdependence of providing benefits and relationship quality is central to the specific perspective on food sharing I am going to take for this study: food sharing seen as a social means to prevent potential conflict situations from becoming open conflicts, since the latter has direct costs for an individual and might damage valuable relationships, thereby reducing their benefits for the interacting individuals in the future (Aureli & de Waal, 2000a).

A situation in which two individuals, only one of them being in possession of food, signal their interest in the food constitutes an interindividual conflict due to incompatible goals of keeping or getting the food, respectively (Cords & Killen, 1998). However, a conflict of interest underlying a food interaction does not necessarily result in aggression. An open conflict may be prevented either when the non-possessor abandons expressing his interest or by food sharing (de Waal, 1996). While the former non-aggressive alternative requires some extent of social tolerance in both individuals and inhibitory control in the presence of food in the non-possessor, the latter is more demanding with regard to socio-cognitive skills and motivation depending on whether the transfer occurs in a passive, reactive or proactive manner as discussed previously (subsection 1.1.4.3, p. 12-13)

Since chimpanzees are one of our two closest living relative species and, therefore, of special interest for comparative behavioural research (Mitani, 2009a), it is not surprising that there is a large body of studies on food sharing in this species. Chimpanzees live in complex social systems; they frequently engage in cooperative behaviour (Boesch, 1994; Gomes, Mundry, & Boesch, 2009), form coalitions (Goodall, 1986; Koyama et al., 2006; Newton-Fisher, 2006; Watts, 2004; Watts & Mitani, 2001) and share food selectively with valuable partners (de Waal, 1997a), both in the wild and in captivity.

In contrast, there is much less known about food sharing in the two orangutan species. The lack of knowledge might only partly be explained by difficulties in observing these arboreal apes in their natural habitat (MacKinnon, 1974; Rijksen, 1978); more fundamentally, it is due to their social organisation, which differs from that of the African great apes and has been described as an individual-based fission-fusion sociality with a mean party size of less than two individuals (van Schaik, 1999). Mother-offspring-associations represent the only stable and long-term groups in orangutans (Delgado & van Schaik, 2000; Mitani, Grether, Rodman, & Priatna, 1991; van Noordwijk et al., 2009; van Schaik & van Hooff, 1996), which are characterised by extraordinarily strong and long-lasting social bonds. Food sharing, which consists mostly in tolerated taking, occurs regularly between mothers and dependent offspring (MacKinnon, 1974, pp. 243-245; Rijksen, 1978; van Noordwijk et al., 2009), and its main function most likely consists in socially learning of diet and foraging skills (Bard, 1992; Jaeggi, Dunkel, et al., 2010a; Jaeggi et al., 2008; van Noordwijk & van Schaik, 2005).

Apart from these close social units, there are few opportunities for food sharing and other prosocial behaviours. Likewise, there is no evidence of cooperative hunting, grooming networks or coalitions in wild orangutans to date. However, since recent studies suggest that social bonds might also play a role for adult orangutans (Mitra Setia et al., 2009), food sharing might be a means for establishing and maintaining social relationships as well (for more details on this topic see Study 2).

Recent reports on occasional food sharing among adults support this suggestion. In some populations, related females with dependent offspring form clusters with overlapping home ranges. Within these clusters, females occasionally feed in proximity and sometimes even share food among each other (Singleton et al., 2009; van Noordwijk et al., 2012; van Noordwijk et al., 2009; van Schaik, 1999). Furthermore, van Noordwijk and van Schaik (2009) reported passive food transfers from males to females within mating consortships, thus suggesting that food sharing might be a means of female partner choice. Nevertheless, food sharing among adult orangutans occurs far less frequently in the wild than e.g. among adult chimpanzees.

In chimpanzees and bonobos, but not in orangutans, food sharing among adults preferentially involves meat after a successful hunt (Gomes & Boesch, 2009; e.g. Hohmann & Fruth, 2008) and large fruits or cultivated plant food (Hockings et al., 2007; Yamamoto, 2015). These are compact, monopolisable and high-valued food items, which seem to elicit food sharing in primates (Jaeggi & Gurven, 2013a). In contrast, all recorded instances of sharing between adult orangutans involved food that had been readily obtainable for both partners (van Noordwijk & van Schaik, 2009), while for the very rare consumptions of vertebrate meat, no sharing among adults has been reported to date (Hardus et al., 2012; Sugardjito & Nurhuda, 1981; Utami & van Hooff, 1997).

Given the limited knowledge on food sharing in wild orangutans, it is interesting that there is no systematic study to investigate food sharing in captivity so far, despite one recently published study that focused on the analysis of communication patterns rather than on actual food sharing and its determinants (Rossano & Liebal, 2014).

Notwithstanding their semi-solitary lifestyle in the wild, orangutans are often kept in zoos in permanent groups comprising one adult male, several females and their offspring and cope with group life quite well (Edwards & Snowdon, 1980; Jantschke, 1972; Poole, 1987), although with some variability between the two species. As a comparative study based on hormone levels demonstrated, the more gregarious Sumatran orangutans are less stressed in captivity than the Bornean species (Weingrill, Willems, Zimmermann, Steinmetz, & Heistermann, 2011). A study on the effect of fission-fusing housing of zoo-living Bornean orangutans on hormonal and behavioural stress parameters revealed that the orangutans under fission-fusion conditions were less affected by social stress factors associated with a large group size than orangutans under conventional housing conditions (Amrein, Heistermann, & Weingrill, 2014).

Although wild orangutans are generally less gregarious than other great apes, captive orangutans are reported to show less aggressive behaviour than chimpanzees in potential conflict situations such as feeding sessions; severe agonistic interactions are rare (Edwards & Snowdon, 1980; Jantschke, 1972; Poole, 1987). These observations suggest that captive orangutans might have adopted strategies to alleviate conflict situations, e.g. increased affiliative and prosocial behaviour (Aureli & Smucny, 1998). Engaging in non-aggressive food interactions that result either in food sharing by the possessor or in abandoning a request by the solicitor might be an appropriate alternative strategy. Recent physiological findings on wild chimpanzees support this suggestion by linking food sharing with increased urinary oxytocin levels (Wittig et al., 2014).

Contradicting earlier views, which even ascribed an “anti-social attitude of adult orang utans […] which precludes the development of food sharing” (Sugardjito & Nurhuda, 1981, p. 415), more recent studies demonstrate that orangutans possess those socio-cognitive predispositions required for passive and active food sharing, such as social tolerance, inhibitory control, and the ability to produce and to comprehend signals (Amici, Aureli, & Call, 2008; Liebal, Pika, & Tomasello, 2006; Pika, Liebal, Call, & Tomasello, 2005). Orangutans strongly depend on social learning during their infancy and adolescence (Jaeggi, Dunkel, et al., 2010b; van Noordwijk et al., 2009; van Noordwijk & van Schaik, 2005), are able to distinguish intentional actions from accidental behaviour (Call & Tomasello, 1998). Furthermore, orangutans in captivity are found to have a large repertoire of gestures and to use them flexibly in communication (Liebal et al., 2006). In experimental settings, they were able to cooperate in a problem-solving task (Chalmeau, Lardeux, Brandibas, & Gallo, 1997), frequently passed token to conspecifics upon request (Pelé, Dufour, Thierry, & Call, 2009), and were ready to help conspecifics in need in an assistance task (Liebal, Vaish, Haun, & Tomasello, 2014).

Taking all these findings from both wild and captive orangutans into account, the central hypothesis (H1) and the derived predictions (P1.1 - P1.3) for this first study are as follows:

(H1) In potential conflict situations created by the unequal distribution of food or objects across individuals, socially housed orangutans perform prosocial behaviours to mitigate the conflict comparable to those in other great apes, using them as a means to cope with group life.[2]

---

[2] In this hypothesis, I expanded the focus by including not only food interactions but also interactions over preferred non-food objects following Jaeggi and van Schaik (2011) who suggested similar psychological mechanisms underlying food and non-food transfer. Captive orangutans are usually highly interested in objects for behavioural enrichment, sheets and material for nest building (KSK, pers. observation). I therefore assumed that the unequal possession of non-food objects might create a similar conflict situation as food and enables analogous possibilities to mitigate the situation. Moreover, it has been suggested that in food contexts the readiness of great apes to act prosocially might be decreased compared to non-food contexts (Yamamoto & Takimoto, 2012). The inclusion of both contexts enabled a comparison of the respective behavioural patterns.

(P1.1) In potential competitive situations regarding the possession of food or objects, captive orangutans are expected to frequently engage in tolerated passive and active transfers depending on the particular partner, rather than in aggressive interactions.

(P1.2) When interacting over food or objects, captive orangutans are expected to frequently perform begging gestures and other, non-aggressive forms of request behaviour until the possessing individual tolerates a transfer, rather than to make a direct attempt to take the food item or object or to take it by force.

(P1.3) The frequency of tolerated transfers is expected to increase when the available space decreases, since the latter is usually correlated with an increase of social tension due to fewer opportunities for the orangutans to avoid each other.

To test my predictions and to elucidate the prosocial potential of orangutans with regard to food and object sharing, I conducted an observational study with a group of Sumatran orangutans under two housing conditions.

2.1.2 Methods

2.1.2.1 Study group and housing conditions

I observed a well-established group of Sumatran orangutans in the zoological garden of Dortmund, Germany.

The group consisted of six individuals: one adult male (*Walter*), three adult females (*Toba*, *Suma* and *Djamuna*), one not fully weaned, semi-dependent female (*Tao*) and one unweaned, dependent female (*Eirina*). The immatures were daughters of *Walter* and *Toba*. The other adult females were not kin-related to any other group member (Table 2). In assigning the age classes, I followed van Noordwijk and van Schaik (2005).

Table 2 Details of observed individuals: sex, age and kin relation with other group members; A and B, respectively, refer to the subgroups formed during the winter

Individual	**Sex**	**Date of birth**	**Age category**	**Subgroup**	**Information on kinship**
Walter (Wa)	male	24/04/1989	adult	A	father of Ta and Ei
Toba (To)	female	07/02/1994	adult	A	mother of Ta and Ei
Tao (Ta)	female	18/11/2004	semi-dependent immature	A	daughter of Wa and To
Eirina (Ei)	female	30/12/2007	dependent immature	A	daughter of Wa and To
Suma (Su)	female	14/03/1993	adult	B	no kin
Djamuna (Dm)	female	28/05/1999	adult	B	no kin

During the summer (at least from April to September, depending on the weather), all individuals were kept together in the outdoor enclosure for the day time. The outdoor enclosure had an area of 1515 m² and contained trees, bushes, grass, and herbs, climbing structures, ropes, a fresh water spring and a tree hut. During the winter, the orangutans were kept in two subgroups (Table 2) in adjacent indoor enclosures (48 m² and 65 m²), each with additional sleeping boxes and alternating temporary access to a third compound (140 m²). Subsequently, the family subgroup consisting of *Walter*, *Toba*, *Tao,* and *Eirina* will be referred to as group A, while the other one consisting of *Suma* and *Djamuna* as group B (Table 2). The indoor enclosures were equipped with climbing structures, platforms, access to fresh water, and poking timbers. Since these indoor enclosures were separated by flexible mesh, the two subgroups had the opportunity to interact with each other through the mesh when kept indoors during the winter.

The main diet consisted of a mixture of vegetables and fruits, but also included leaves, branches, yoghurt, curd, cooked eggs, occasionally cooked meat, and special food items for behavioural enrichment.

2.1.2.2 Data collection

I conducted group observations between September 2011 and July 2012 using *continuous recording* as the recording rule and *behavioural sampling* as the sampling rule (Altmann, 1974; P. Martin & Bateson, 2007). This resulted in a total observation time of 157 h 30 min of which 74 h 21 min were collected outdoors in autumn 2011 and summer 2012, and 83 h 9 min indoor observations in winter 2012. Observations were distributed over the daily main activity period of 15 days each split in two intervals of consecutive days both for outdoor observation (10 days in September 2011 and 5 days in June and July 2012) and indoor observations (10 days in February and 5 days in March 2012). On average, the observation time per day lasted 5 h 30 min outdoors and 5 h indoors, respectively. The observations were conducted from the visitor area during opening hours. I continuously video-recorded the whole group and focused on all visible social interactions. When filming, I was additionally taking notes on social interactions in previously defined contexts (cf. next section) and on particular events or circumstances, e.g. when individuals were hidden from view. When interactions took place within more than one dyad at the same time and could not be video-taped simultaneously, I used the audio function of the camcorder to record a spoken description. All observations were conducted using a digital camcorder CANON Legria FS200.

2.1.2.3 Definitions and data coding

Based on both the footage and the written protocol, I coded previously defined behaviours in the contexts of uneven food and object possession using *all occurrences sampling* (also called *behaviour sampling*) as the sampling rule (Altmann, 1974; P. Martin & Bateson, 2007) by applying the coding scheme below (Fig. 2). Additionally, for each context-specific interaction I coded the identity of the interacting individuals, the enclosure, the date, on- and offset time and the food or object type. The respective codes were defined as follows (see also Table 1 on p. 14 and Tables A1-A2 in the Appendix). All coding was performed using the coding software INTERACT®, Version 14.3.

A ***food interaction*** was defined as a dyadic interaction regarding a defensible food item between a food-possessing and a non-possessing, but food-interested individual.

An ***object interaction*** was defined analogously as a dyadic interaction over a defensible object or parts of it between an object-possessing and a non-possessing, but object-interested individual.

An individual was referred to as ***possessor*** if she held food or a non-food item with her hand, mouth or any other body part or had it put into the vision field within arm's length, so that it was potentially defensible. Only interactions where the possessor had the opportunity to defend her possession were considered as food or object interactions, respectively. Consequently, a sudden snatching of food or the object, which could not have been prevented by the possessor, did not count as a food or object interaction.

A non-possessing individual who showed interest in the food or object was called ***solicitor***. Showing interest has been ascribed if the non-possessor was located in the visual field of the possessor with her body orientated towards the possessor either (i) within a distance up to two arm's lengths (i.e. in proximity) gazing at the food/object or chewing mouth and/or performing request behaviour; or (ii) outside a distance of two arm's lengths performing request behaviour. Mere gazing did only count as showing interest, if it occurred in proximity and persisted for at least 5 s (unless it led to transfer within less than 5 s). For all other request behaviours no minimum duration was required. There was one exception to this definition of showing interest: In case of proactive, i.e. possessor-initiated transfer the receiver was called solicitor as well, though the criteria of showing interest in the first instance were not fulfilled.

Food indicated all eatable items provided during daily feeding sessions and behavioural enrichment, furthermore grass, herbs, leaves, and twigs collected by the orangutans in their enclosures, but also regurgitated food. ***Object*** usually indicated not-eatable items, which were used as tools, for nest building or for play, e.g. cloths of different sizes, coconut shells, cardboard, wood wool, balls, stones, pieces of wood or bamboo. Objects might be compact or dividable.

In case an item could be regarded both as food and as an object, e.g. a twig or leaves, then its actual use or function was decisive: If the possessor would use it as food, then it was seen as *food*; if she used it in non-nutritional ways, then it was seen as an *object*.

Onset and offset of a food or object interaction were determined from the perspective of the solicitor: A food or object interaction started when the solicitor began to show interest (or with the possessor-initiated transfer in the case of proactive transfer) and ended either when a piece of food or the object or parts of it had been transferred or when the solicitor had not shown interest for at least 5 s.

A food or object interaction usually comprised one or more of the following elements: request, resistance, and/or transfer.

A ***request*** consisted in a single request behaviour or a combination of several request behaviours, which ranged from gestures like *peering*, *extend arm*, *hand under mouth*, *touch food/object or body part*, to actions like *grab food/object, grab body part*, *follow*, *chase*, *use of attention getters*, vocalisations such as *whimpering* up to *tantrums*. I categorised request behaviours with regard to their intensity: no request, mild request (including gestures without body contact, e.g. *directed approaching*, *peering*, *hand under mouth*, *extend hand/open palm*, *vocalisations*, *contact sitting*), moderate request (including *reaching for food*, *touch body/food*, *follow*), strong request (including *grab/pull food*, *grab/pull body part*, *taking attempts*) and threat/chase. When behaviours of different intensities have been combined, the most intense behaviour determined the category. (For more details, cf. Appendix, Table A1.)

In a strict sense, only active behaviour of the possessor which had been performed to prevent a transfer was considered as ***resistance***, with one exception: when a possessor had shown no reaction until the solicitor ceased showing interest, then this passive ‘ignoring’ was also referred to as resistance. I distinguished between five degrees of resistance depending on its intensity: no reaction (*ignoring*), slight resistance (e.g. *turn away*), moderate resistance (e.g. *shield food*), strong resistance (e.g. *move away* or *struggle*) and threat (e.g. *threat face* or *bite*). In case different resistance behaviours had been combined, the category with regard to the strongest behavioural element had to be chosen (for more details, cf. Appendix, Table A1).

A food or object interaction resulted either in transfer or not. No transfer occurred when the possessor either successfully resisted or when a transfer attempt failed, e.g. when offered food dropped outside the solicitor’s reach. The first case was referred to as ***no transfer (resistance)*** and the latter as ***failed transfer***. Transfers that occurred could either be non-tolerated or tolerated. A transfer was called ***non-tolerated*** if it occurred despite the possessor’s undiminished resistance. Tolerated transfers might occur without any resistance – indicated as ***tolerated transfer (no resistance)*** – or with initial resistance – indicated as ***tolerated transfer (initial resistance)***. The crucial criterion to distinguish *tolerated transfer (initial resistance)* from *non-tolerated transfer* was that the possessor had to cease his resistance and, finally, enabled an unresisted transfer.

Transfers could be performed in several ways: ***Forced taking*** indicates a non-tolerated transfer. ***Collect near*** was defined as the solicitor's taking food or the object, which was discarded, but still defensibly by the possessor. ***Tolerated taking*** occurred when the solicitor was permitted to take food or the object, but not assisted by the possessor. In case, the solicitor was not only permitted to take food or the object, but also assisted by the possessor, the transfer was called ***facilitated taking***. The passing over of food or the object by the possessor was indicated as ***active giving***, when it occurred upon previous request, and as ***offering***, when it occurred without request. Tolerated transfers for which the exact transfer type was indeterminable were indicated merely as tolerated

Food sharing was defined as the tolerated transfer of a defensible food item from a possessor to a solicitor (Feistner & McGrew, 1989). This included tolerated transfers with and without initial resistance. Non-tolerated transfers and no transfers due to resistance were regarded as ***no food sharing***. Neither of both categories could be reliably ascribed to failed transfers.

Object sharing was defined analogously as the tolerated transfer of a defensible object or parts of this object from a possessor to a solicitor.

Different types of sharing could be distinguished with regard to the extent of the active involvement of the possessor. In ***passive sharing***, the solicitor was allowed to take food or the object without resistance or assistance by the possessor. ***Active sharing*** involved an action by the possessor that facilitated or performed the transfer and could either be ***reactive***, i.e. upon request, or ***proactive***, i.e. possessor-initiated (Jaeggi, Burkart, et al., 2010).

Table 1 (section 1.1.4.3, p.14) provides an overview of the different transfer types distinguished in this study, alongside with an operational definition and a categorisation regarding tolerance and the possessor's active involvement, accomplished by references to analogous concepts from previous studies on food transfer.

All data coding was done by me. To assess interrater reliability, a second person who has been naïve to the hypotheses coded 11 % of the data again using the same coding scheme. As a measure of interrater reliability, I calculated Cohen's kappa coefficient of agreement (Cohen, 1960) using the function `kappa2` from the R package irr (Gamer, Lemon, Fellows, & Puspendra, 2012). It demonstrated a good agreement between the two raters with respect to both the occurrence of sharing ($\kappa = 0.79$, $n = 138$, $p < 0.001$) and the active involvement of the possessor ($\kappa = 0.72$, $n = 138$, $p < 0.001$).

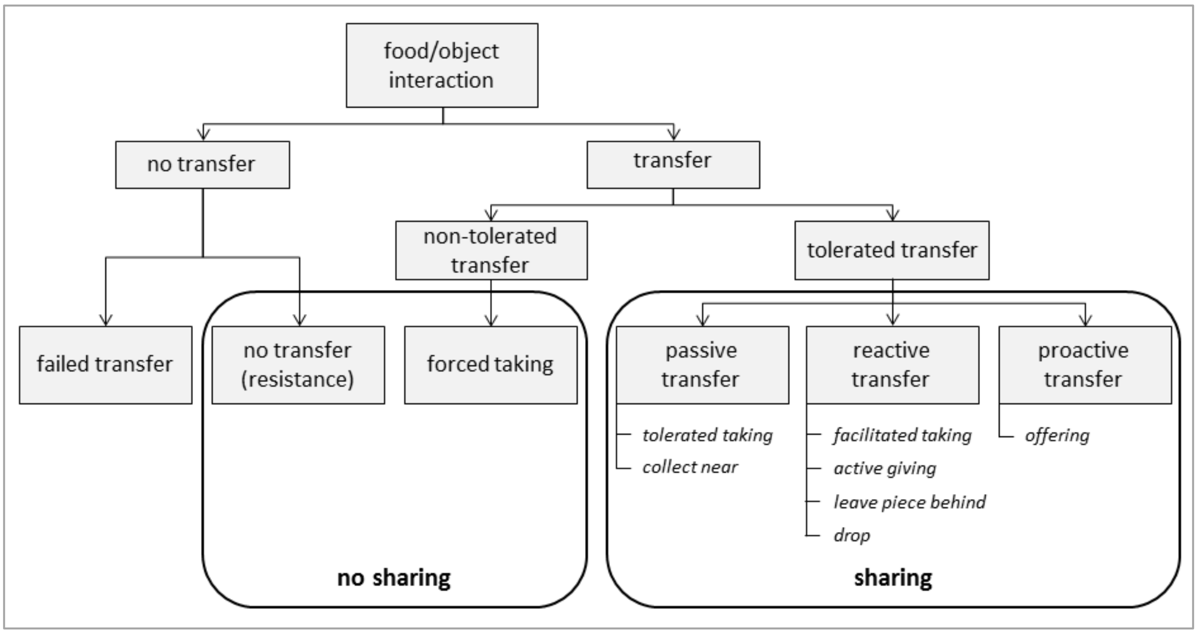

Fig. 2 Coding scheme for food and object interactions[3]

2.1.2.4 Data analysis

For all analyses, I used Microsoft Excel® 2010 and the statistics software R 3.2.4 (R Core Team, 2016) with appropriate packages for analysing and plotting, e.g. car (J. Fox & Weisberg, 2011).

Due to the small sample size and unequal contribution of the particular individuals and dyads to the data set, I applied descriptive and non-parametric statistics both on pooled data and on data differentiated at an individual and dyadic level. I computed absolute and relative frequencies of food and object interactions with regard to the occurrence of sharing, the active involvement of the possessor, the particular interaction types, combination of request behaviours and the intensity of resistance.

To test for the occurrence of reciprocity, I calculated the Pearson's product-moment correlation for the willingness to share food/object and the food/object getting success for dyads using R function `cor.test` from R package stats.

With regard to the effect of housing conditions, I investigated the effect of the two housing conditions (large outdoor vs. smaller indoor enclosure) on the frequency of food and object interactions in general and on sharing by descriptive statistics first. I applied a Wilcoxon signed rank test to test my prediction about the housing effect on food and object interactions and on sharing using the R function `wilcox.exact` from R package exactRankTests (Hothorn & Hornik, 2015) with statistical significance assessed at the α-Level of 0.05.

---

[3] This coding scheme was already included – in a slightly adapted form – in the prior publication of Study 2 (Kopp & Liebal, 2016, Fig. 1, doi:10.1007/s00265-016-2130-2).

Finally, I compared the data for food and object interactions on a dyadic basis. To test for correlations between food and object interactions and between the willingness to share food and objects, respectively, I calculated the Pearson's product-moment correlation using R function `cor.test` from R package stats.

2.1.3 Results

I report the results with regard to predictions P1.1 to P1.3 for food and object interactions separately, followed by a brief comparison of the main findings for both contexts. For each prediction, I report results for pooled data on group level and on an individual and/or dyadic with subheadings summarising the respective main findings.

2.1.3.1 Food context

P1.1 confirmed for food context: Non-aggressive food interactions and frequent passive and active sharing depending on the particular partner, rather than open conflict

(i) Orangutans predominantly engaged in non-aggressive food interactions and shared food frequently with high proportions of active transfers

In total, I observed 908 food interactions of which 719 were determinable with respect to the occurrence of a transfer. These food interactions resulted in 346 food sharing events (48%). In 339 cases (47%), no food sharing took place: either due to the food possessor's successful resistance (*n* = 311, 43%) or because a transfer took place despite the undiminished resistance of the possessor (*n* = 28, 4%). For the remaining 34 cases (5%), it could not be determined whether the transfer had been tolerated or not. Passive (*n* = 166, 23%) and active transfers (*n* = 157, 22%) occurred nearly equally frequently. For the remaining cases of food sharing (*n* = 23, 3%), it could not be determined whether they were passive or active. The majority of active transfers was reactive, i.e. it took place upon request (*n* = 138, 19%), the remaining cases were proactive, i.e. initiated by the possessor without previous request (*n* = 18, 2.5%), with the exception of one case for which the initiator could not be determined. (Fig. 3, cf. also Table 4)

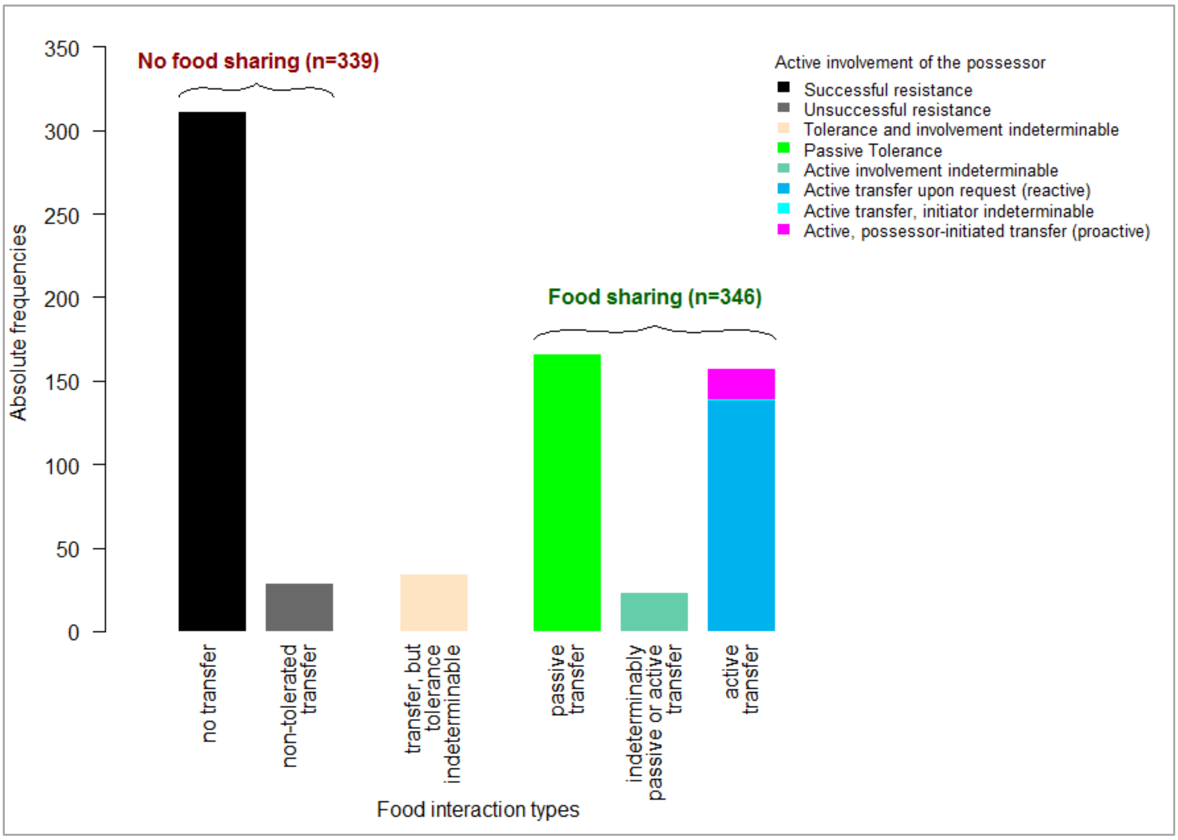

Fig. 3 Absolute frequencies of food interactions in the study group differentiated with regard to sharing tolerance and active involvement of the food possessor across the observation periods

Individuals engaged considerably differentially frequent in food interactions. There were differences among the individuals in the general engagement in food interactions. *Toba* was involved in more than a half of all food interactions (*n* = 377, 52%), followed by *Suma* (*n* = 269, 37%), *Tao* (*n* = 262, 36%), *Eirina* (*n* = 223, 31%) and *Djamuna* (*n* = 202, 28%). *Walter* generally engaged much less in food interactions than all females (*n* = 105, 15%). Furthermore, the individuals differed with regard to the frequency of their role as possessor or solicitor when they were interacting over food. While both *Toba* and *Walter* were mainly in the role of the possessor when they were involved in food interactions (in 85% and 83%, respectively), the two immatures *Eirina* and *Tao* were mostly in the role of the solicitor (91% and 79%, respectively). *Suma* and *Djamuna* were nearly as often possessor as they were solicitor (51% vs. 49% for *Suma*, 49% vs. 51% for *Djamuna*). (Fig. 4)

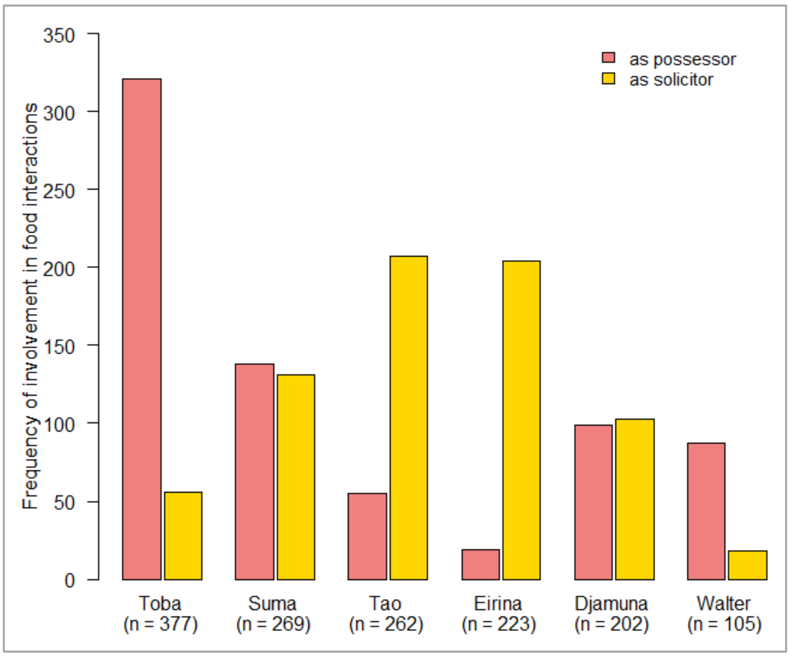

Fig. 4 Frequencies of food interactions for each individual differentiated between being involved as possessor (red bars) and solicitor (yellow bars), respectively. Numbers in parenthesis below the individual name indicate the total number of food interactions in which the particular individual had been involved

(ii) Sharing with immatures was mainly passively, while adults predominantly shared actively among each other

Considering the extent of active involvement of the possessor with regard to the identity of the solicitor revealed, that both immatures *Eirina* and *Tao* received more often food by passive than by active transfer, though the proportion of active sharing was higher for the older, semi-dependent *Tao* (*n* = 32, 33%) than for the dependent *Eirina* (*n* = 30, 24%). All adult individuals received relatively more often food by active (46% ± 9%) than by passive transfer (22% ± 7%). Among adults, *Suma* showed with 55% (*n* = 48) the highest proportion and *Walter* with 33% (*n* = 3) the lowest proportion of active transfers as recipient. All adults received food without previous request at least twice, while all active transfers towards immatures occurred upon request. (Fig. 5)

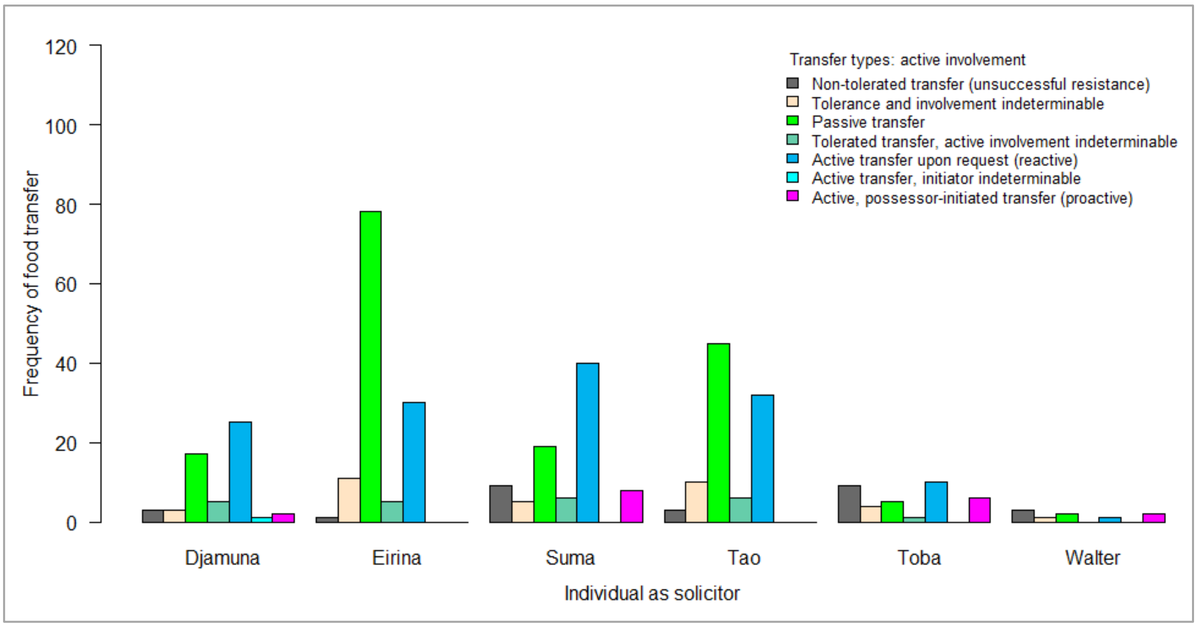

Fig. 5 Absolute frequencies of the particular food transfer types for each individual in the role as solicitor. Dark grey bars indicate non-tolerated transfers, beige bars indicate transfers for which it was not determinable whether they had occurred tolerated or not. All other coloured bars indicate tolerated transfers with active involvement of the possessor increasing from left to right.

Restricting the analysis to dyads which consisted of adults only, the average proportion of active sharing exceeded that of passive sharing (mean$_{active}$ = 0.54 ± 0.35, mean$_{passive}$ = 0.26 ± 0.23). (Fig. 6)

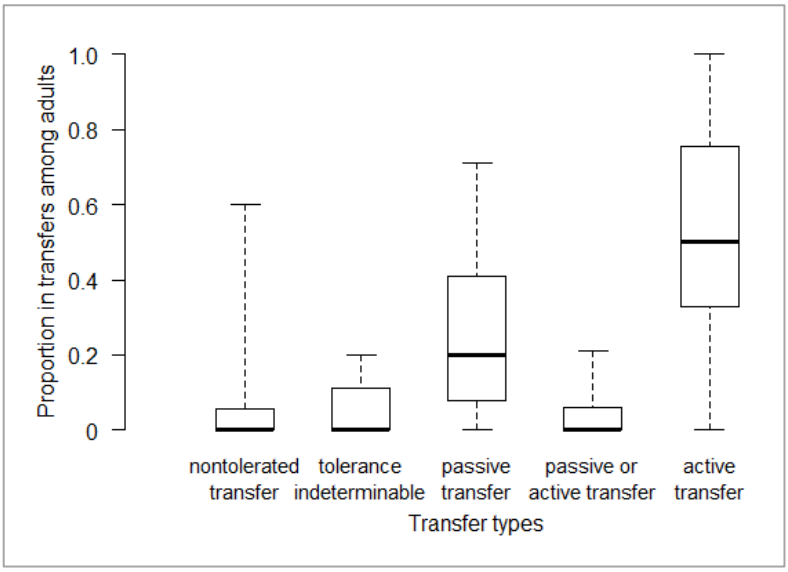

Fig. 6 Proportion of transfer types across adult-adult dyads (*n* = 11) with regard to the possessor's active involvement. Horizontal lines indicate medians, boxes indicate interquartile ranges, and whiskers indicate minima and maxima, respectively

(iii) All orangutans preferentially interacted over and shared food with particular partners

Individuals did not engage equally frequently in food interactions with all groupmates. Taking the solicitor's perspective, the intra-individual frequencies for soliciting food from a groupmate varied similarily and their means ranged from 4 ± 2 for *Walter* up to 41 ± 29 for *Tao* and 41 ± 61 for *Eirina* (Fig. 7a). There was a comparable intra-individual variation of frequency for individuals to be involved as possessor, here the means ranged from 4 ± 2 for *Eirina* up to 64 ± 53 for *Toba* (Fig. 7c).

From the solicitor's perspective, the food-getting success (FGS) varied both among and within the individuals with means ranging from 30% ± 24% for *Toba* up to 53% ± 17% for *Djamuna* (Fig. 7b). Likewise, from the possessor's perspective, the willingness to share (WtS) varied inter- and intra-individually with means ranging from 25% ± 20% for *Suma* up to 57% ± 8% for *Tao* (Fig. 7d).

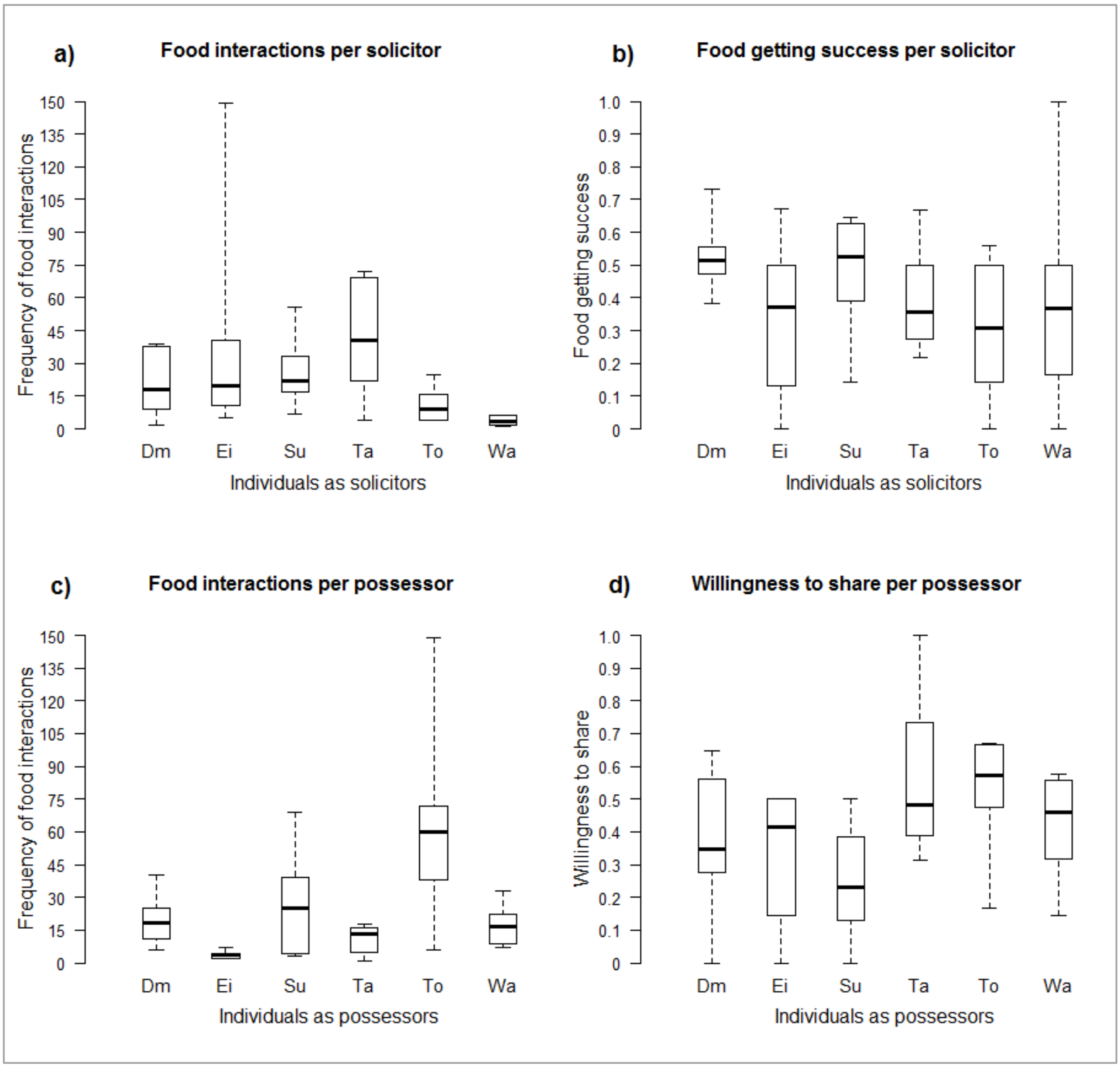

Fig. 7 Frequencies of food interactions, food getting success and willingness to share summarised for each individual across dyads from the solicitor's and the possessor's perspective, respectively. a) Absolute frequencies of food interactions per solicitor. b) Food getting success, i.e. proportion of food interactions which resulted in food sharing, per solicitor. c) Absolute frequencies of food interactions per possessor. d) Willingness to share, i.e. proportion of food interactions which resulted in food sharing, per possessor. Horizontal lines indicate medians, boxes indicate interquartile ranges, and whiskers indicate minima and maxima, respectively

Especially the found intra-individual variances with regard to frequencies of food interactions and sharing suggest individual preferences to interact and/or share with particular partners which becomes obvious when analysing the data on a dyadic level. Across dyads, the average frequency of engaging in food interactions with another individual was 24 but showed a considerable variation (sd = 31); the average proportion of food sharing per dyad was 41% (sd =24%).

Most food interactions by far occurred between *Toba* as possessor and her younger, dependent daughter *Eirina* as solicitor (*n* = 149, i.e. 21% of all food interactions) with a high proportion of food sharing (*n* = 100, 67%) followed by food interactions between *Toba* and her older daughter *Tao* (*n* = 72, i.e. 10% of all food interactions) with an equally high proportion of food sharing (*n* = 48, 67%). In contrast, while there were nearly as much food interactions with *Suma* as possessor and *Tao* as solicitor (*n* = 69) as between *Toba* and *Tao*, much less of the interactions between the former finally led to food sharing (*n* = 15, 22%). The directed dyads *Tao→Walter*, *Eirina→Walter*, *Eirina→Djamuna* and *Suma→Walter* were those dyads in which the least food interactions took place (1, 2, 2 and 3, respectively). (Fig. 8)

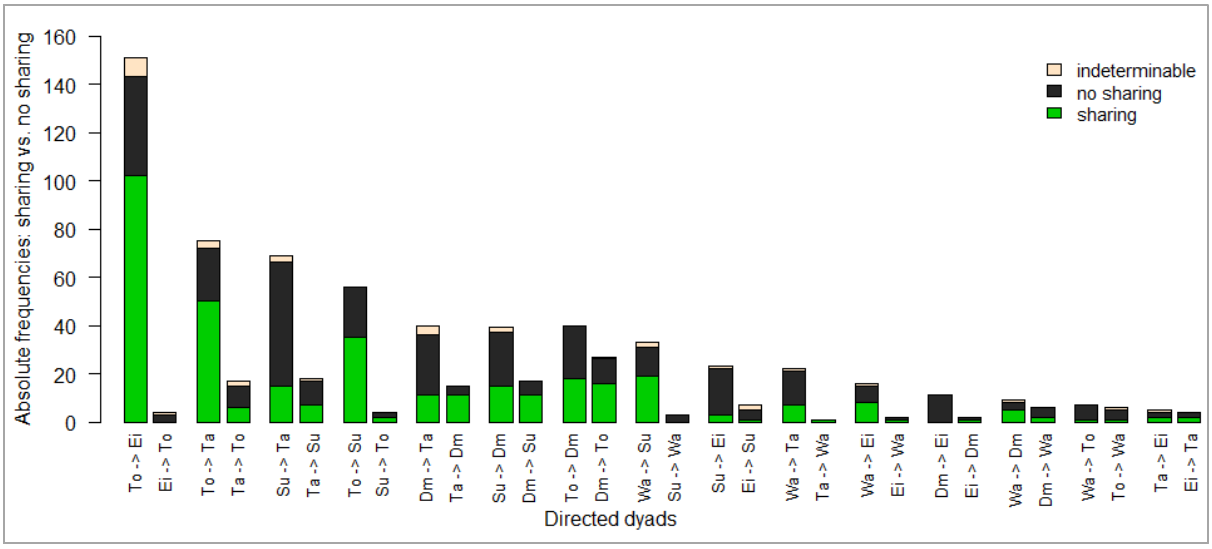

Fig. 8 Absolute frequencies of food interactions for each directed dyad. Dyads consisting of the same individuals with reverse roles are placed next to each other. Green sections of the bars indicate the respective proportion of food sharing (i.e. *food getting success* from the solicitor's perspective and *willingness to share* from the possessor's perspective, respectively). Black sections indicate those food interactions which did not resulted in food sharing, beige sections indicate those cases for which it was not determinable, whether the transfer had been tolerated or not

(iv) Reciprocal exchange of food could neither be demonstrated, nor be ruled out

A comparison of the proportion of food sharing between two individuals and the proportion of food sharing between the same individuals with reverse roles revealed no evidence for the occurrence of reciprocity (Pearson's product-moment correlation: r = -0.21, *N* = 15, *p* = 0.45, confidence intervals with statistical significance assessed at the α-level of 0.05: lower CI = -0.65, upper CI = 0.34). (Fig. 9)

Furthermore, the data were partly extremely unbalanced with regard to the number of food interaction both across dyads (confer e.g. dyads *Toba↔Eirina* vs. *Tao↔Eirina*; Table 3) and within dyads (confer e.g. *Toba→Eirina* and *Eirina→Toba*; Table 3).

Therefore, conclusions about reciprocity – i.e. a positive correlation between the willingness to share as a possessor with an individual on the one hand and the food getting success as solicitor in interactions with this particular partner on the other – based on these data are to be treated with caution.

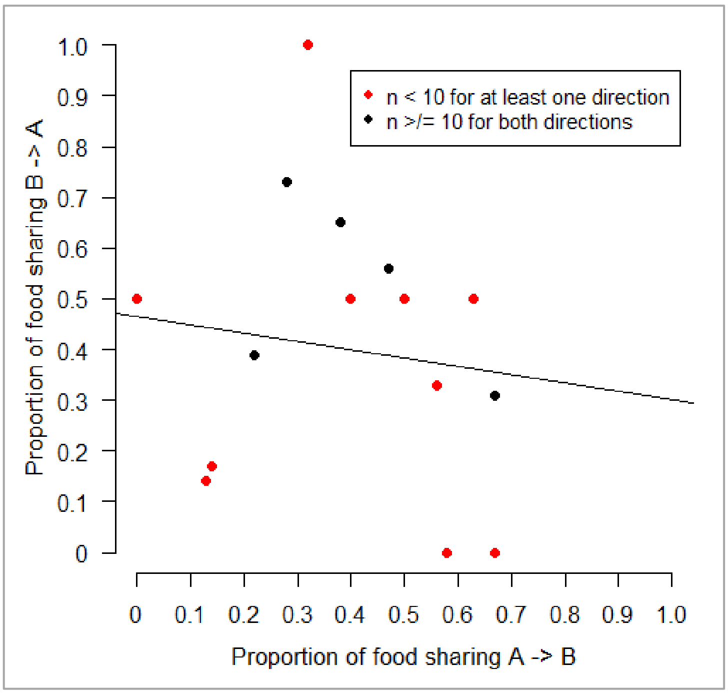

Fig. 9 Proportions of food sharing within dyads plotted against proportions of food sharing between the same individuals with reverse roles as possessor and solicitor. Black dots indicate those dyads with more than 9 food interactions for each direction; red dots indicate those dyads with less than 10 food interactions for at least one or for both directions

Table 3 Comparison of absolute frequencies of food interactions and proportions of food sharing for each dyad with regard to the respective role of the involved individuals as possessor or solicitor. The majority of dyads demonstrates unbalanced data with respect to the number of food interactions for the directed dyads. Red shadings indicate dyads for which the number of food interactions for one direction is at least twice as much as the one for the reverse direction (11 out of 15 dyads). Red boxes indicate frequencies of food interactions less than 10 (for 7 dyads in one direction, for another 3 dyads in both directions)

Dyad (A↔B)	Number of food interactions (A→B)	Proportion of food sharing (A→B)	Number of food interactions (B→A)	Proportion of food sharing (B→A)
Toba↔Eirina	149	67%	4	0%
Toba↔Tao	72	67%	16	31%
Suma↔Tao	69	22%	18	39%
Toba↔Suma	56	63%	4	50%
Djamuna↔Tao	40	28%	15	73%
Suma↔Djamuna	39	38%	17	65%
Toba↔Djamuna	38	47%	25	56%
Walter↔Suma	33	58%	3	0%
Suma↔Eirina	23	13%	7	14%
Walter↔Tao	22	32%	1	100%
Walter↔Eirina	16	50%	2	50%
Djamuna↔Eirina	11	0%	2	50%
Walter↔Djamuna	9	56%	6	33%
Walter↔Toba	7	14%	6	17%
Tao↔Eirina	5	40%	4	50%

P1.2 confirmed for food context: Non-aggressive communication generally preceded food transfer

(i) Solicitors predominantly signaled their interest using gestures first, rather than trying to obtain food directly

In a minority of food interactions, the non-possessing individual did not perform any detectable request behaviour (*n* = 33, 5%). These were cases of either proactive transfers (*n* = 18), passive transfers (*n* = 13) or forced taking (*n* = 2). The vast majority of food interactions were initiated by a single request behaviour (*n* = 263, 37%) or a combination of two (*n* = 245, 34%), three (*n* = 131, 18%), four (*n* = 31, 4%), five (*n* = 6, 0.8%) up to six (*n* = 4, 0.6%) behaviours per request. For six cases, the request behaviour was not determinable. The most frequent behavioural element was *peering/approach face* (*n* = 292) – both as a single request behaviour and in combination with other behaviours; followed by *taking attempt from hand or mouth* (*n* = 154), *directed approaching* (*n* = 135), *touch food or body* (*n* = 129), *grab/pull body part* (*n* = 99), *contact sitting* (*n* = 89), *grab/ pull food* (*n* = 79), *mouth under/near mouth* (*n* = 77), *mouth-mouth contact* (*n* = 64), *manual gestures* (*n* = 47), *reach for food* (*n* = 47) and *follow* (*n* = 25). Occasionally, other behavioural elements were performed, such as *vocalisations* (*n* = 6), *use of attention getters* (*n* = 3) or *chase* (*n* = 3). *Threat display* was observed only once.

There were several behaviours which often occurred in combination with each other, the most frequent of these pairs were: *peering/approach face* combined with either *touch food or body* (*n* = 51), *contact sitting* (*n* = 50), *directed approaching* (*n* = 45), mouth under/near mouth (*n* = 39) or *facial expression* (*n* = 35) as well as *taking attempt* combined with *directed approaching* (*n* = 45), *grab/pull body part* (*n* = 32) or *touch food or body* (*n* = 31).

With regard to intentensity, strong requests were most frequent (*n* = 281, 39%), followed by mildly intense requests (*n* = 244, 34%), moderate requests (*n* = 142, 20%) and threat/chase (*n* = 4, 0.6%). In 33 cases no request behaviour occurred and for another 15 cases, the intensity was not determinable. Strongly intense requests resulted more often in sharing (food getting success: 58%) than moderate or mild request (food getting success: 33% and 41%, respectively). However, since mild requests demonstrated a higher success rate than moderate requests, the food getting success seems not to increase with increasing intensity, or at least not with increasing physical involvement which had been applied as the defining criterion.

(ii) Possessors frequently complied with requests, otherwise their resistance was generally non-aggressively

The behavioural spectrum of the possessors was manifold as well. In 18 cases (2.5%) the possessor initiated the food transfer without previous request, and in another 258 cases (36%) the possessor did not show any resistance. Resistance behaviour (*n* = 443) consisted either of *no reaction* (*n* = 108, 15%), a single behaviour (*n* = 229, 32%) or a combination of two (*n* = 67, 9%), three (*n* = 7, 1%) up to four behavioural elements (*n* = 2, 0.3%). Another 30 responses to solicitations (4%) were not determinable with regard to their behavioural elements.

Ignoring the request without detectable reaction until the solicitation stopped was the most performed resistance behaviour (*n* = 108), followed by *shielding* (*n* = 75), *turn away* (*n* = 69), *move away* (*n* = 64), *push* (*n* = 39), *withdraw food* (*n* = 34), *hold on food* (*n* = 33), *hold food out of reach* (*n* = 17), *threat/agonistic behaviour* (*n* = 14), *struggle* and *grab/pull* (*n* = 12, each). All other behaviours were observed less than 8 times.

Resistance behaviours was mostly of moderate intensity (*n* = 142, 32%), followed by strong resistance (*n* = 109, 25%), no reaction (*n* = 108, 24%) and slight resistance (*n* = 40, 9%). Threat or other agonistic behaviour was rare (*n* = 14, 3%). For 30 cases (7%), the intensity was not determinable.

(iii) Orangutans interacted over various food types and shared usually, though not exclusively, small amounts of food

Food interactions occurred over a broad range of food types. Most food interactions regarded food that had been chewed or regurgitated (*n* = 162, 23%) – regurgitation and redigestion (R/R) was a frequent habit of all adult females immediately after feeding sessions, especially when feeding fruits (for research on the prevalence of and factors influencing R/R in captive orangutans cf. Cassella, Mills, & Lukas, 2012). On 148 occasions (21%), food interactions were over moderately preferred food as vegetables or less sweet fruits, e.g. apples, while 114 food interactions (16%) regarded highly preferred food, especially meat, nuts, bread and sweet fruits, e.g. melon, grapes or pomegranate. But also less preferred food such as grass, bamboo, wild herbs, leaves or leftovers, e.g. carrot peelings, was object of soliciting (*n* = 99, 14%), often even when the begging individual had the opportunity to gather the same food by herself. On 53 occasions (7%), food interactions regarded items that were no food in a strict sense, as e.g. pompoms of wood wool, but were used by the orangutans to chew on. Additionally to solid food, there were 34 interactions (5%) over water or tea, in these cases the solicitors had access to water or tea by herself, nevertheless they begged from other individuals. In 109 cases (15%) it was not possible to determine the respective food type, usually when a solicitor was begging from an already chewing individual, whose food intake had not been visible. The amounts of food which were transferred were usually small, mostly a bite or less. But there were some exceptions to this rule, e.g. when *Toba* tolerated *Tao*'s taking of a large piece of melon or when *Toba* handed over a whole carrot to *Suma*. In one remarkable case, when *Tao* grabbed a pumpkin possessed by *Toba*, *Toba* took a pumpkin back from *Tao*, divided it and handed the larger piece back to *Tao*.

P1.3 confirmed for food context: Increase of food interactions and sharing under less spacious housing conditions

(i) Overall interaction and sharing rates were only slightly affected by housing conditions.

With regard to the overall rate of food interactions (number per hour), there was no difference between the housing conditions: food interactions occurred as frequently in the outdoor as in the indoor enclosure (rates: 4.55 and 4.59 food interactions/hour, respectively).

The proportion of food sharing in food interactions was with 204 of 378 instances (54%) slightly higher in the indoor enclosure than in the outdoor enclosure with 142 of 341 instances (42%). However, since the proportion of transfers for which it was indeterminable whether they occurred tolerated or not was greater outdoors (*n* = 26, 8%) than indoors (*n* = 8, 2%), the actual difference between housing conditions regarding the proportion of foodsharing might be even less.

(ii) Inverted frequency relation of passive and active transfers: more active than passive sharing under less spacious conditions

Considering solely those tolerated transfers for which the active involvement of the possessor could be determined (*n* = 137 outdoors, *n* = 186 indoors) revealed, that transfers were slightly more frequently active than passive for the indoor condition (53% active vs. 47% passive), while the relation was reverse for the outdoor condition (42% active vs. 58% passive).

A closer examination of the indoor data demonstrated that the majority of active transfers occurred through the mesh, i.e. between individuals housed in neighboring inclosures, (*n* = 79 between subgroups, *n* = 20 within subgroups), while most passive transfers occurred within the subgroups (*n* = 8 between subgroups, *n* = 79 within subgroups). Figure 10 demonstrates the frequencies of food interaction types with regard to both the general housing conditions and the special condition for the indoor enclosure. (see also Table 4)

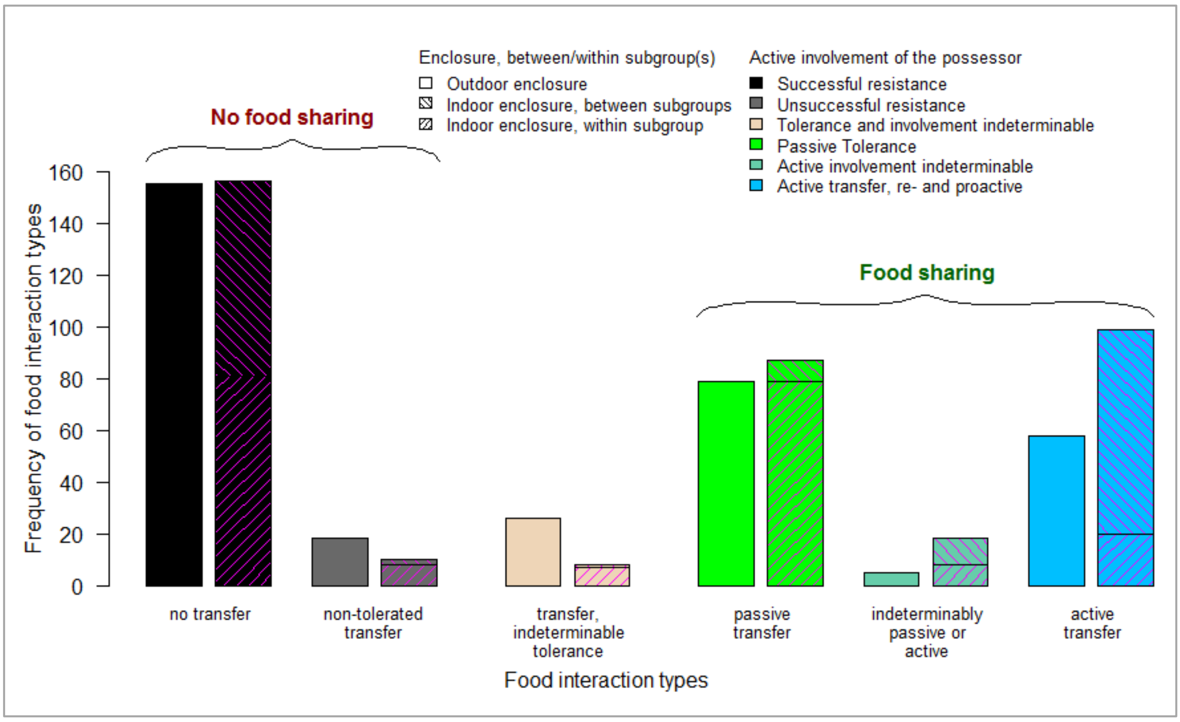

Fig. 10 Absolute frequencies of food interaction types differentiated with regard to interaction types and housing conditions. The different colours indicate the particular food interaction types. For each interaction type, coloured bars without shaded lines on the left indicate food interactions, which occurred in the outdoor enclosure, while coloured bars with shaded lines on the right indicate those which occurred in the indoor enclosure. Of the latter bars, the lower sections (shaded lines with an angle of 45°) indicate food interactions within a subgroup, the upper sections (shaded lines with an angle of 135°) indicate those between the two subgroups, i.e. which occurred through the mesh.

Table 4 Absolute and relative frequencies of food interaction types for housing conditions. The data for the indoor enclosure are additionally subdivided into food interactions which occurred within a subgroup and those which occurred between the subgroups. Percentages relate to the total of food interactions for the respective housing condition.

Housing / Food interaction type	Outdoor enclosure		Indoor enclosure		Indoors: within a subgroup		Indoors: between subgroups		Total	
All food interaction types	341 (rate: 4.59/h)		378 (rate: 4.55/h)		203		175		719 (rate: 4.57/h)	
No food sharing	173	50.7%	166	43.9%	89	43.8%	77	44.0%	339	47.1%
No transfer (resistance)	155	45.5%	156	41.3%	81	39.9%	75	42.9%	311	43.3%
Non-tolerated transfer	18	5.3%	10	2.6%	8	3.9%	2	1.1%	28	3.9%
Indeterminable tolerance	26	7.6%	8	2.1%	7	3.4%	1	0.6%	34	4.7%
Food sharing	142	41.6%	204	54.0%	107	52.7%	97	55.4%	346	48.1%
Passive transfer	79	23.2%	87	23.0%	79	38.9%	8	4.6%	166	23.1%
Passive or active transfer	5	1.5%	18	4.8%	8	3.9%	10	5.7%	23	3.2%
Reactive transfer	55	16.1%	83	22.0%	19	9.4%	64	36.6%	138	19.2%
Re- or proactive transfer	0	0.0%	1	0.3%	0	0%	1	0.6%	1	0.1%
Proactive transfer	3	0.9%	15	4.0%	1	0.5%	14	8.0%	18	2.5%

(iii) Unrelated adult females interacted and shared significantly more among each other when kept indoors, while interaction rates in most of the other dyads decreased

Although the overall rates of food interactions did not differ between outdoor and indoor housing (cf. Table 4), a comparison on a dyadic level revealed considerable differences with regard to the frequency of food interactions in both conditions. While for most dyads the frequency of food interactions decreased when housed in the indoor enclosure, food interactions within the dyads *Toba→Eirina*, *Tao→Djamuna*, *Tao→Eirina*, and among all adult females increased, even between females housed in adjacent enclosures (Fig. 11, Table 5).

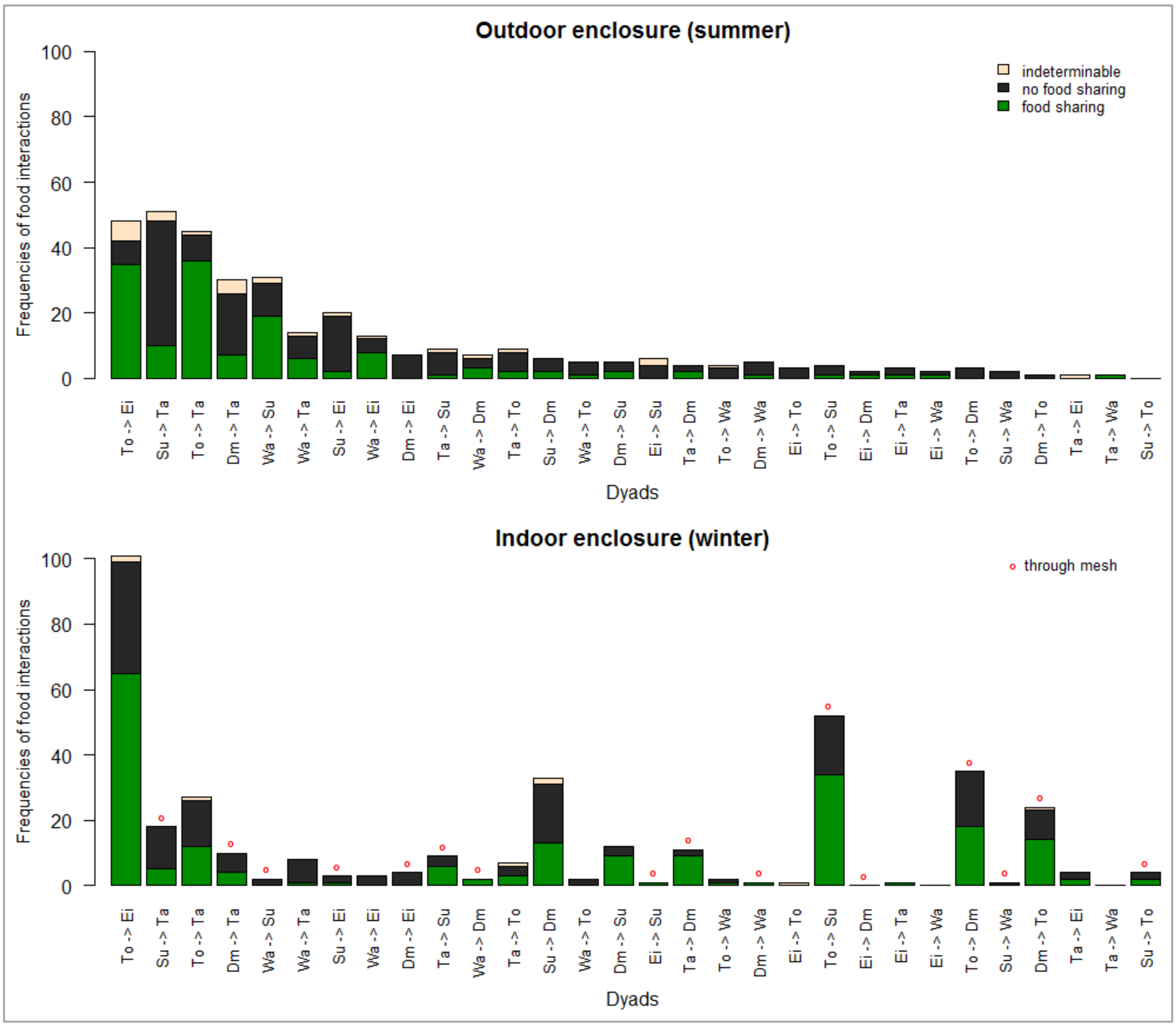

Fig. 11 Frequencies of food interactions per dyad differentiated with regard to housing conditions. In the upper figure, dyads are sorted by decreasing frequencies. In the lower figure, the order of dyads remains unchanged to enable comparison between outdoor and indoor condition. Bars represent frequencies of food interactions for each directed dyad with green sections indicating the proportion of interactions which resulted in food sharing, black sections indicating the proportion of interactions which did not result in food sharing and beige sections indicating food transfers for which it was not determinable whether they were tolerated or not. Red circles in the lower figure indicate those dyads that consisted of individuals housed in neighbouring enclosures. Within these dyads, the food interactions took place through the separating steel mesh

Taking the slightly differing total durations of outdoor and indoor observation into account and calculating rates of food interactions per hour for each directed dyad did not change these results: the rate of food interactions decreased in the majority of dyads, but increased among all adult females as well as within the dyads *Toba*→*Eirina*, *Tao*→*Eirina* and *Tao*→*Djamuna* (Table 5).

Table 5 Number of food interactions and food sharing events, interaction rates and proportions of food sharing for each directed dyad differentiated by their occurrence in the outdoor and indoor enclosures, respectively. Red shadings indicate proportions of sharing for dyads consisting of unrelated adult females (including *Tao*). All of them demonstrated an increased willingness to share with each other under indoor conditions.

Dyad	Inter-actions outdoors	Inter-actions indoors	Inter-action rate outdoors	Interaction rate indoors	Number sharing outdoors	Number sharing indoors	Proportion sharing outdoors	Proportion sharing indoors
To→Ei	48	101	0.646	1,215	35	65	73%	64%
To→Su	4	52	0.054	0.625	1	34	25%	65%
To→Dm	3	35	0.040	0.421	0	18	0%	51%
Su→Dm	6	33	0.081	0.397	2	13	33%	39%
To→Ta	45	27	0.605	0.325	36	12	80%	44%
Dm→To	1	24	0.013	0.289	0	14	0%	58%
Su→Ta	51	18	0.686	0.216	10	5	20%	28%
Dm→Su	5	12	0.067	0.144	2	9	40%	75%
Ta→Dm	4	11	0.054	0.132	2	9	50%	82%
Dm→Ta	30	10	0.403	0.120	7	4	23%	40%
Ta→Su	9	9	0.121	0.108	1	6	11%	67%
Wa→Ta	14	8	0.188	0.096	6	1	43%	13%
Ta→To	9	7	0.121	0.084	2	3	22%	43%
Su→To	0	4	0.000	0.048	0	2	0%	50%
Dm→Ei	7	4	0.094	0.048	0	0	0%	0%
Ta→Ei	1	4	0.013	0.048	0	2	0%	50%
Su→Ei	20	3	0.269	0.036	2	1	10%	33%
Wa→Ei	13	3	0.175	0.036	8	0	62%	0%
To→Wa	4	2	0.054	0.024	0	1	0%	50%
Wa→Dm	7	2	0.094	0.024	3	2	43%	100%
Wa→Su	31	2	0.417	0.024	19	0	61%	0%
Wa→To	5	2	0.067	0.024	1	0	20%	0%
Dm→Wa	5	1	0.067	0.012	1	1	20%	100%
Ei→Su	6	1	0.081	0.012	0	1	0%	100%
Ei→Ta	3	1	0.040	0.012	1	1	33%	100%
Ei→To	3	1	0.040	0.012	0	0	0%	0%
Su→Wa	2	1	0.027	0.012	0	0	0%	0%
Ei→Wa	2	0	0.027	0.000	1	0	50%	---
Ei→Dm	2	0	0.027	0.000	1	0	50%	---
Ta→Wa	1	0	0.013	0.000	1	0	100%	---
Mean:	11.4	12.6	0.153	0.151	4.7	6.8	29%	46%

Comparing the outdoor and the indoor data across all dyads demonstrated a significantly increased willingness to share, with assessed statistical significance at the α-level of 0.05 (exact one-tailed Wilcoxon signed rank test: T = 68, N = 24 (3 ties, 3 NAs), p = 0.009). Restricting the analysis to unrelated adult females (including *Tao*) revealed an even clearer difference between both conditions (exact one-tailed Wilcoxon signed rank test: T = 0, N = 10 (0 ties, 0 NA), p = 0.002) (Fig. 12)

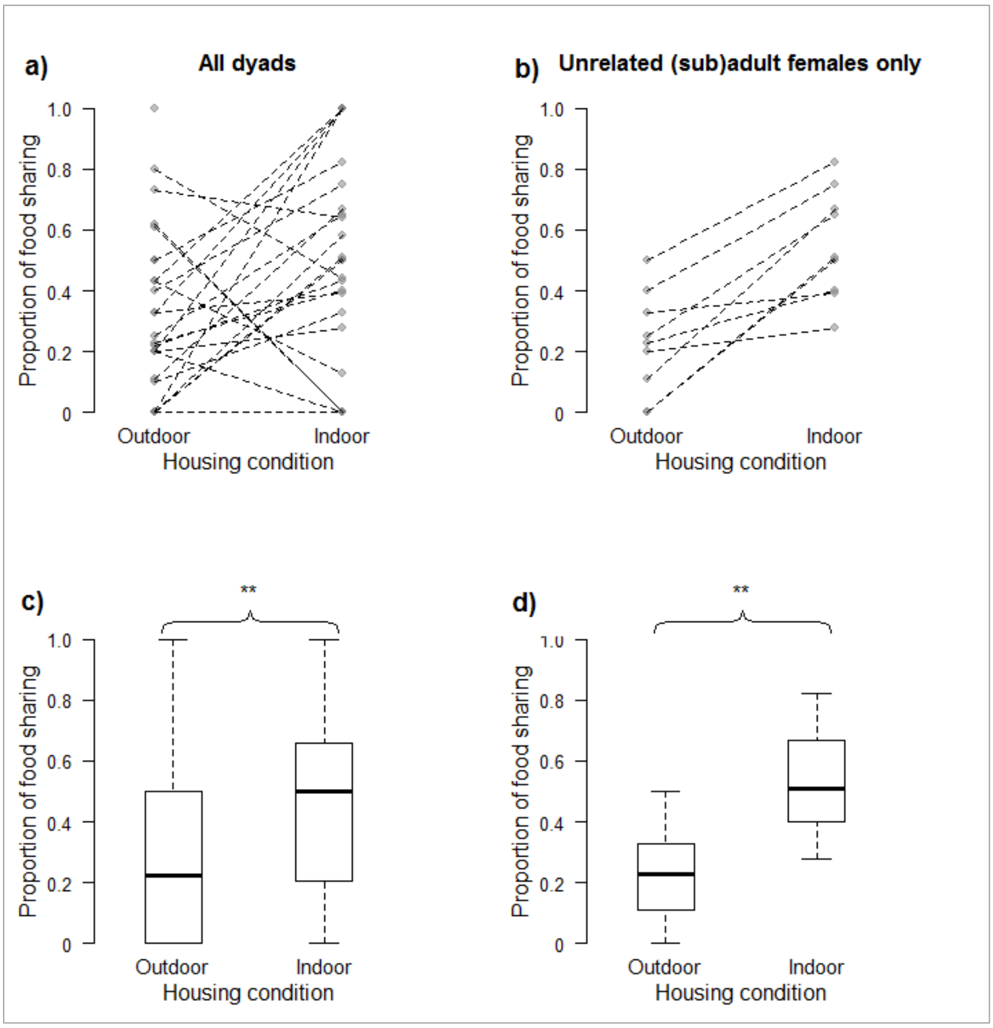

Fig. 12 Proportion of food sharing for outdoor and indoor conditions across all dyads (left side) and restricted to unrelated adult females including *Tao* (right side). In figures 11a and 11b, each data point refers to a particular dyad; dashed lines connect data points which belong to the same dyad. In figures 11c and 11d, boxplots illustrate the data for each condition. Horizontal lines indicate medians, boxes indicate the interquartile range and whiskers indicate 1.5 times interquartile range. Curly brackets with two asterisks indicate significant differences between the two housing conditions (assessed statistical significance at the α-level of 0.05)

2.1.3.2 Non-food context

P1.1 confirmed for non-food context: Non-aggressive object interactions and frequent tolerated passive and sharing depending on the particular partner, rather than open conflict

(i) Orangutans predominantly engaged in non-aggressive object interactions which frequently resulted in tolerated, mostly passive transfers

In total, I observed 302 dyadic interactions over objects; three of these interactions had to be excluded from the further analysis because for these cases it was not determinable whether a transfer had taken place or not. Of the remaining 299 object interactions, 138 interactions (46%) resulted in tolerated transfers (sharing) of the respective object or parts of it and 126 interactions (42%) did not result in sharing either due to successful resistance of the possessor (*n* = 90, 30%) or when a transfer occurred despite the undiminished resistance of the possessor (*n* = 36, 12%). For another 35 transfers (12%) it was not determinable whether they were tolerated or not.

The vast majority of object sharing was passive (*n* = 117, 39 % of all object interactions and 85% of all tolerated transfers), only 20 cases (7% of all object interactions and 14.5% of all tolerated transfers) were active. Of these active transfers, 14 sharing events occurred upon request, and 6 transfers were initiated by the possessor. In one case it was not determinable whether the tolerated transfer occurred passive or active. (Fig. 13)

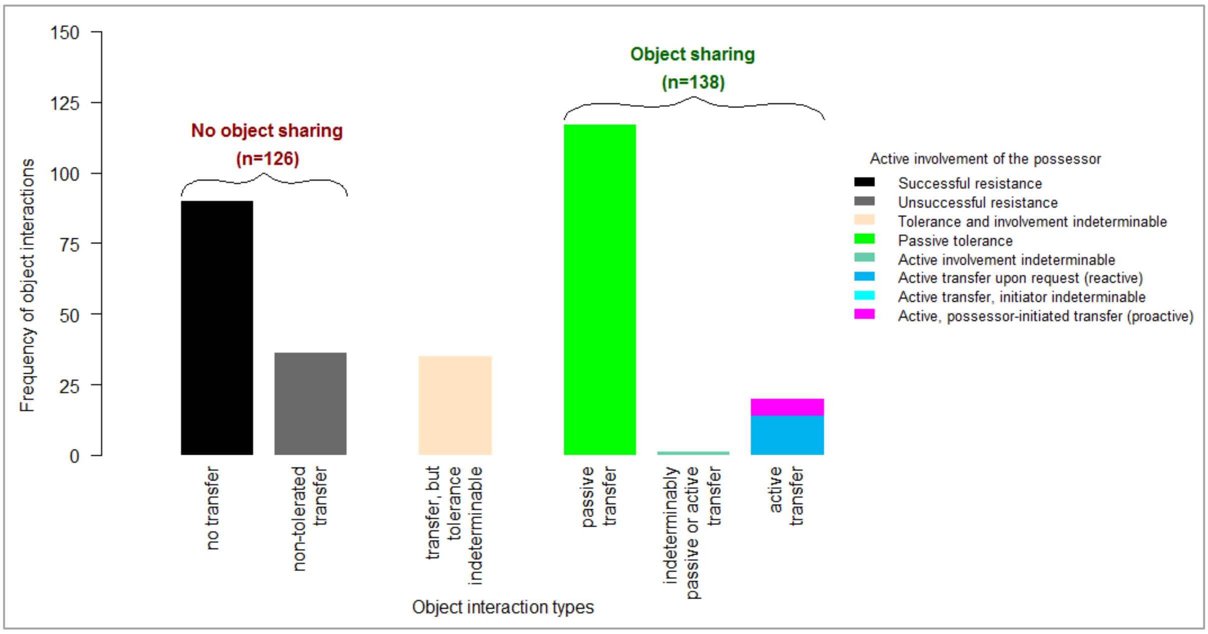

Fig. 13 Absolute frequencies of object interactions in the study group differentiated with regard to sharing tolerance and active involvement of the object possessor across the observation periods

As already demonstrated for food interactions, the frequency of being involved in object interactions differed among the individuals. Again, *Toba* was most frequently involved in interactions over objects (*n* = 163, 55% of all interactions), followed by *Djamuna* (*n* = 143, 48%) and

Tao (*n* = 133, 44%). *Eirina* and *Suma* were less frequently involved in object interactions (*n* = 68, 23% and *n* = 64, 21%, respectively). *Walter* engaged only rarely in object interactions (*n* = 27, 9%).

With regard to object interactions, the proportion of acting as possessor or as solicitor was not as biased within individuals as with regard to food interactions (cf. section 2.1.3.1, p. 36). While *Toba* acted more often as possessor than as solicitor (66% vs. 34% of food interactions she was involved in) and the immatures were less often possessor than solicitor (*Eirina*: 35% vs. 65%, *Tao*: 38% vs. 62%), for the other individuals the relation was about 1:1 (50% vs. 50% for *Djamuna*, 47% vs. 53% for *Suma* and 52% vs. 48% for *Walter*). (Fig. 14)

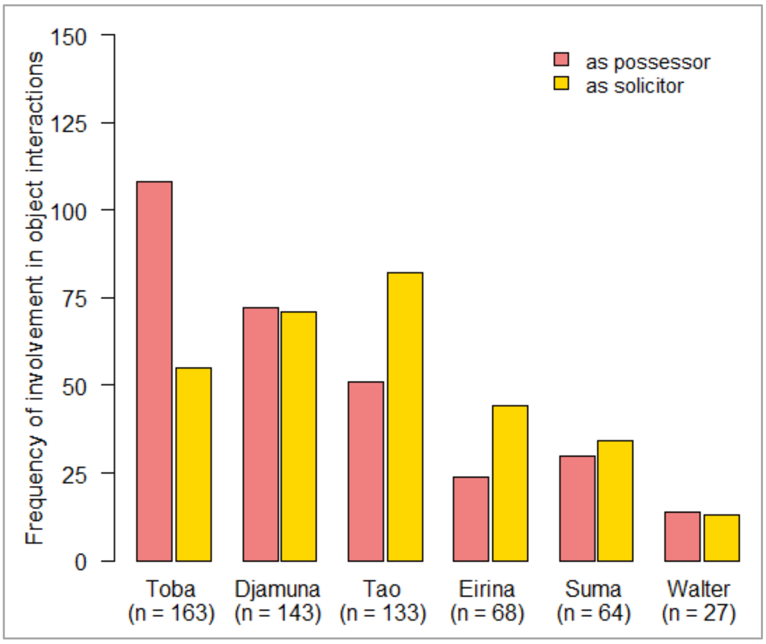

Fig. 14 Frequencies of object interactions for each individual differentiated between being involved as possessor (red bars) and solicitor (yellow bars), respectively. Numbers in parenthesis below the individual name indicate the total number of object interactions in which the particular individual had been involved

(ii) Sharing was passive in general, there was no difference in the proportions of active sharing with immatures and adults, respectively

Contrary to food interactions, the most frequent form of object transfer was passive, both for sharing with immatures and with adults. The proportion of active transfers was considerable low compared to food transfers and ranged from 0% with *Walter* as recipient to 17% (*n* = 7) with *Djamuna* as recipient. Furthermore, *Djamuna* was the individual who received most of the proactively transferred objects (*n* = 4). (Fig. 15)

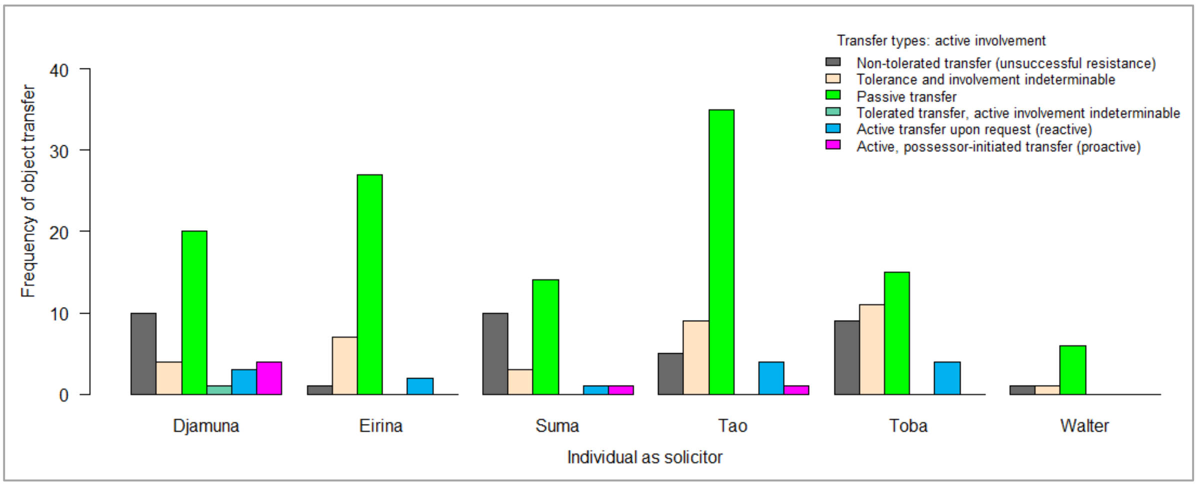

Fig. 15 Absolute frequencies of the particular object transfer types for each individual in the role as solicitor. Dark grey bars indicate non-tolerated transfers, beige bars indicate transfers for which it was not determinable whether they had occurred tolerated or not. All other coloured bars indicate tolerated transfers with active involvement of the possessor increasing from left to right.

(iii) All orangutans preferentially interacted over and shared objects with particular partners

As with food interactions, individuals did not equally often engage in object interactions with all of their groupmates. The average frequency of interacting over objects was 10, but the variations across dyads was considerable (sd = 11). From the solicitor's perspective, there was a similar variation of the intra-individual frequencies for soliciting food from another individual with means ranging from 3 ± 3 for *Walter* up to 14 ± 11 for *Djamuna* and 16 ± 12 for *Tao* (Fig. 16a). Analogously, the average intra-individual frequency of being a possessor ranged from 3 ± 2 for *Walter* up to 22 ± 16 for *Toba* (Fig. 16c).

Across dyads, the average proportion of object interactions resulting in object sharing was 40% ± 29%. Taking the solicitor's perspective, the object-getting success (OGS) varied both among and within the individuals with means ranging from 31% ±32% for *Eirina* up to 63% ± 33% for *Walter* (Fig. 16b). Similarily, the willingness to share (WtS) varied both inter- and intra-individually with means ranging from 14% ± 18% for *Eirina* up to 66% ± 26% for *Toba* (Fig. 16d).

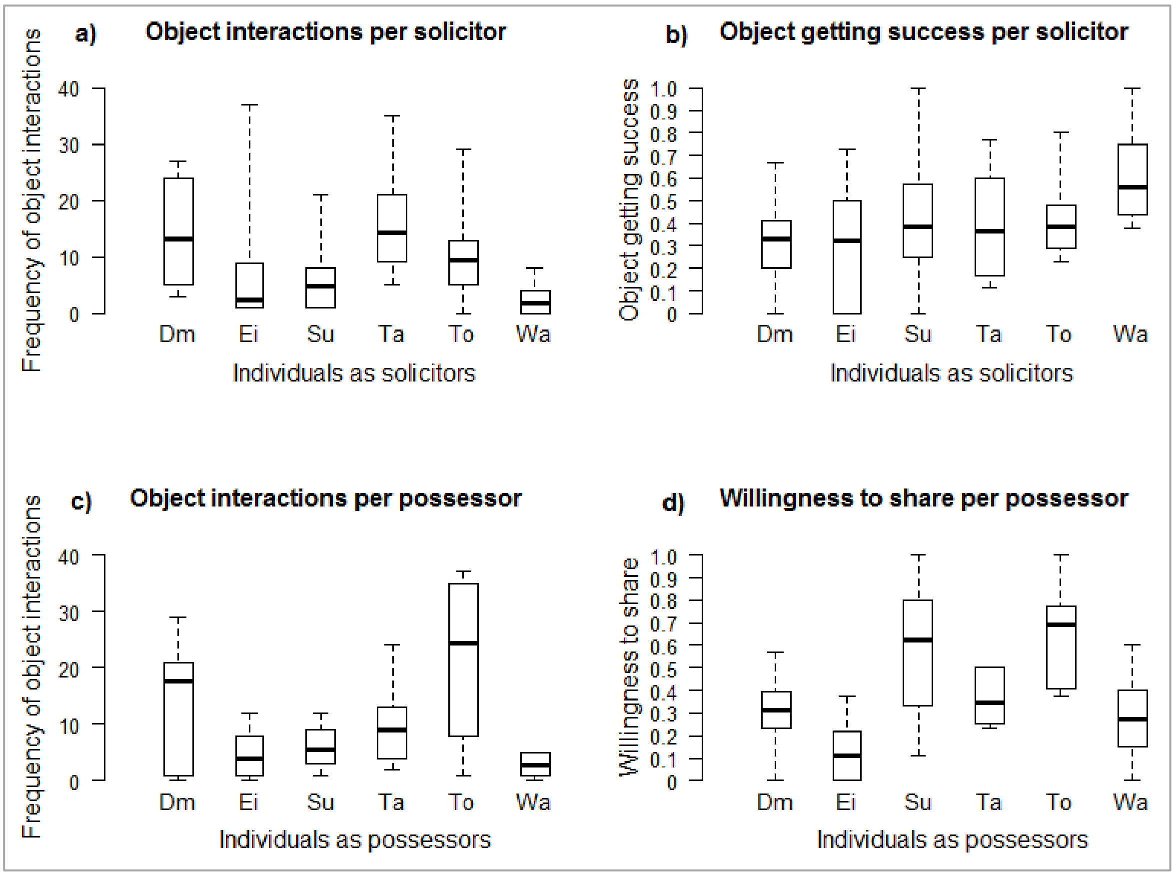

Fig. 16 Frequencies of object interactions, object getting success and willingness to share summarised for each individual across dyads from the solicitor's and the possessor's perspective, respectively. a) Absolute frequencies of object interactions per solicitor. b) Object getting success, i.e. proportion of object interactions which resulted in object sharing, per solicitor. c) Absolute frequencies of object interactions per possessor. d) Willingness to share, i.e. proportion of object interactions which resulted in object sharing, per possessor. Horizontal lines indicate medians, boxes indicate interquartile ranges, and whiskers indicate minima and maxima, respectively

As the demonstrated inter- and interindividual variance in the frequency of involvement in object interactions already suggested, individuals were selective regarding with whom they interact over objects. Most object interactions occurred with *Toba* as possessor and her two daughters as solicitor (*n* = 37 with *Eirina*, *n* = 35 with *Tao*). In both directed dyads, *Toba* showed a high willingness to share (73% with *Eirina*, 77% with *Tao*). *Eirina* and *Tao*, on the other hand, were less often involved in object interactions as possessors with *Toba* (*n* = 8 and *n* = 13, respectively), and their willingness to share was considerably lower (38% and 23%, respectively). *Toba* and *Djamuna* also often engaged in object interactions during which both individuals had been almost equally often possessor and solicitor (*n* = 27 for the dyad *Toba→Djamuna*, *n* = 29 for *Djamuna→Toba*). *Toba* tolerated the object transfer in 41%, while *Djamuna* tolerated it in 31% of these cases. Object interactions between *Suma* and *Tao* were likewise balanced with 24 cases for the dyad *Tao→Djamuna* and 21 cases for the dyad *Djamuna→Tao*. Both *Tao* and *Djamuna* tolerated object transfer in 33% of the interactions. Regarding object interactions between *Suma* and *Djamuna*, there were twice as many interactions with *Djamuna* as possessor (n = 21) than with *Suma* as possessor (n = 12). However, both individuals were comparably equally tolerant to each other (willingness to share: 57% for *Djamuna* and 67% for *Suma*). *Tao* and *Eirina* mostly interacted over objects with *Eirina* in object possession (n = 12), but *Eirina*'s willingness to share was low (17%). There were only few object interactions within the other dyads. However, on the rare occasions in which *Suma* and *Toba* interacted over an object, all of these interactions but one for which it was not determinable resulted in tolerated transfer. There were no object interactions at all within the dyads *Walter*→*Toba*, *Djamuna*→*Walter* and *Eirina*→*Walter*. (For more details cf. Fig. 17)

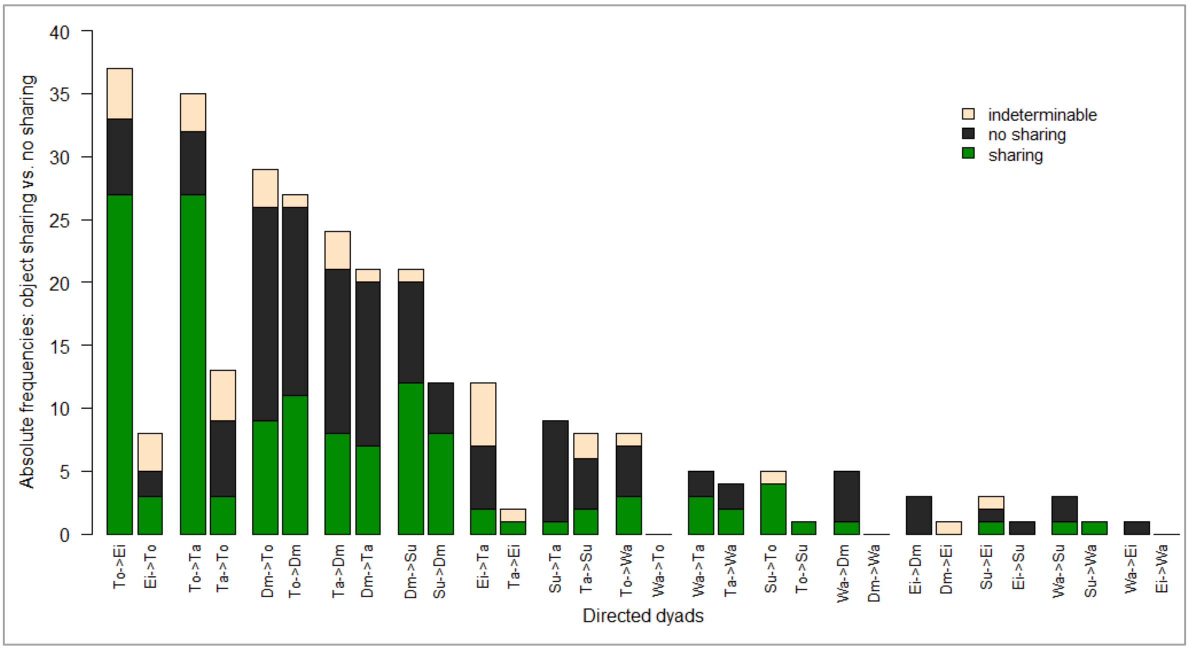

Fig. 17 Absolute frequencies of object interactions for each directed dyad. Dyads consisting of the same individuals with reverse roles are placed next to each other. Green sections of the bars indicate the respective proportion of object sharing (i.e. *object getting success* from the solicitor's perspective and *willingness to share* from the possessor's perspective, respectively). Black sections indicate those object interactions which did not resulted in sharing, beige sections indicate those cases for which it was not determinable, whether the transfer had been tolerated or not.

(iv) Reciprocal exchange of objects could neither be demonstrated, nor be ruled out

Relating the proportion of object sharing between two individuals and the proportion of object sharing between these individuals with reverse roles might suggest a correlation between the willingness to share with a particular individual and the object getting success in interactions with this particular groupmate as a possessor (Pearson's product-moment correlation, one-tailed: $r = 0.48$, $N = 12$, $p = 0.058$, confidence intervals with assessed statistical significance at the α-level of 0.05: lower CI = -0.027, upper CI =1.0). However, there were only four dyads whith more than 10 object interactions in both directions (indicated with black dots in Fig. 18), therefore reciprocity might be only an artifact due to the small sample size. (Fig. 18, red boxes in Table 6 indicate frequencies of object interactions less than 10)

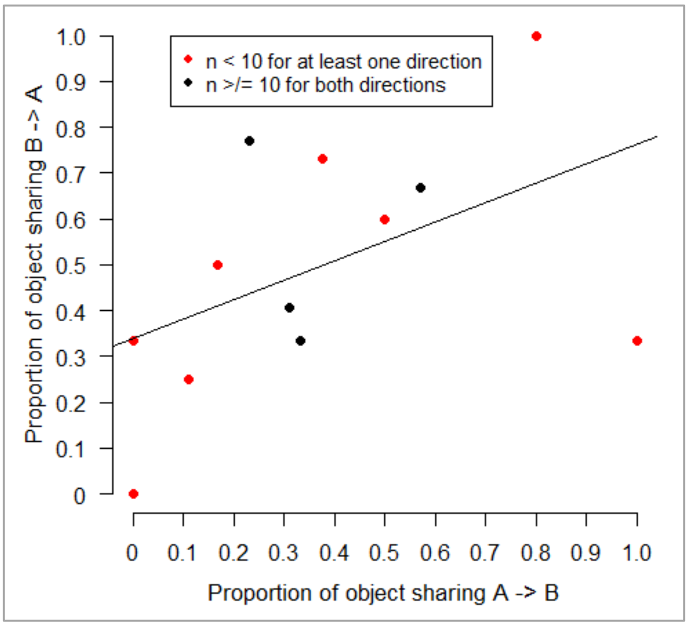

Fig. 18 Proportions of object sharing within dyads plotted against proportions of object sharing between the same individuals with reverse roles as possessor and solicitor. Black dots indicate those dyads with 10 or more object interactions for each direction; red dots indicate those dyads with less than 10 object interactions for at least one or for both directions

Table 6 Comparison of absolute frequencies of object interactions and proportions of object sharing for each dyad with regard to the respective role of the involved individuals as possessor or solicitor. Red boxes indicate frequencies of food interactions less than 10 (for 2 dyads in one direction, for another 9 dyads in both directions)

Dyad (A↔B)	Number of object interactions (A→B)	Proportion of object sharing (A→B)	Number of object interactions (B→A)	Proportion of object sharing (B→A)
Djamuna↔Toba	29	31%	27	41%
Toba↔Tao	35	77%	13	23%
Tao↔Djamuna	24	33%	21	33%
Toba↔Eirina	37	73%	8	38%
Djamuna↔Suma	21	57%	12	67%
Suma↔Tao	9	11%	8	25%
Eirina↔Tao	12	17%	2	50%
Walter↔Tao	5	60%	4	50%
Toba↔Walter	8	38%	0	---
Suma↔Toba	5	80%	1	100%
Walter↔Djamuna	5	20%	0	---
Eirina↔Djamuna	3	0%	1	0%
Suma↔Eirina	3	33%	1	0%
Walter↔Suma	3	33%	1	100%
Walter↔Eirina	1	0%	0	---

While the data were comparably unbalanced with regard to the number of object interactions across dyads as found for food interactions, they were less unbalanced within dyads. The strongest differences were found within both mother-daughter dyads, where *Toba* was considerably more in the role as possessor (*n* = 37 and *n* = 35, respectively) than either *Eirina* (*n* = 8) or *Tao* (*n* = 13).

P1.2 partly confirmed for non-food context: Non-aggressive communication generally preceded food transfer, however, request behaviour was predominantly object-directed and begging gestures were less frequent

(i) Solicitors predominantly signalled their interest in objects in a non-aggressive, though mainly object-directed way; begging gestures were performed less frequently

Request behaviours were generally non-aggressive; there were only three exceptions when the solicitor performed slightly aggressive behaviour as reaction to strong resistance or – in two cases – threat by the possessor. Requests consisted either of a single behaviour (*n* = 174, 58%) or a combination of two (*n* = 84, 28%), three (*n* = 22, 7%) or four (*n* = 3, 1%) different types of behaviour. On 8 occasions no request behaviour was observed, of which the possessor initiated the transfer in 6 cases, in the remaining 2 cases the solicitor collected the object without previous signalling while it lay within the possessor's reach (*collect near*). For 7 interactions, the request behaviour was not determinable.

The most frequent request behaviour was *grab and/or pull object* which was performed 137 times as a single behaviour and 78 times in combination with other behaviours. The second most frequent behaviour was *directed approaching* (*n* = 62), here – in contrast to the former – were only two cases in which approaching alone resulted in object transfer; in all other 60 cases *directed approaching* had been combined with other request behaviours. Other frequent behaviours were *reach for object* (*n* = 41) and *taking attempt from hand or mouth* (*n* = 32). All other behaviours such as *peering* (*n* = 14), *touch body or object* (*n* = 12), *grab and/or pull body part* (*n* = 12), *follow* (*n* = 11), *contact sitting* (*n* = 5) or *extend hand with open palm* (*n* = 3) were performed less frequently.

In contrast to food interactions, the request behaviour to get objects revealed to be generally more straightforward. While especially *peering* and hand gestures were frequently observed in connection with requesting food (cf. p. 42), they were only occasionally performed to signal interest in an object.

(ii) Possessors frequently complied with requests, otherwise their resistance was generally non-aggressively

Similarly to food interactions, responses to requests for objects were also generally non-aggressive; there were only two cases of threat (<1%), while in about one third of all object interactions the possessor showed no resistance at all (*n* = 106, 35%). On 174 occasions (58%), the possessor showed – at least initially – resistance in various ways and intensities: Most resistance behaviours were of moderate intensity (n = 130, 43% of all interactions, 75% of all cases of resistance) and consisted in one or a combination of the following behaviours: *hold on object*, *withdraw object*, *shielding* and *hold object out of reach*. Strong resistance was performed in 37 cases (12% of all interactions, 21% of all cases of resistance) and included one or two of the behaviour types *move away*, *struggle* and *grab and/or pull object/body part* mostly combined with less intense resistance behaviours. Slight resistance which consisted of *turn away* or *reach for object* occurred in 4 cases (1% of all interactions, 2 % of all cases of resistance); and *no reaction* occurred only once. For 19 object interactions (6%) the resistance behaviour was not determinable.

(iii) Object interactions regarded a variety of object types, which have usually not been divided for sharing

Interactions occurred over several different object types: Most interactions (n = 176, 59%) were over cloth, mainly sheets, followed by wood wool (n = 44, 15%) and sticks or twigs (n = 27, 9%). The remaining interactions regarded various objects such as empty coconut shells, cardboard or balls.

In contrast to food sharing where usually small and occasionally large parts of the possessed food were transferred (cf. p. 44), sharing an object mainly consisted in the transfer of the whole object – despite some interactions over wood wool. However, there were two remarkable exceptions: Responding to request behaviour by *Eirina* and *Tao*, respectively, regarding a large sheet, on both occasions *Toba* actually ripped the sheet apart and left the respective daughter one part (Fig. 19).

Fig. 19 Sequence of four video stills showing *Toba* (on the left) dividing a sheet for sharing with *Tao* (on the right). (a) *Tao* grabs the sheet, *Toba* starts ripping the sheet apart. (b) *Toba* has nearly finished dividing the sheet but for the seam. (c) *Toba* divides the seam using her teeth. (d) *Tao* leaves with one part of the sheet.

P1.3 neither confirmed nor contradicted: Increase of object interactions and sharing under less spacious housing conditions in particular female-female dyads, but no overall housing effect

(i) Analysis of pooled data suggested a housing effect on interaction rate and the proportion of object sharing

The overall rate of object interactions was 1.8 interactions per hour, and the overall proportion of sharing (*n* = 138, 46%) nearly as high as the proportion of no sharing (*n* = 126, 42%); for the remaining cases (*n* = 35, 12%) it was not determinable whether they were tolerated or not.

Differentiated with regard to the housing conditions, the interaction rate was with 2.1 interactions per hour higher indoors than outdoors whith 1.6 interactions per hour. The proportion of sharing was by 10% higher indoors compared with outdoors. For indoor conditions, half of the object inteactions resulted in sharing (*n* = 89, 50%), while 39% did not (*n* = 69); 19 transfers were indeterminable with regard to tolerance. Outdoors, the sharing rate was 40% (*n* = 49), while 47% of the interactions did not result in sharing (*n* = 57) and 16 cases were indeterminable (13%).

Considering only cases of tolerated transfer, the proportion of active transfer was by 10% increased indoors (*n* = 16, 18%) compared to outdoors (*n* = 4, 8%). Six cases of sharing indoors were initiated by the possessor, while no single case of proactive transfer has been observed outdoors.

Differentiating the indoors data with regard to interactions within and between the subgroups, respectively, demonstrated that while 59% of the determinable within-group interactions resulted in sharing (*n* = 60), it was only 39% between subgroups. But, since 15% of the within-group interactions were not determinable with respect to tolerance, this difference between the two conditions might be less strong. Both conditions differ from each other in another aspect: As already seen for food sharing, the majority of active sharing, i.e. 13 out of 16 cases and especially all cases of proactive transfer, occurred between the subgroups. The relation of passive to active sharing was 19:1 for sharing within and nearly 1:1 for sharing between the subgroups. (cf. Fig. 20 and Table 7 for more details)

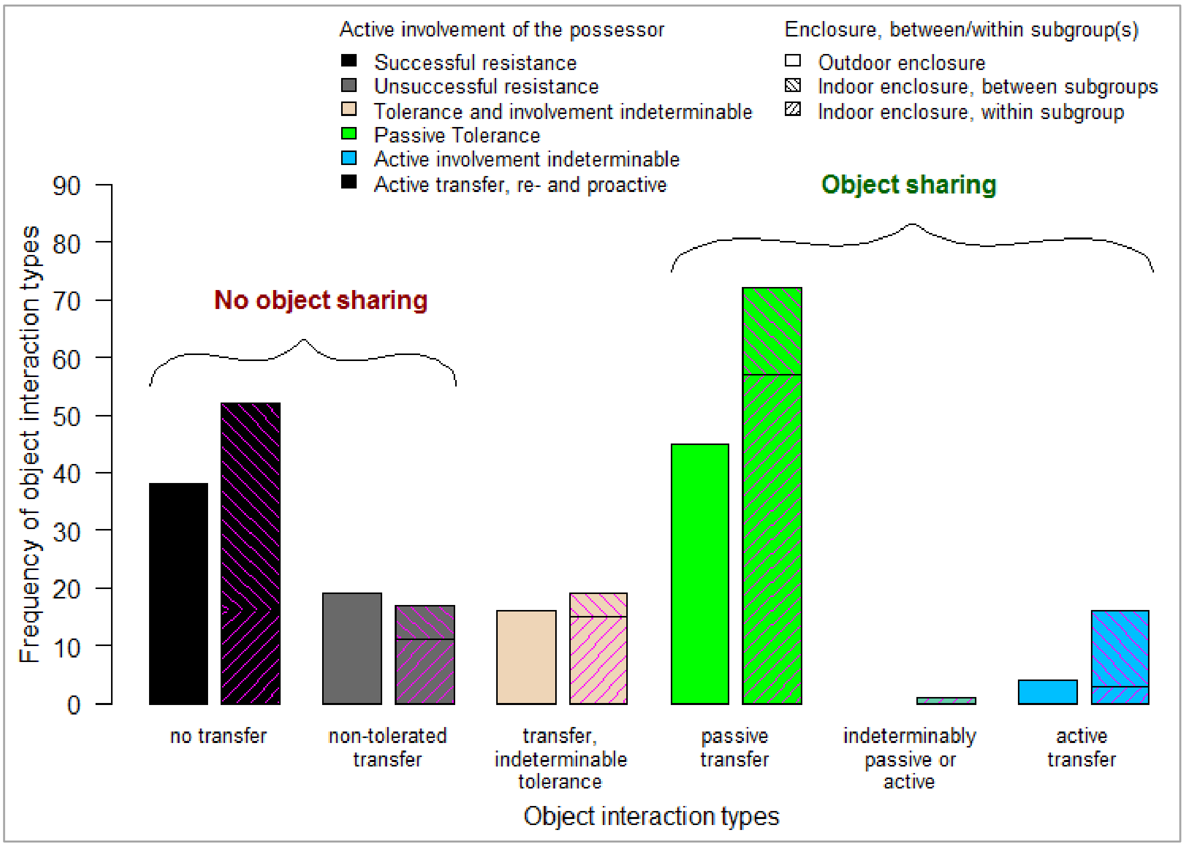

Fig. 20 Absolute frequencies of object interactions differentiated with regard to interaction types and housing conditions. The different colours indicate the particular object interaction types. Coloured bars without shaded lines indicate food interactions which occurred in the outdoor enclosure, coloured bars with shaded lines indicate those which occurred in the indoor enclosure. Of the latter bars, the lower sections (shaded lines with an angle of 45°) indicate object interactions within a subgroup, the upper sections (shaded lines with an angle of 135°) indicate those between the two subgroups, i.e. which occurred through the mesh

Table 7 Absolute and relative frequencies of object interaction types for housing conditions. The data for the indoor enclosure are additionally subdivided into object interactions which occurred within a subgroup and those which occurred between the subgroups. Percentages relate to the total of object interactions for the respective housing condition.

Housing Object interaction type	Outdoor enclosure		Indoor enclosure		Indoors: within a subgroup		Indoors: between subgroups		Total	
All object interaction types	122		177		102		75		299	
No object sharing	57	47%	69	39%	27	26%	42	56%	126	42%
No transfer (resistance)	38	31%	52	30%	16	16%	36	48%	90	30%
Non-tolerated transfer	19	16%	17	10%	11	11%	6	8%	36	12%
Indeterminable tolerance	16	13%	19	10%	15	15%	4	5%	35	12%
Object sharing	49	40%	89	50%	60	59%	29	39%	138	46%
Passive transfer	45	37%	72	41%	57	56%	15	20%	117	39%
Passive or active transfer	0	0%	1	1%	0	0%	1	1%	1	0.3%
Reactive transfer	4	3%	10	6%	3	3%	7	9%	14	5%
Proactive transfer	0	0%	6	3%	0	0%	6	8%	6	2%

(ii) More differentiated analyses demonstrated increased indoor object interactions and sharing for several female-female dyads, but no housing effect in general

Though the total rate of object interactions was higher indoors than outdoors (cf. p. 58), an examination of the data on a dyadic level revealed, that the found difference was not a general trend but due to an increasement of object interactions in 16 of 30 dyads, especially in 8 dyads in which the number of object interactions increased by 5 to 13 cases. For the other 8 dyads with an increased interaction rate, the found difference consisted of only one to three interactions. In three dyads, the interaction rate was the same both under outdoor and indoor conditions; and for 11 dyads, the interaction rate decreased for indoor conditions. The most obvious increase of object interactions when housed indoors was found between *Toba* and *Djamuna* on the one hand and *Suma* and *Djamuna* on the other. Whithin these dyads the interaction rate increased in both directions (*Toba*→*Djamuna* and *Djamuna*→*Toba*: increase by 11 interactions each; *Suma*→*Djamuna* and *Djamuna*→*Suma*: increase by 12 and 13 interactions, respectively). While *Toba* and *Djamuna* were housed in neighbouring indoor enclosures, *Suma* and *Djamuna* shared the same indoor enclosure. However, contrary to food interactions where the interaction rate increased indoors for all dyads consisting of unrelated adult females, there was no such clear pattern with regard to dyadic age-sex combinations for object interactions. (Fig. 21 and Table 8)

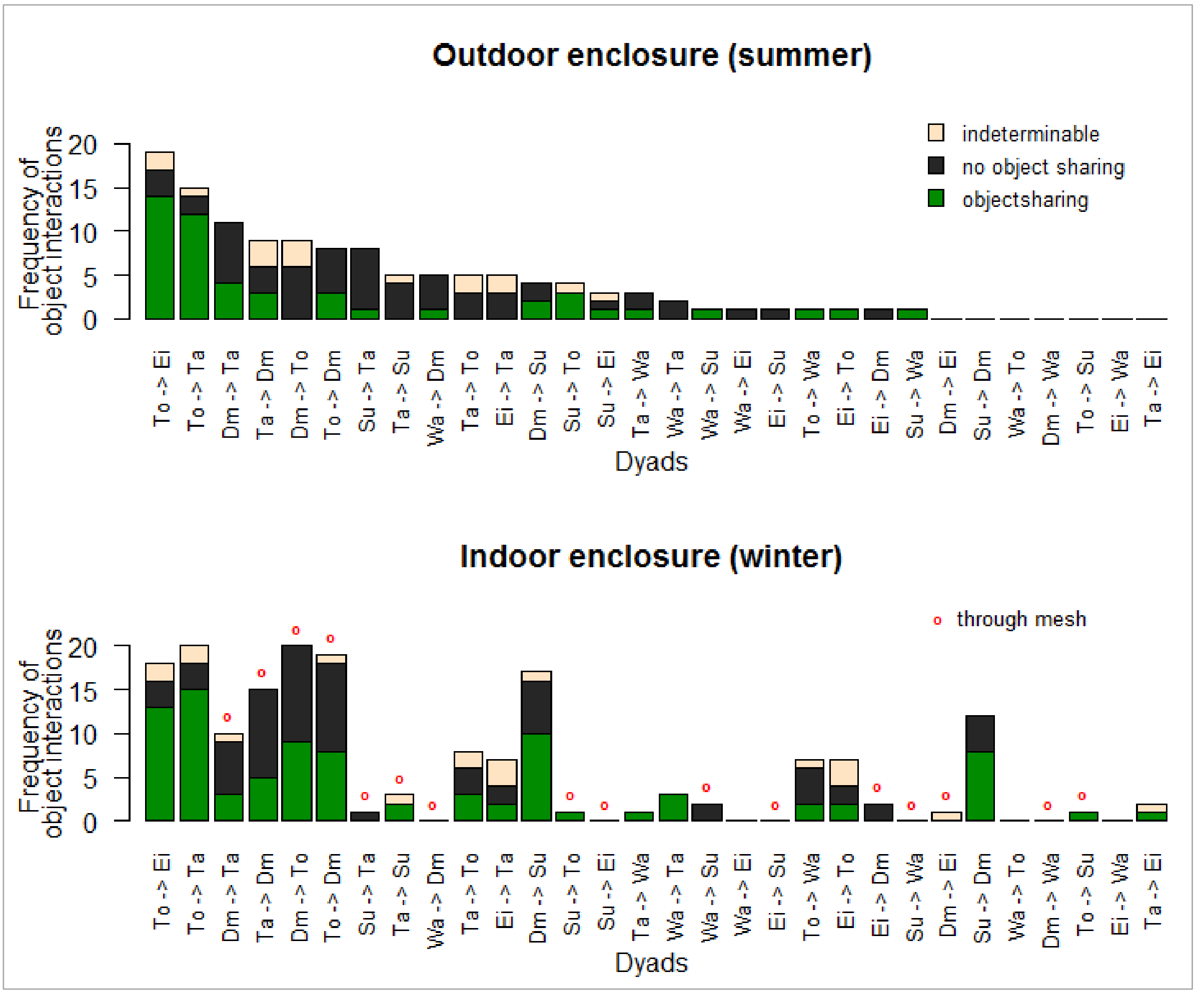

Fig. 21 Frequencies of object interactions per dyad differentiated with regard to housing conditions. In the upper figure, dyads were sorted by decreasing frequencies. In the lower figure, the order of dyads remains unchanged to enable comparison between outdoor and indoor condition. Bars indicate frequencies of object interactions for each directed dyad with green sections indicating the proportion of interactions which resulted in object sharing, black sections indicating the proportion of interactions which did not result in object sharing and beige sections indicating object transfers for which it was not determinable whether they were tolerated or not. Red circles in the lower figure indicate those dyads that consisted of individuals housed in neighbouring enclosures. Within these dyads, the object interactions took place through the separating steel mesh

Table 8 Number of object interactions and object sharing events, interaction rates and proportions of object sharing for each directed dyad differentiated by their occurrence in the outdoor and indoor enclosures, respectively. Red shadings indicate proportions of sharing for dyads consisting of unrelated adult females (including *Tao*).

Dyad	Interactions outdoors	Interactions indoors	Interaction rate outdoors	Interaction rate indoors	Number sharing outdoors	Number sharing indoors	Proportion sharing outdoors	Proportion sharing indoors
To→Ta	15	20	0.202	0.241	12	15	80%	75%
Dm→To	9	20	0.121	0.241	0	9	0%	45%
To→Dm	8	19	0.108	0.229	3	8	38%	42%
To→Ei	19	18	0.256	0.216	14	13	74%	72%
Dm→Su	4	17	0.054	0.204	2	10	50%	59%
Ta→Dm	9	15	0.121	0.180	3	5	33%	33%
Su→Dm	0	12	0.000	0.144	0	8	---	67%
Dm→Ta	11	10	0.148	0.120	4	3	36%	30%
Ta→To	5	8	0.067	0.096	0	3	0%	38%
Ei→Ta	5	7	0.067	0.084	0	2	0%	29%
Ei→To	1	7	0.013	0.084	1	2	100%	29%
To→Wa	1	7	0.013	0.084	1	2	100%	29%
Ta→Su	5	3	0.067	0.036	0	2	0%	67%
Wa→Ta	2	3	0.027	0.036	0	3	0%	100%
Wa→Su	1	2	0.013	0.024	1	0	100%	0%
Ei→Dm	1	2	0.013	0.024	0	0	0%	0%
Ta→Ei	0	2	0.000	0.024	0	1	---	50%
Su→Ta	8	1	0.108	0.012	1	0	13%	0%
Su→To	4	1	0.054	0.012	3	1	75%	100%
Ta→Wa	3	1	0.040	0.012	1	1	33%	100%
Dm→Ei	0	1	0.000	0.012	0	0	---	0%
To→Su	0	1	0.000	0.012	0	1	---	100%
Wa→Dm	5	0	0.067	0.000	1	0	20%	---
Su→Ei	3	0	0.040	0.000	1	0	33%	---
Ei→Su	1	0	0.013	0.000	0	0	0%	---
Su→Wa	1	0	0.013	0.000	1	0	100%	---
Wa→Ei	1	0	0.013	0.000	0	0	0%	---
Dm→Wa	0	0	0.000	0.000	0	0	---	---
Ei→Wa	0	0	0.000	0.000	0	0	---	---
Wa→To	0	0	0.000	0.000	0	0	---	---

Comparing the outdoor and the indoor data across all dyads demonstrated no significant increase of the willingness to share when housed indoors (exact one-tailed Wilcoxon signed rank test, statistical significance assessed at the α-level of 0.05: *T* = 56.5, *N* = 16 (2 ties, 12 NAs), *p* = 0.285). Restricting the analysis to unrelated adult females (including *Tao*) revealed no significant difference either, though there seemed to be a trend for an increased willingness to share when kept indoors (exact one-tailed Wilcoxon signed rank test, assessed statistical significance at the α-level of 0.05: *T* = 10, *N* = 9 (1 tie, 2 NAs), *p* = 0.082). However, since the data were unbalanced with regard to the number of food interactions across dyads with several individuals engaging in object interactions with each other only once or twice, the calculated proportions of object sharing might not be representative. Therefore, these results hardly enable reliable conclusions. (Fig. 22)

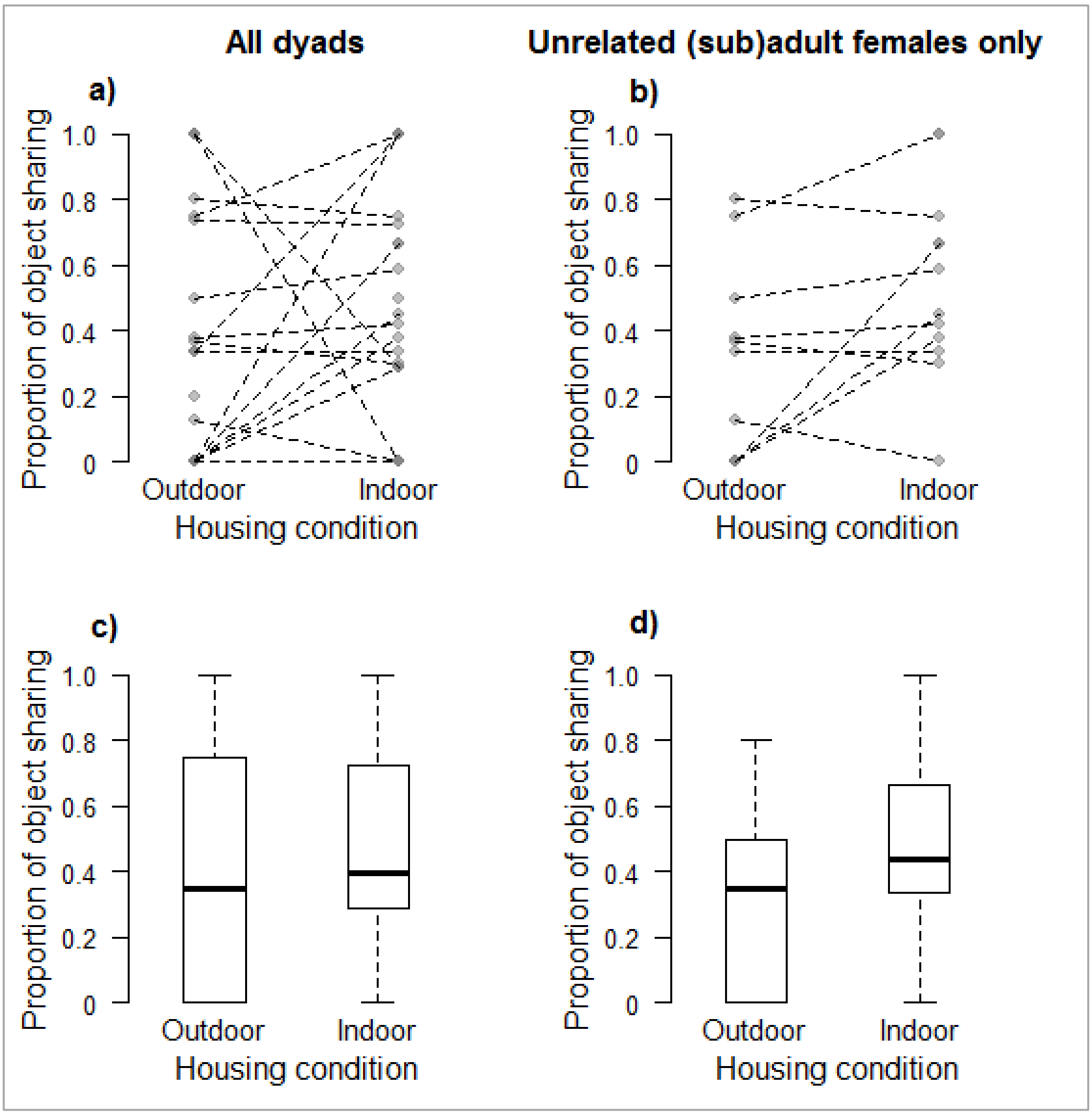

Fig. 22 Proportion of object sharing differentiated for outdoor and indoor conditions across all dyads (left side) and restricted to unrelated adult females including *Tao* (right side). In figures 22a and 22b, each data point refers to a particular dyad; dashed lines connect data points which belong to the same dyad. In figures 22c and 22d, boxplots summarise the data for each condition. Horizontal lines indicate medians, boxes indicate the interquartile range and whiskers indicate 1.5 times interquartile range.

2.1.3.3 Summary of the results – food and non-food contexts compared

Food interactions occurred more frequently and within more dyads compared with object interactions. However, the frequencies of food and object interactions across dyads revealed to be significantly correlated, i.e. those individuals who frequently interacted over food were also often engaged in object interactions (Pearson's product-moment correlation: r = 0.65; *N* = 30, *p* < 0.001, one-tailed, confidence intervals with assessed statistical significance at the α-level of 0.05: lower CI = 0.425, upper CI =1.0).

In contrast, while the average willingness to share food and to share objects was equally high, though also equally variable, (41% ± 24% and 40% ± 29%, respectively), the data might suggest only a weak correlation (Pearson's product-moment correlation: r = 0.205; *N* = 27, *p* = 0.152, one-tailed, confidence intervals with statistical significance assessed at the α-level of 0.05: lower CI = -0.127, upper CI = 1.0).

However, since in most dyads object interactions were rare, the calculated proportions of sharing might be not representative. (Fig. 23)

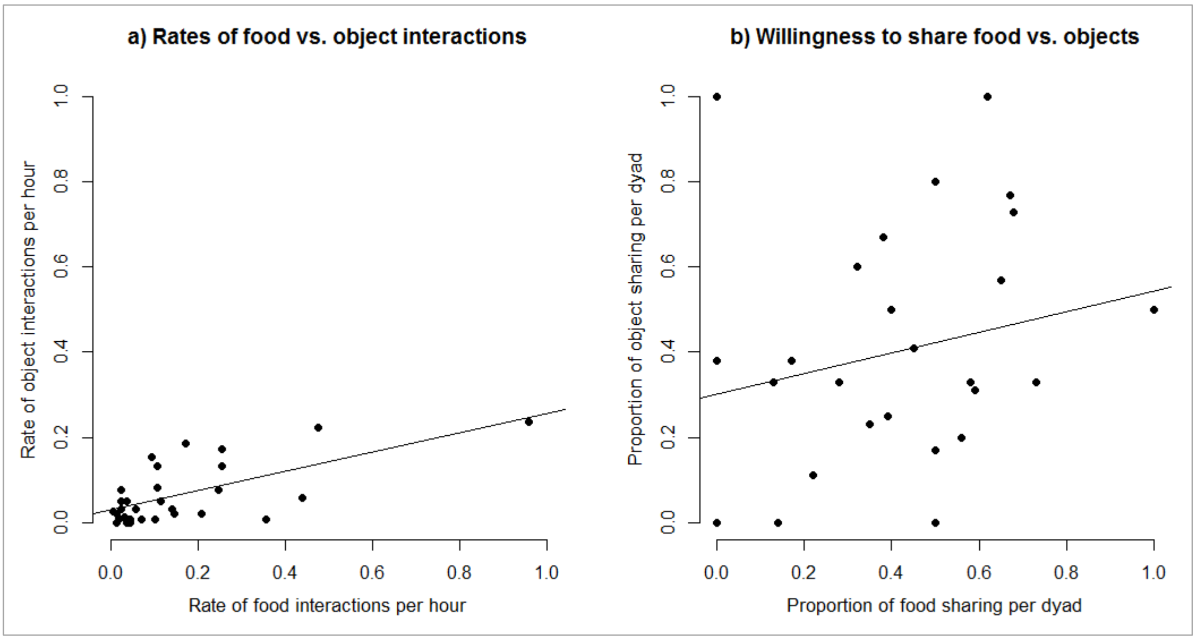

Fig. 23 Rates of food interactions per hour plotted against rates of object interactions per hour (a) and willingness to share food plotted against willingness to share objects (b). Dots indicate data points for each dyad; lines indicate the estimated correlations between both contexts

The analyses on group, individual and dyadic level demonstrated that potential conflict situations regarding food or non-food objects barely led to open conflict, i.e. aggressive competition over food or objects. On the contrary, all individuals of the study group frequently engaged in tolerated food transfers with each other or resisted requests in non-aggressive ways. However, the proportion of forced transfers was larger for object than for food interactions (12% vs. 4%). Depending on the particular partner, each individual varied with regard to interaction rates and the willingness to share both food and objects. Food and object sharing differed with regard to the active involvement of the possessor. While food sharing with immatures occurred mainly passively, adults received food more frequently by active than by passive transfer. Tolerated object transfers, on the other hand, occurred mostly passively regardless the age of the solicitor. In sum, the findings for both contexts fully met the expectations of prediction P.1.1.

The vast majority of food interactions included at least one request behaviour signalling interest in the food by the solicitor. The observed request behaviour mostly consisted of a combination of begging gestures and actions. Direct attempts to take the food without communicative signals or taking food by force were very rare. The finding, that adults nearly equally often transfer food passively and actively when interacting among each other, reflects the communicative nature of food sharing in particular. Compared to food interactions, the request behaviours regarding objects were more straightforward and consisted mainly of actions directed at the object, especially *grab and pull*. Contrary to food interactions, non-tactile gestures such as *peering/approach face* or manual gestures as well as more reserved tactile gestures such as *touch body* were less common. However, forced transfers, though occurring more often regarding objects than food, constituted the minority of transfers. Responses to requests for objects were generally non-aggressive and often tolerant, as also found for food interactions.

In summary, the individuals of the study group both signalled their interest in the respective food or objects and responded to these requests generally by non-aggressive means. Nevertheless, the communicative patterns of object interactions were less elaborated than those of food interactions. Therefore, while the results regarding communication over food fully met the expectations of prediction P.1.2, those regarding communication met them only partially.

According to the expectations of prediction P.1.3, the comparison of the two housing conditions revealed an increase both of the rate of food interactions and of the proportion of food sharing when less space was available, with the exception of the male *Walter* who engaged generally less in food interactions when kept indoors. Especially all unrelated adult females shared significantly more frequently among each other under less spacious conditions, even when they were kept in adjacent enclosures. In contrast, the comparison of object interactions with respect to the two housing conditions provided no reliable evidence for my prediction P.1.3. While the data might suggest a respective trend for unrelated adult females, no above average difference could be found with regard to all dyads. In sum, the findings for the food context met the expectation of prediction P.1.3 regarding a housing effect; however, there was no clear evidence for the non-food context.

2.1.4 Discussion

The present study investigated social interactions in potential competitive situations regarding food or objects in a group of captive orangutans during their daily life. The results provide evidence for the hypothesis on prosocial behaviour being a means for captive orangutans to cope with group life.

Easing conflict situations by tolerant food and object interactions

Conflicts of interest due to an unequal distribution of food or non-food objects are common in the daily group life of captive orangutans. However, such potential conflict situations barely escalated into actual conflicts within the study group; both requests by force and aggressive responses were rare. In comparison, the orangutans showed less aggressions in feeding contexts than reported e.g. for captive chimpanzees (de Waal, 1989a). Potentially competitive situations were instead generally mitigated by non-aggressive interactions which frequently resulted in tolerated transfers. These findings are also consistent with the more general observation that captive orangutan rarely engage in severe agonistic interactions (Edwards & Snowdon, 1980; Jantschke, 1972; Poole, 1987). The found rarity of aggressions and the high frequency of non-aggressive food and object interactions suggest communicating over food and non-food items and subsequent sharing to be an effective way to ease these types of conflicts (de Waal, 1996). Especially among unrelated adult females, food interactions and sharing seemed to be the preferred way to deal with conflicts of interest regarding food.

Enhanced frequency of food interactions and willingness to share among adult females under less spacious conditions

The comparison of outdoor and indoor interactions revealed, on the one hand, a decrease of food and object interactions within dyads that included the male, and, on the other hand, an increase of food and object interactions and food sharing among females. Although other factors than higher spatial density, such as seasonal effects, cannot be excluded, the found seemingly contradicting changes of behaviour are in line with reports on varying strategies to cope with increased social tension under crowded conditions (de Waal, 1989b; Judge, 2000). Coping strategies may depend on several aspects, e.g. on the duration of crowding, the general social tolerance, the species-specific social organisation, as well as on kin-relatedness, relationship quality or the sex of the particular individuals (Caperos, Sánchez, Peláez, Fidalgo, & Morcillo, 2011; Judge & de Waal, 1997; Novak, Oneill, & Suomi, 1992). For example, Aureli and de Waal (1997) investigated the effect of short-term high density conditions on the social behaviour of captive chimpanzees and observed a general decrease of social interactions including both affiliative and agonistic behaviour among adults, but simultaneously an increase of juvenile play. The authors suggest the general reduction of adult social activity to be an inhibition strategy to reduce opportunities for conflicts during short-term crowding (see also Aureli, van Panthaleon van Eck, & Veenema, 1995; Judge & de Waal, 1993; van Wolkenten, Davis, Lee Gong, & de Waal, 2006). An earlier study by Nieuwenhuijsen and de Waal (1982) on a group of zoo-living chimpanzees with a seasonal outdoor and indoor housing similar to the present study (about 6 months each) demonstrated an increase of social interactions including agonistic, but also submissive and affiliative behaviour under higher density conditions which has been suggested to be a coping strategy under longer lasting crowding.

In the current study, unrelated adult females significantly increased their food interaction rates and their willingness to share food among each other under less spacious conditions. The fact that this was true also for females kept in adjacent enclosures further suggests that tolerant and prosocial interactions were preferred over mere avoidance which would have been an alternative and less demanding strategy to deal with potential conflict situations (de Waal & Aureli, 1997). These frequently observed food interactions and sharing events through the mesh seem to contrast results of a comparative study on the preference of common marmosets (*Callithrix jacchus*), bonobos and chimpanzees to feed alone or accompanied by a tolerant partner using a door-opening paradigm (Bullinger, Burkart, Melis, & Tomasello, 2013). In this experimental study, all participating individuals did not seek company for feeding by letting another individual enter their compartment, regardless whether they belonged to a more or less tolerant species. However, both settings differ in an essential aspect, which might – at least partly – explain the differences in the behaviour: The orangutans who were going to feed near the mesh had still maximal control over their food, i.e. they were still able to decide *whether*, *with whom*, *what* and *how much* to share. The individuals in the Bullinger et al. study, on the other hand, would not have had such full control once they had opened the door, since the food had been distributed throughout the compartment. Therefore, feeding in proximity to their group mates at the mesh was potentially less costly for the orangutans than it would have been for the individuals in the door-opening experiment. Nevertheless, food possessing orangutans voluntarily approached the mesh and frequently passed over food of varying amount and quality upon more or less intense begging, which suggests that these food interactions might have a social function, such as negotiating social relationships, rather than a mere nutritional one (see also Slocombe & Newton-Fisher, 2005).

Selective food and object interactions and sharing

In accordance to my expectations, food or object possessing individuals interacted and shared selectively with particular partners. This supports the view that the essential function of prosocial behaviour as a means of conflict management consists in protecting, maintaining and probably establishing valuable social relationships rather than in general tension reduction (Wittig et al., 2014).

However, given the heterogeneity of circumstances in which food and object interactions took place, the data collected in this study did not allow for determining specific factors, such as food type, degree of repletion or relationship quality which might determine the probability of sharing. To investigate the possible influence of these factors under more controlled conditions, I conducted a quasi-experimental study using monopolisable food in which I included a further zoo-group of orangutans. This study is described in detail in the next section (2.2).

High proportion of active food sharing

Surprisingly and – to my knowledge – contrasting all food sharing studies on primates so far (Jaeggi & Gurven, 2013a; Jaeggi & van Schaik, 2011), the majority of food transfers among adult orangutans included active support by the possessor. However, the comparability with previous studies in captivity is debatable since most active sharing occurred among females who were separated by a wire mesh, i.e. in a context uncommon to other primate groups in zoos (Fig. 10). Therefore, though frequently active and selective sharing supports my hypothesis on the social function of food sharing and probably indicates characteristics in the sharing psychology of Sumatran orangutans, I do not want to over-interpret this result in comparison to other great apes. However, the design of the second study (cf. section 2.2) dealt with this issue and enabled a valid comparison with findings on other great apes.

With respect to psychological aspects, mitigating potentially food and non-food conflicts by tolerant behaviour – especially active sharing – demonstrates the presence of certain socio-cognitive skills in orangutans: social tolerance, inhibitory control in the presence of food and preferred objects, and the capability to produce and comprehend signals of need in both interacting individuals (Burkart et al., 2009; Jaeggi & Gurven, 2013a). These abilities are prerequisites for selective sharing (cf. p. 12), which in turn is most likely an essential means for reciprocating favours and thereby developing and maintaining social bonds (Jaeggi & Gurven, 2013a).

Differences of food and non-food sharing

Supporting findings of a pilot study on communication over food in orangutans (Rossano & Liebal, 2014), requests regarding food frequently involved persistent periods of peering and begging gestures awaiting a reaction, which reflects inhibitory control in the presence of food on the part of the solicitor. Request behaviour regarding non-food items, on the other hand, was usually directed at the object and involved explicit begging gestures or peering to a less extent. Nevertheless, although forced transfers of objects occurred more often than forced food transfers, they represent only the minority of object transfers.

Furthermore and probably related to the first difference, food sharing among adults was predominantly performed actively; object transfers, in contrast, occurred mostly passively. This finding seems to contradict common explanations regarding a better prosocial performance of chimpanzees in non-food than in food contexts, e.g. due to a lack of inhibitory control in the presence of food (Warneken & Tomasello, 2009). However, this is not necessarily a contradiction, since different selection pressures might have shaped species-specific sharing psychologies of orangutans and chimpanzees differentially (Jaeggi & Gurven, 2013a) resulting in lower self-control in the presence of food for chimpanzees compared to orangutans.

Moreover, from a methodological point of view, it is questionable whether a comparison of the prosocial performance in instrumental helping tasks, on the one hand, which are often given as examples for non-food contexts (Warneken & Tomasello, 2009; Yamamoto & Tanaka, 2009), and in provisioning experiments, on the other, is a feasible one. While in an assistance task including tools, the potential helper is usually required to pass over an object (tool) from which she herself could not gain any direct benefit; in the case of food sharing, she has to tolerate a diminution of a direct benefit. A tolerated transfer of an object which is – in a narrower sense – not a tool for the helper, but for the individual in need, is different from a tolerated transfer of an object which is likewise valuable for the possessor, e.g. nesting material. Only the second case fulfils the requirements of sharing, since sharing presupposes an interest in the respective object by both the solicitor and the possessor, as defined in several studies including the present one (e.g. Feistner & McGrew, 1989; Jaeggi & van Schaik, 2011; Silk, Brosnan, et al., 2013). Therefore, it might be more appropriate to differentiate between contexts regarding an object of some sort which is controlled by the potential prosocial actor and valuable for both interacting individuals, and those contexts in which the object is not or less valuable for the possessor, than to discriminate between food and non-food contexts *per se*. This view is also in line with Jaeggi and van Schaik (2011) who assume that similar psychological mechanisms underlie food and tool transfers in primates. The current study enabled a direct comparison of the respective interactions, since both food and object interactions regarded items in which the possessor and the solicitor were interested in.

The found difference with respect to the active involvement of the possessor in tolerated transfers of food and non-food objects may have several reasons. An alternative explanation to *food vs. non-food* might be *divisibility vs. indivisibility*: in contrast to food, which has been transferred in usually small or sometimes larger pieces, object transfers mostly regarded the whole, undivided object. An individual who has control over some food or a non-food object can selectively tolerate a transfer depending on the identity of the solicitor both while sharing passively or actively. In active transfers, however, he has additional control over the quality and the amount of the shared item. If the respective item was either not divisible, e.g. a ball, or dividing it would have made it useless for the possessor, e.g. when a large sheet had been used to construct a hammock, then the decision was only about *keep it* or *let it go*. The question about *which part* or *how much* would have been irrelevant in this case. A comprehension of these differing situations by both interacting individuals might explain the found differences in the request and in the response behaviour when it came to food or non-food transfers. This interpretation is supported by two, already described transfer events with *Toba* dividing a sheet for sharing it (cf. Fig. 19, p.58). In both cases, *Toba* had draped the sheet around herself when a daughter was approaching. Then, upon request, *Toba* ripped the sheet apart resulting in two pieces which were still large enough to be used by both individuals in the previous way. In contrary to most other transfers including cloth, these transfers were active. However, further investigations under controlled conditions are necessary to test whether the food vs. non-food aspect or the divisibility of an object influences the type of transfer.

Summary

In this first study I investigated prosocial behaviour in potential conflict situations caused by the unequal distribution of food and preferred non-food objects which occurred in a group of zoo-living Sumatran orangutans during their daily life. The main finding was that conflicts of interest regarding food and non-food objects only very rarely led to open conflicts, but were usually communicated by non-aggressive interactions which frequently resulted in tolerated transfers. These results strongly support the proposed function of prosocial behaviour as a means to mitigate potential conflict situations and thereby to cope with the challenges of permanent group life.

Sharing food and objects turned out to be selectively with regard to particular group mates. Especially within dyads of adult females, the frequency of food interactions and active sharing increased under less spacious housing conditions during the winter, which supports the proposed function of food sharing as a social means to negotiate and maintain social relationships. Moreover, the observed complex interactions over food and non-food objects indicate a remarkable flexibility of orangutan’s social behaviour in captive settings, since permanent group-living differs essentially from their social organisation under natural conditions.

2.2 STUDY 2: SELECTIVE AND ACTIVE FOOD SHARING AND ITS CORRELATION WITH SOCIAL BONDS IN CAPTIVE SUMATRAN ORANGUTANS[4]

After exploring the prosocial behaviour of captive Sumatran orangutans in potential conflict situations regarding food and objects occurring in daily group life, the second study aimed at investigating patterns and dynamics of food sharing in more detail under controlled conditions which allow for a comparison with similar studies on other great apes. A particular focus of this study is directed at proximate factors, especially at the strength of social bonds, which might influence the willingness of an individual to share food.

---

[4] This chapter is largely based – with slight adaptations – on a prior published research article in *Behavioural Ecology and Sociobiology* (Springer-Verlag Berlin, Heidelberg): Kopp, K. S., & Liebal, K. (2016). Here you are! - Selective and active food sharing within and between groups in captive Sumatran orangutans (*Pongo abelii*). *Behavioural Ecology and Sociobiology*, 1219-1233. doi:10.1007/s00265-016-2130-2. In conformance with the doctorate regulations (Gemeinsame Promotionsordnung zum Dr. phil./Ph.D. der Freien Universität Berlin vom 02.12.2008), my supervisor, Prof. Dr. Katja Liebal, gave her approval to include the article as a part of my doctoral thesis. The inclusion of this article into this doctoral thesis is also in accordance with the Copyright Transfer Statement agreed to on the 25th of April 2016. The original publication is available at http://link.springer.com or http://dx.doi.org/10.1007/s00265-016-2130-2. *Due to copyright reasons, this study is not available in the online version of this dissertation.*

Due to copyright reasons, pages 72-94 are not available in the online version of this dissertation. Please see the original article at http://dx.doi.org/10.1007/s00265-016-2130-2. You may also contact the author for a copy of the manuscript at kathrin.kopp@fu-berlin.de.

2.3 STUDY 3: PROSOCIAL BEHAVIOUR AS A MEANS OF CONFLICT MANAGEMENT IN CAPTIVE SUMATRAN ORANGUTANS

While Study 1 and 2 aimed at investigating prosocial behaviour, particularly sharing food, as a social means both for mitigating potential conflicts and social bonding, the objective of the present study is to elucidate the abilities of group-living orangutans to cease ongoing conflicts and to reduce direct and potential indirect costs when conflicts have been escalated.

2.3.1 Introduction

Despite all its benefits, living in a group of conspecifics – as most diurnal primates including humans do – is an everyday challenge for each individual. Conflicting interests with groupmates may lead to open conflicts, potentially resulting in direct and/or indirect costs. Direct costs may include e.g. the loss of possession, physical injuries or even violent death. The loss of reputation or dominance status and especially the destabilisation of close, valuable relationships rank among indirect costs, which might turn out to be even more costly for an individual and also for the whole group in the long run than immediate costs (cf. subsection 1.1.4.1 for a detailed discussion about the benefits and costs of sociality).

Since conflicts are inevitable when living in groups, conflict management is "[...] a critical component of the social life of any group-living species" (Aureli & de Waal, 2000a, p. 4). Acknowledging this, mechanisms of conflict management became a highly investigated topic among behavioural scientists during the last three decades. As already referred to in detail in the General Introduction (especially in the subsections 1.1.4.1, pp. 6-8, and 1.1.4.4), a broad range of strategies and behaviours has been evolved in gregarious species in order to prevent open conflicts, to cease them or to alleviate their consequences – or in other words: to minimise the costs of group life (Cords & Killen, 1998).

Especially in primates, but also in some non-primate species, conflict management strategies include special types of prosocial behaviour, such as *third party interventions* to terminate conflicts and affiliative post-conflict behaviour involving former opponents, i.e. *reconciliation*, or additionally uninvolved bystanders, i.e. *post-conflict third party affiliation* (de Waal, 2000; Judge, 2003). These types of prosocial conflict management are in the focus of the present study.

An essential part of our knowledge on prosocial conflict resolution comes – as also for the case of food sharing – from studies with chimpanzees. In fact, with their study on reconciliation and consolation among chimpanzees in 1979, de Waal and van Roosmalen initiated a perspective shift in the study of conflicts from aggression to conflict management and its important role for gregarious species.

The social systems of chimpanzees, bonobos and modern humans are characterised by a large community size and a high degree of fission-fusion dynamics demonstrating social flexibility (Aureli et al., 2008). On the other hand, long-term social relationships, cooperation and other prosocial interactions play a crucial role in these closely related species (Boesch, 1994; Furuichi & Ihobe, 1994; Jaeggi, Burkart, et al., 2010; H. S. Kaplan et al., 2009; Langergraber, Mitani, & Vigilant, 2009; Mitani, 2009b; Mitani & Watts, 2005; Seyfarth & Cheney, 2012). Given the importance of social bonds and group cohesion (Bliege Bird & Power, 2015; Silk, 2007a; van Hooff & van Schaik, 1994), advanced conflict resolution strategies should have been established in these species to protect valuable relationships from being jeopardized and groups from being destabilised by aggressive conflicts (Aureli et al., 2002; Flack et al., 2006). A large body of studies confirms these expectations by providing evidence for partial and impartial third party intervention, reconciliation and post-conflict third party affiliations in chimpanzees, bonobos and humans (e.g. Cords & Killen, 1998; de Waal & Aureli, 1997; Fraser & Aureli, 2008; Fraser et al., 2008; Fry, 2000; Palagi & Norscia, 2013; Palagi et al., 2004; Preuschoft, Wang, Aureli, & de Waal, 2002; Rudolf von Rohr et al., 2012; Watts, 2006). Furthermore, also gorillas, who live in more stable and cohesive groups, engage in prosocial conflict resolution (Cordoni et al., 2006; Scott & Lockard, 2007; Watts, 1995a, 1997). As outlined in the General Introduction (subsection 1.1.4.4), several functions are in discussion for each of these conflict management strategies, which not necessarily mutually exclude another. For humans, chimpanzees, bonobos and partly also for gorillas, the usage of these three strategies may result – probably beside other effects – in protecting valuable partners from (further) harm or restoring violated valuable relationships (Cords & Killen, 1998; Kutsukake & Castles, 2004; Palagi et al., 2004; Silk, 2002a; Wittig, Crockford, Wilkberg, Seyfarth, & Cheney, 2007) and/or in the reduction of conflict-related anxiety in one or more involved individuals (de Waal & Aureli, 1997; Fraser et al., 2008; Romero & de Waal, 2010).

In contrast, very little is known on possible conflict resolution strategies in orangutans. Although wild and especially Bornean orangutans are generally less cohesive than the other great apes (Aureli et al., 2008), their social system is also characterised by individual-based fission-fusion dynamics (van Schaik, 1999) and extraordinary strong and long-term bonds between mothers and their dependent offspring (van Noordwijk et al., 2009). Furthermore, in orangutans, females appear to be the philopatric sex, resulting in clusters of overlapping home ranges of related females and their offspring (van Noordwijk et al., 2012). In these kin associations, as already outlined in the subsections 2.1.1 and 2.2.1, social play among infants and feeding in proximity are common, and even food sharing among females has been observed (Singleton et al., 2009). Related females in association show significantly less aggressive behaviour than females in non-kin associations. In the latter case, aggressions always result in breaking up the association, which is not the case for associations of related females (van Noordwijk et al., 2012). These recent findings on female clusters as well as the occurrence of mating associations, which may last for several weeks, and travel bands of related or unrelated individuals are hints that social relationships might actually be more important for wild orangutans than it has been acknowledged so far (Mitra Setia et al., 2009; Utami Atmoko, Singleton, et al., 2009).

Taking these considerations as well as the close phylogenetic relatedness of all extant hominids into account, conflict management mechanisms for protecting valuable relationships might be expected also in orangutans, similar to respective strategies shared by humans and the African great apes (Aureli et al., 2002).

However, while a few cases of impartial third party intervention have been reported for captive orangutans (Tajima & Kurotori, 2010; Zucker, 1987), until very recently, conflict resolution was thought to be absent in wild orangutans (Knott, 2009). The first and – so far only – evidence of policing by a wild Bornean orangutan male, which was simultaneously the first evidence of a collaborative and lethal attack against a female, came from observations published only a few months ago by Marzec et al. (2016): A young female in coalition with an associated unflanged male repeatedly attacked a resident adult female. After the arrival of the resident flanged male, the unflanged male retreated. The flanged male protected the already most seriously injured female by positioning himself between the opponents and stayed in proximity during the next days, repeatedly policing whenever the younger female was renewing attacks.

These observations of policing both in the wild and in captivity confirm the orangutan’s ability for impartial intervention as one form of prosocial conflict management shared with the other great apes. Post-conflict affiliations of any kind, though, have not been reported so far – neither from the wild nor from captivity.

The lack of studies and hence of knowledge about conflict management abilities in orangutans is puzzling, because orangutans in captivity, especially in zoos, are usually kept in permanent groups and so potentially provide ideal conditions for observing social interactions. Zoo-living orangutans are known for their quiet group life, which is astonishing given their semi-solitary life in the wild (Jantschke, 1972; Maple, 1980; Poole, 1987). Their ability to cope with living in groups cannot be explained by a generally low social activity rate, because captive orangutans engage in a variety of social interactions, including play (Jantschke, 1972; Zucker et al., 1986; Zucker et al., 1978), interactions over food and objects (studies 1 and 2 in this thesis, cf. sections 2.1 and 2.2) and copulations (Maple, 1980). On the contrary, it may indicate the presence of prosocial conflict resolution strategies, which captive orangutans might apply to prevent and resolve conflicts.

With the first study presented in this thesis (section 2.1), I provided evidence for prosocial strategies in orangutans to prevent conflicts of interest from escalating into open conflicts. In the present study, I address possible prosocial strategies for reducing direct and indirect costs of escalated conflicts.

The spectrum of contexts that might lead to open conflicts in captive orangutans is largely, but not entirely similar to that of captive chimpanzees and bonobos. While the latter generally live in multi-male/multi-female groups, orangutans are usually kept in groups comprising one adult male, several females and their offspring. The relationship of flanged males in the wild is agonistic; usually they successfully avoid encounters, but if they meet, they engage in aggressive interactions which may result in serious injuries or death (Utami Atmoko, Singleton, et al., 2009). Therefore, adult males cannot be kept together in a single zoo-group. Given these circumstances, which account for the natural dispersal strategy of male orangutans (Knott, 2009), aggressive competition among adult orangutan males over access to females is precluded in zoo-groups.

A second difference with regard to possible contexts of conflicts consists in the occurrence of different forms of sexual coercion. Indirect sexual coercion, e.g. sexual harassment or coerced mate guarding, to control female future sexual behaviour is known for many species (Clutton-Brock & Parker, 1995b; Smuts & Smuts, 1993), including chimpanzees (Muller, Kahlenberg, Thompson, & Wrangham, 2007; Muller, Thompson, Kahlenberg, & Wrangham, 2011) and humans (Muller & Wrangham, 2009; Wrangham & Muller, 2009). In contrast, direct sexual coercion, i.e. forced copulations, is absent in the African great apes, but occurs regularly in humans (Emery Thompson, 2009) and orangutans (Knott, 2009). Coerced copulations constitute a specific context of mutual inter-sex aggression in orangutans. Although adult orangutan males are as twice as heavy and much stronger than females and therefore able to force females to copulate despite their resistance, the resistance behaviour of orangutan females is of extraordinary intensity (Utami Atmoko, Mitra Setia, et al., 2009). Observations of wild orangutans revealed that the extent of force by the male correlates with the extent of the female’s resistance, however, there is no evidence so far that orangutan males inflict injuries when forcing copulations with females (Knott, 2009). Furthermore, when an orangutan female with a small infant is forced, the offspring usually attacks the male (Utami Atmoko, Mitra Setia, et al., 2009). Although, in such situations, the male tries to push the infant aside and sometimes to bite its hands, an actual harming of an intervening infant has never been observed so far (M. A. van Noordwijk, pers. communication).

Acknowledging these differences, typical contexts in which open conflicts in captive orangutans might be expected are: competition over food or non-food objects, weaning, dominance competition and direct sexual coercion.

Taken the outlined theoretical considerations and empirical findings on conflict resolution strategies in great apes, evidence and hints for a probable importance of social relationships for orangutans, the revealed social flexibility of orangutans in captivity and the phylogenetic relatedness of all great apes together, the third main hypothesis of this thesis is as follows:

(H3) The behavioural repertoire of orangutans includes strategies of conflict resolution which are comparable to those of the other great apes. Group-living orangutans use these strategies in order to prevent conflicts from escalating and to reduce direct and indirect costs of open conflicts.

From this hypothesis I derived the following predictions in order to test them in the present study:

(P3.1) Socially housed orangutans should engage rarely in open aggressive interactions if there is the opportunity to avoid confrontations. With decreasing available space, an increased number of both open conflicts and conflict management behaviours in order to cease them are expected.

(P3.2) When potential conflict situations escalate into severe aggressive conflicts, third parties are expected to intervene to cease the aggressive interaction.

(P3.3) In the immediate aftermath of open conflicts, former opponents are expected to increasingly engage in affiliative contacts with each other.

(P3.4) Immediately subsequent to aggressive interactions, an increased number of affiliative contacts between former victims and third parties is expected.

2.3.2 Methods

2.3.2.1 Study group and housing conditions

This study was conducted with the same study group of Sumatran orangutans in the Zoo Dortmund, Germany, as the first study of this thesis. For details concerning the particular individuals and housing conditions, please confer the respective section 2.1.2.1 (pp. 29 et seq.).

2.3.2.2 Data collection

I recorded the data for this study during group observations on 30 days during September 2011, February/March 2012 and June/July 2012 as described in section 2.1.2.2 (p. 30) which resulted in a video footage of 157 h 30 min. Using a digital camcorder CANON Legria FS200, I continuously videotaped – if possible – the whole group with focus on individuals who engaged in previously defined social interactions, which were, regarding this study, aggressions and subsequently affiliative interactions involving the victim of aggression. When more than one dyadic interaction took place which could not be video-recorded simultaneously, I recorded a spoken description using the audio function of the camcorder. Additionally, I took notes on interactions and circumstances, as for instance the presence of noisy visitors or when a female had been in oestrus or other factors that might have affect the behaviour of the orangutans.

2.3.2.3 Data coding

All data coding for which I used Microsoft Excel® 2010 and the coding software INTERACT® Vers. 14.3 has been conducted on the basis of the video footage and protocols. I applied *all occurrences sampling* (Altmann, 1974) to code aggressive interactions and third party interventions. To code post-conflict affiliative contacts of the victim, I combined this sampling method with *focal sampling* (Altmann, 1974; P. Martin & Bateson, 2007).

An ***aggressive interaction*** indicated an interaction between two (sometimes more) individuals that comprised an initial aggression against and a respective reaction by a target individual.

Aggression was defined as a directed behaviour of an individual towards a group member in order to cause bodily injury or to signalize the readiness for such behaviour by threat displays (adapted from Aureli & de Waal, 2000b, p. 387). The initiator of an aggression was referred to as ***aggressor***.

I distinguished three levels of aggression with regard to intensity: low, medium and high intensity. The first level comprised behaviour which consisted of threat displays, e.g. *bared teeth face* or fast, directed approaching resulting in displacement, without any physical attack; mild physical attacks, e.g. *push*, *grab*, *hold on*, and *chase,* were subsumed as aggressions of medium intensity; while severe physical attacks as *hit*, *bite*, *fight*, *rough grab and pull* were indicated as aggression of high intensity. When behaviours from different levels of aggression were combined, the highest level had to be chosen. To discriminate whether an interaction like wrestling or chase occurred in a context of play or conflict, the reaction of the recipient of this behaviour was important. If the behaviour in question caused distress, e.g. expressed by vocalisations as *kiss squeaks*, *whimpering*, *screaming*, *struggle to escape*, *pilo-erection while fast moving away*, this behaviour had to be coded as aggressive.

A ***reaction*** to an aggression could consist in avoidance, non-aggressive behaviour to cease the attack, counter-aggression or redirection, or in a combination of these types of behaviour. The initial target of an aggression and performer of the reactive behaviour was referred to as ***victim***.

Avoidance usually consisted in *backing away* or *moving away*. ***Non-aggressive behaviour to cease the attack*** comprised e.g. *withdraw body (part)*, *struggle to escape*, or vocalisations like *whimpering*, *kiss squeaks* or *screaming*. ***Counter-aggression*** was defined as an aggressive action by the victim towards the initial aggressor. ***Redirection***, on the other hand, indicated an aggressive action by the victim against a third individual or more individuals (Aureli & de Waal, 2000b, p. 387).

An aggressive interaction started with the aggression and ended when both aggression and reaction had ceased. Additionally to the behaviour, I coded the situation in which the aggressive interaction had occurred, especially to distinguish the contexts of *food competition*, *weaning*, *spontaneous aggression* and *sexual coercion*.

Sexual coercion generally indicated sexual harassment among females and forced (attempted) copulations by a male. While I treated female sexual coercion like aggressive interactions in other contexts, I analysed male sexual coercion separately with regard to associated prosocial behaviour, since coerced copulations form a special type of aggression, which does not occur – with the exception of humans – in other great apes.

Sexual harassment among females could be distinguished from consensual sexual interactions by *stalking* and/or rough behaviour of the initiating female as e.g. *grab*, *pull*, *hold on tight* while mounting or masturbating using a hand or other body parts of the other female, and by the resistance behaviour of the other female, which may include *move away*, *struggle to escape* and/or vocalisations like *kiss squeaks*.

Male sexual coercion, i.e. forced copulation and forced copulation attempt, could be distinguished from *a consensual mating* by the aggressive behaviour of the male, which mostly included *long call, chase, grab*, *pull*, *hold on tight*, and often also *hit* or *bite*, and the resistance behaviour of the female, which mostly includes *flee*, *struggle to escape*, and often *hit*, *bite* and sometimes *fight*.

Three types of prosocial behaviour were expected with regard to aggressive interactions: *third party intervention*, *reconciliation* and *post-conflict third-party affiliation*.

A ***third party intervention*** was defined as the attempt of an individual who was originally not involved in the conflict to cease the aggressive interaction by appeasement behaviour, shielding the victim, threat display or actions like pulling the victim away from the aggressor or attacking the aggressor (Petit & Thierry, 2000). An intervention by a bystander could be either ***partial***, which includes an agonistic support of one of the opponents, or ***impartial***, which includes no agonistic behaviour against any of the opponents (Rudolf von Rohr et al., 2012).

Reconciliation indicated the affiliative reunion of the opponents of a conflict which probable function consisted e.g. in repairing their social relationship, reducing anxiety or uncertainty and/or preventing further aggression (de Waal & van Roosmalen, 1979; Kappeler & van Schaik, 1992).

Post-conflict third party affiliation (PCTA) was here defined as the first affiliative interaction following a conflict between a previously uninvolved individual and the recipient of the aggression, which has often been called *consolation* (e.g. de Waal & van Roosmalen, 1979). In general, I followed the definition provided by Aureli and de Waal (2000b, p. 387), especially in proposing that post-conflict third party affiliation may have several functions including consolation, but also tension reduction, appeasement or reassurance; therefore I do not use the term consolation synonymously with post-conflict third party affiliation. However, in contrast to their definition, I did not include affiliative interactions with the former aggressor, but restricted the concept to first affiliations with the former victim (cf. also subsection 1.1.4.4, p. 19).

While third party interventions could have been directly coded with regard to their on- and offset, the identity of the intervening individual, the particular behaviour and the success of the intervention, this was not possible for reconciliation and post-conflict third party affiliation, which required particular post-hoc observations based on the recorded material. To attribute certain affiliative interactions following a conflict as post-conflict behaviour necessitated additional criteria to distinguish them from affiliative behaviour that occurred independently of the conflict. For this I analysed the video footage by applying the post-conflict/matched-control observation method (PC-MC method, de Waal & Yoshihara, 1983).

PC-MC method

In applying the PC-MC method, I examined the video recording of the first 10 min immediately following an aggressive interaction with focus on the victim and determined the time interval (one minute length each) in which the first affiliative interaction between the former opponents as well as between the victim and a third party had occurred. In case the conflict had been resumed within the first 3 min of the PC interval, I stopped this PC and restarted a new PC immediately following the end of the resumed aggressive interaction.

On the next possible day, preferentially the next day at exact the same time, but – if not possible – at least within a time slot of maximum +/- 60 min with regard to the onset of the exactly matched time, I examined the video recordings focussing the former victim for 10 min and determined the time of the first affiliative contact between the former opponents as well as with a third party. In case the required MC recording of the next day was not available, I used time-matched video footage of observations on a previous or following day within a maximum time window of +/- 7 days. If a conflict had taken place within 10 min prior to the planned MC interval, I chose the interval nearest to the matched time within a time slot of maximum +/- 60 min which followed an interval without conflict of at least 10 min. This resulted in PC-MC pairs which were used to analyse whether and how conflicts changed the subsequent behaviour of the opponents and of other group members towards the victim (Veenema et al., 1994) as explicated in detail in the next section (p. 103).

2.3.2.4 Statistical analysis

All statistical computations were conducted by using statistics software R vers. 3.2.4 (R Core Team, 2016) with additional packages, e.g. car (J. Fox & Weisberg, 2011), sfsmisc (Maechler et al., 2016) and other specific packages (cf. next sections for more references).

(i) Aggressive interactions

In a first step, I analysed the frequencies of aggressive interactions, including male sexual coercion, with regard to their general occurrence, intensity and contexts using descriptive statistics. To compare the frequencies of aggressive interactions with regard to the housing conditions, I conducted a Wilcoxon signed rank test using the R function `wilcox.exact` from the R package exactRankTests (Hothorn & Hornik, 2015) with statistical significance assessed at the α-level of 0.05.

Then I investigated aggressive interactions on an individual as well as on a dyadic level using descriptive statistics. For visualising behavioural patterns as a social network, I used the R package tnet (Opsahl, 2009, pp. 104-122).

Since forced copulations form a specific class of aggression which is uncommon in other non-human great apes and differs from other aggressive behaviours, I subdivided the dataset for further analyses of third party intervention and post-conflict affiliations into two subsets to consider them separately. The main subset included aggressive interactions of all contexts but male sexual coercion, while the latter constituted the second subset. Forced sexual interactions among females, on the other hand, were considered as common aggressive behaviour and were therefore included into the general analysis.

(ii) Third party intervention

Due to the rare occurrence of aggressive interactions, only descriptive statistics was applicable to analyse third party intervention on a dyadic and an individual level with regard to the context, intensity of the aggression, individuals involved and the housing conditions.

(iii) Reconciliation and post-conflict third party affiliation

To examine, whether reconciliation and post-conflict third-party affiliation occurred, I applied the PC-MC method as established by de Waal and Yoshihara (1983) in a first step. For each PC-MC pair received as described above (p. 103), I compared the time of the first affiliation for PC and MC.

A PC-MC pair was indicated as *attracted* if the affiliative interaction took place earlier in the PC than in the MC, or only in the PC. It was indicated as *dispersed* if the affiliative interaction took place earlier in the MC than in the PC, or only in the MC. And it was indicated as *neutral* if either the affiliative interaction occurred in both observation intervals at the same time or not at all (Fig. 29).

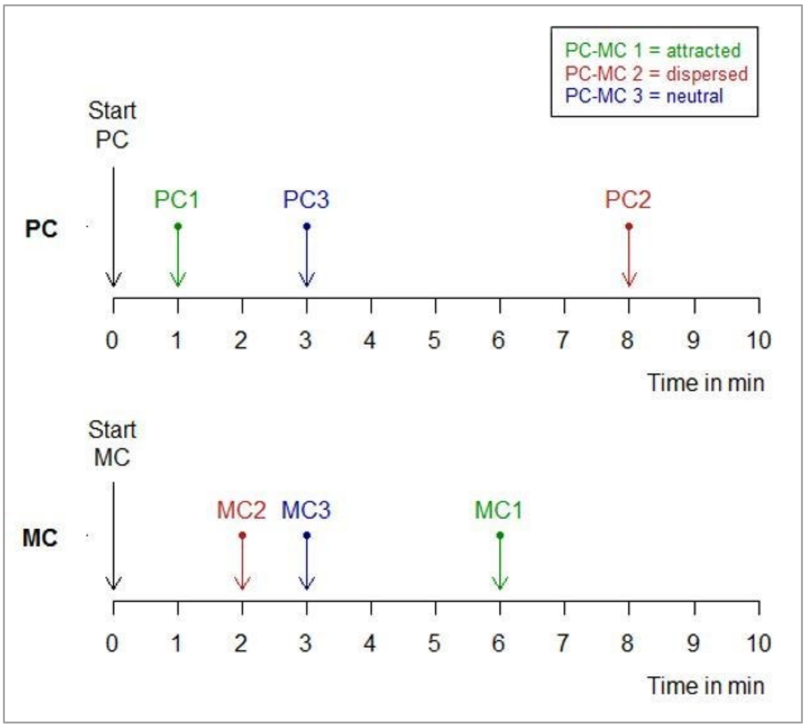

Fig. 29 Principle of determining PC-MC pairs as attracted, dispersed or neutral

To determine, whether a higher proportion of attracted vs. dispersed PC-MC pairs was above chance, which would – following de Waal and Yoshihara (1983) – demonstrate the occurrence of reconciliation in the study group, I conducted an exact Wilcoxon signed rank test on the proportions for attracted and dispersed pairs for each focal individual (Fraser & Aureli, 2008, p. 1116) using R function `wilcox.exact` from the R package exactRankTests (Hothorn & Hornik, 2015) with statistical significance assessed at the α-level of 0.05.

As an alternative way to determine whether reconciliation or post-conflict third-party affiliation occurred, I applied the time rule method (Aureli et al., 1989). For each PC-MC pair, I indicated the one-minute interval in which the first affiliative contact occurred in the PC as well in the respective MC and computed the cumulative distributions (i.e. the cumulated relative frequency) over time for PC and MC. Following Aureli et al. (1989) I applied a two sample Kolmogorov-Smirnov test with assessed statistical significance at the α-level of 0.05 using R function `ks.test` to investigate whether the distributions differed. In case a significant difference could be demonstrated, again following Aureli et al. (1989, p. 42), I determined the post-conflict time interval with the maximum difference between the cumulative relative frequencies of PC and MC. Then I operationally defined each affiliative post-conflict contact between former opponents within this time interval as reconciliation.

As suggested by Aureli and van Schaik (1991, p. 7), I controlled for possibly influential dyads by conducting an exact Wilcoxon signed rank test with statistical significance assessed at the α-level of

0.05 on PC-MC pairs for each undirected dyad in the time window which had been determined as relevant for reconciliation using R function `wilcox.exact` from the R package exactRankTests (Hothorn & Hornik, 2015).

With regard to the determined time window for reconciliation, I considered the types of affiliative behaviour between former opponents to determine whether a specific behaviour was typically performed using descriptive statistics.

Finally I investigated whether there were differences in the *conciliatory tendency* across the dyads of former opponents which would have indicated selectivity with regard to reconciliation. The conciliatory tendency has been originally introduced as a measure by de Waal and Yoshihara (1983) who defined it as the number of attracted PC-MC pairs divided by the total number of PC-MC pairs. The concept has been subsequently altered by Veenema et al. (1994) to account for different baseline levels of affiliation among dyads. I used this improved measure and computed the *corrected conciliatory tendency* (hereafter referred to as conciliatory tendency or *CCT*) as suggested by Veenema and colleagues:

$$CCT = \frac{attr - disp}{total}$$

In this equation *attr* indicates the number of attracted, *disp* the number of dispersed and *total* the total number (i.e. attracted, dispersed and neutral pairs) of PC-MC pairs for a particular undirected dyad.

Unfortunately, the number of PC-MC pairs per dyad was too small as to allow for comparison across all dyads. Therefore, a meaningful conclusion about a general selectivity in conciliating was not possible, so I only reported the results of the calculation.

All coding was done by me. To assess inter-rater reliability, 20% of the aggressive interactions as well as the affiliations during the respective PC- and MC-periods were coded by a second rater who was unfamiliar with the hypotheses. A comparison of the coded behaviours revealed a proportion of agreement between the raters in 87%.

2.3.3 Results

2.3.3.1 Aggressive interactions

P3.1 confirmed: Orangutans generally engaged rarely in social conflicts – especially when housing conditions allowed for avoiding conflicts (i.e. given lower social density)

(i) Aggressive interactions were generally rare and of moderate intensity

Aggressive interactions occurred relatively rarely. Across all observation days I recorded 114 aggressive interactions which also include 16 cases of coerced copulation or attempted copulation. While 85 aggressive interactions were distinct events with no other aggression following within 4 min. The remaining 29 cases occurred in sequences of two, three or four causally connected interactions, either when a further attack followed within 4 min or when counter-aggression was performed.

The duration of all aggressions but coerced copulations was 34 s (*sd* = 42 s, *median* = 20 s), the average duration of male sexual coercion was 204 s (*sd* = 312 s, *median* = 48 s).

The majority of aggressions seemed to occur spontaneously (*n* = 49, 43%) without any detectable reason, followed by aggressions in the contexts of sexual coercion (*n* = 26, 23%) and weaning (*n* = 17, 15%). Aggression due to direct food competition was observed on 9 and due to object competition on 6 occasions (8 % and 5%, respectively). There was one case of punishment when *Toba* attacked *Djamuna* immediately subsequent to *Djamuna's* aggression against *Tao*. For the remaining cases (*n* = 6, 5%) the particular context was not determinable.

Half of all aggressions was of *medium intensity* (*n* = 57, 50%), followed by *high intensity* (*n* = 37, 32.5%) and *low intensity* (*n* = 14, 12.3%). In 6 cases (5.3%), the intensity of aggression could not be determined. However, even though nearly one third of all aggressions was indicated as of high intensity, only 16 cases included biting or bite attempts. Overall, only one severe aggression occurred which resulted in a minor injury of the victim.

(ii) Aggressions varied in their intensity across contexts

The contexts of aggressive conflicts differ with regard to the intensity of aggression (Table 13). Most high-level aggression occurred during sexual coercion (*n* = 16, 43%), while most low-level aggressions occurred in the context of weaning (*n* = 12, 86%).

Table 13 Frequencies of aggressions with regard to their level of intensity and context. Percentages indicate the proportion of the levels of intensity for each context and the overall proportions both of contexts and of levels of intensity. Numbers within red boxes indicate the highest frequencies of aggression for each level of intensity.

Intensity Context	High		Medium		Low		Indeterminable		Total	Proportion of contexts
Spontaneous	13	27%	33	67%	1	2%	2	4%	49	43%
Sexual coercion	16	62%	9	35%	0	0%	1	4%	26	23%
Weaning	3	18%	2	12%	12	71%	0	0%	17	15%
Food competition	0	0%	8	89%	1	11%	0	0%	9	8%
Object competition	3	50%	3	50%	0	0%	0	0%	6	5%
Punishment	1	100%	0	0%	0	0%	0	0%	1	1%
Indeterminable	1	17%	2	33%	0	0%	3	50%	6	5%
Across contexts	37	32%	57	50%	14	12%	6	5%	114	

(iii) Under less spacious housing conditions, aggressive interactions increased in their frequency of occurrence and intensity.

Frequencies and rates of aggressive conflicts (pooled data) differed substantially between the housing conditions. While in autumn and summer a total of only 23 aggressive interactions (20% of all cases) had been observed in the outdoor enclosure, resulting in a rate of 0.31 aggressions/h, the number of aggressive conflicts almost quadrupled in the indoor enclosures in winter (*n* = 91, 80%), resulting in a rate of 1.09 aggressions/h.

Likewise, the intensity of aggression increased with decreasing available space. While in the outdoor enclosure, 70% of the aggressive interactions were of medium and 13% of high intensity, this relation changed indoors to 45% vs. 37%, mainly due to male sexual coercion. (Fig. 30)

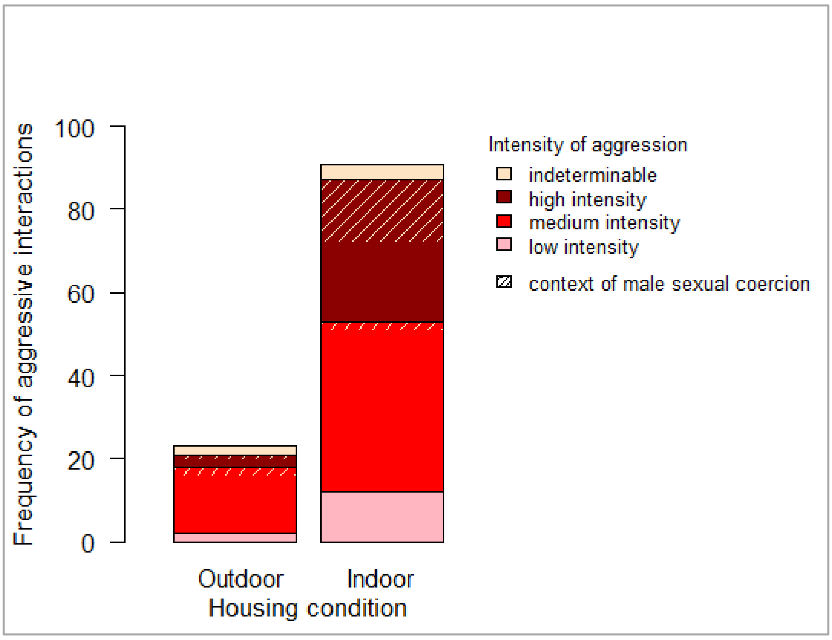

Fig. 30 Comparison of housing conditions with regard to aggression intensity. Bars indicate the absolute number of aggressive interactions per housing condition. The respective proportions of low, medium and highly intensive aggression are indicated with different hues (light pink, red and dark red, respectively; beige for indeterminable cases). Additionally, the respective proportions of conflicts in the context of male sexual coercion are indicated with shaded lines

However, aggression rates varied across dyads and housing conditions, all outdoor-aggressions occurred within 8, all indoor-aggressions within 14 of 30 possible dyads (Fig. 31). The number of indoor-conflicts between *Toba* and *Djamuna* was drastically increased compared to outdoors, despite the fact that both females were kept in adjacent, but separate indoor enclosures. In contrast, there were fewer aggressions by *Toba* against *Suma* under indoor conditions. Open conflicts between *Toba* and *Tao* were also considerably increased in frequency under indoor conditions, though most of them occurred in the context of weaning.

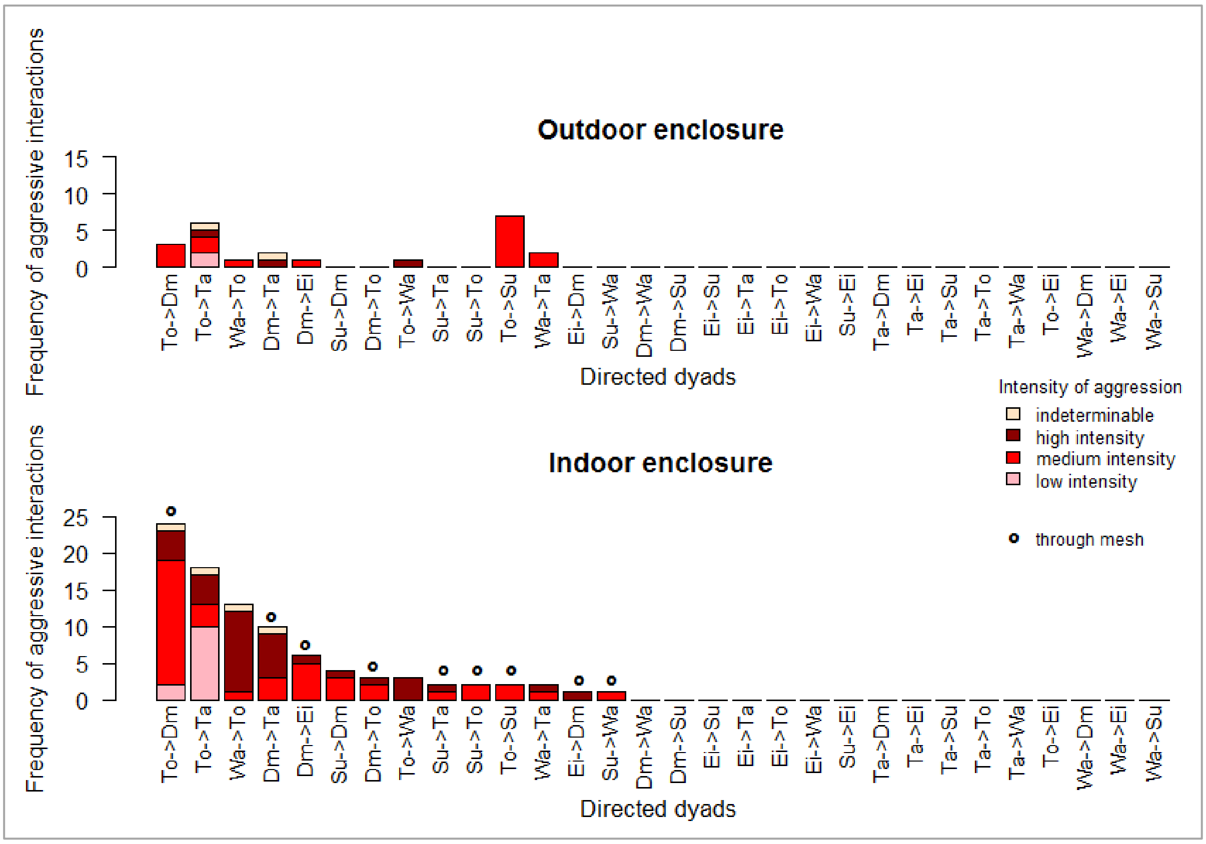

Fig. 31 Comparison of the number and intensity of aggressions for each dyad under two different housing conditions

The average aggression rate across dyads (number of aggression per hour) increased from 0.010 (*sd* = 0.023) under outdoor conditions to 0.036 (*sd* = 0.070) under indoor conditions (Fig. 32). An exact Wilcoxon signed rank test comparing frequencies on a dyadic level demonstrated a significant difference between the frequencies of aggressions of outdoor vs. indoor enclosure (N = 14 ,T = 11, p = 0.006, assessed statistical significance at α-level = 0.05).

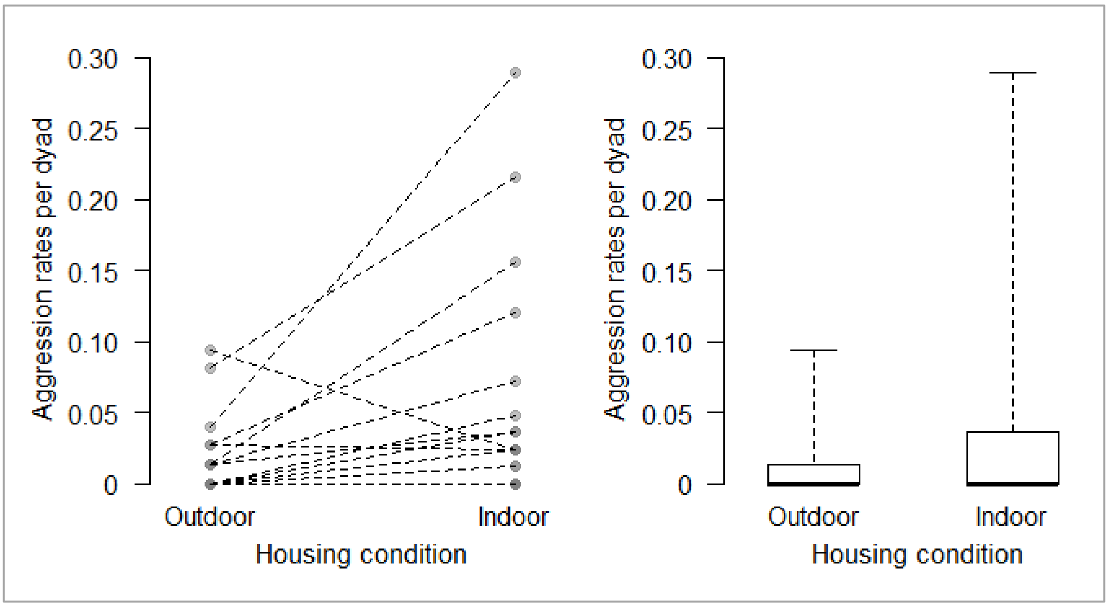

Fig. 32 Comparison of rates of aggressive interactions on a dyadic level. In the left figure, each data point refers to a particular dyad; dashed lines connect data points which belong to the same dyad. In the right figure, boxplots summarise the data for each condition. Horizontal lines indicate medians, boxes indicate the particular interquartile range and whiskers indicate maxima

(iv) Behavioural patterns in the context of coerced copulations differed from those of other contexts

Aggressions consisted of a single behaviour or a sequence of two or more behaviours. The main behaviour types were: *grab* or *grab attempt* (*n* = 53), *forced sexual interaction* (*n* = 20), *pull* (*n* = 39), forced sexual interaction (*n* = *chase* (*n* = 17), *threat* (*n* = 16), *bite* or *bite attempt* (*n* = 16), hold tight (n= 13), *push* (10), *hit* (*n* = 7). On 56 occasions, a single aggressive behaviour had been performed; on the other occasions, two (*n* = 23), three (*n* = 19), four (*n* = 12) or five (*n* = 2) behaviours had been combined. In the remaining two cases the particular aggressive behaviour was not determinable.

Reactions by the victim consisted of the following main behaviour types or combination of them: *vocalisation* (*n* = 50), *avoidance* (*n* = 49), *non-aggressive behaviour to cease the conflict* (*n* = 37), *counter-aggression* (*n* = 20), *no reaction* (*n* = 9). No case of *redirection* has been observed. On 60 occasions, a single behaviour type had been performed; on the other occasions, two (*n* = 44) or three (*n* = 10) behaviour types had been combined. The majority of combinations (*n* = 40) included vocalisations ranging from soft *hoo* vocalisations, *kiss squeaks*, *whining*, *whimpering*, to loud *screaming*.

Interaction patterns in the context of male sexual coercion differed from those of other contexts. All forced copulations but one occurred in the indoor enclosure in winter and most of them were preceded by an audible disturbance either from a distressed groupmate or due to visitors or other external circumstances. In contrary to agreed copulations, forced copulations or copulation attempts were always initiated by *Walter* who was obviously aroused emitting long calls and/or showing dominance display when approaching *Toba* or – in two cases of unsuccessful copulation attempt – *Tao*. In each case, aggressive behaviour involved *grab* and *hold tight*, often *pull* and *forceful repositioning*. *Hit* and *bite* were performed when the female heavily struggled to escape or reacted aggressively, e.g. hit and/or bit. In all cases of sexual coercion against *Toba*, *Eirina* was clinging on her mother, usually at her front. On 4 occasions, *Toba* attacked and bit *Walter* immediately following the copulation when they were still in body contact.

(v) Particular individuals were predominantly aggressors, others mostly the target of aggression

Although all individuals but one (*Tao*) had acted as aggressors at least once and all individuals had been victims at least once, the frequency of being involved in an aggressive interaction as aggressor or victim varied considerably across individuals (Fig. 33). While *Toba* was the most frequent aggressor (*n* = 66, 56%), but a less frequent victim (*n* = 19, 17%), *Tao* who never initiated an aggressive interaction was the most frequent target of aggression (*n* = 42, 37%). *Djamuna* was both the second frequent aggressor (*n* = 22, 19%) and victim (*n* = 32, 28%), followed by *Walter* as aggressor (*n* = 18, 16%) who had rarely been attacked (*n* = 5, 4%). *Suma* was equally often aggressor and victim (*n* = 9, 8%) and *Eirina* was least frequently involved in conflicts, one time as aggressor (1%) and seven times as victim (6%).

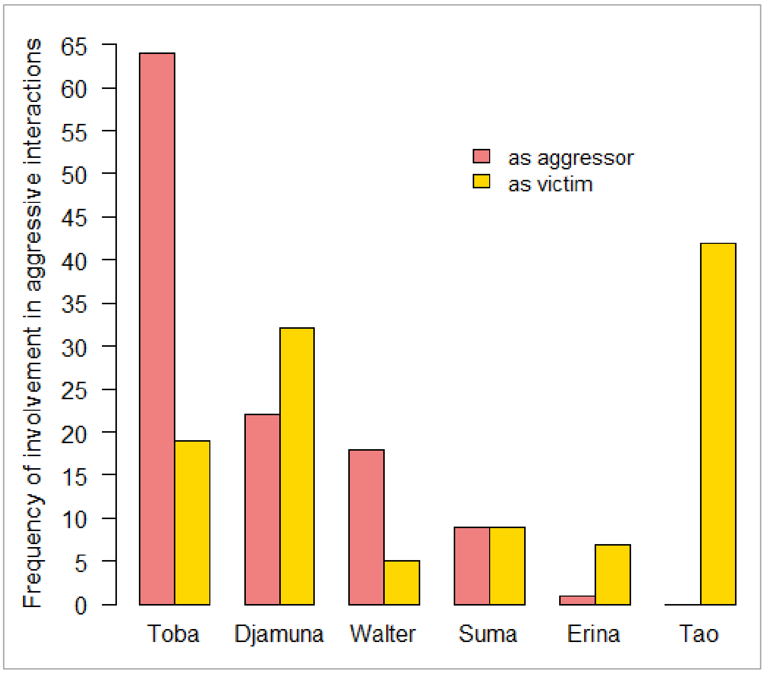

Fig. 33 Absolute frequency of involvement in aggressive interactions as aggressor (red bars) and victim (yellow bars) for each individual

(vi) Dyads differed with regard to the frequency of open conflicts

With respect to the aggressor-victim dyads, aggressions were observed within 14 of 30 possible dyads. Most aggressions occurred by *Toba* against *Djamuna* (*n* = 27, 28%) and against *Tao* (*n* = 24, 21%), most of the latter occurred in the context of weaning (*n* = 17), followed by *Walter* against *Toba* (*n* = 14, 12%), all of them coerced copulations, *Djamuna* against *Tao* (*n* = 12, 11%), *Toba* against *Suma* (*n* = 9, 8%) and *Djamuna* against *Eirina* (*n* = 7, 6 %). Aggression occurred four times (4%) in each of the dyads *Toba-Walter*, *Walter-Tao* and *Suma-Djamuna*, three times (3%) between *Djamuna* and *Toba*, two times in each of the dyads *Suma-Toba* and *Suma-Tao,* and there was one single case (1%) of aggression between *Suma* and *Walter* and *Eirina* and *Djamuna, respectively*. Figure 34 represents these dyadic patterns as social networks.

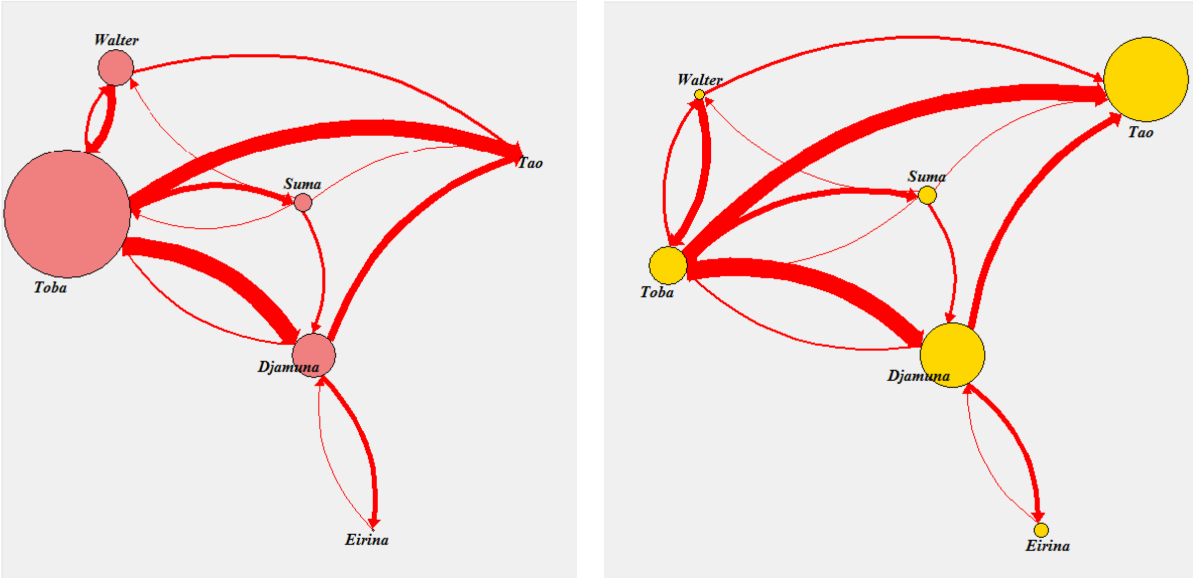

Fig. 34 Dyadic patterns of aggressive interactions demonstrated as weighted graphs. Red edges indicate aggressive interactions, with arrows showing the direction of aggression and edge size indicating the frequency for the particular directed dyad. Vertices indicate the particular individuals. In the left-hand figure, the vertex size corresponds with the number of cases in which the particular individual was involved as aggressor (red coloured vertices). In the right-hand figure, it corresponds with the number of cases in which the particular individual was involved as victim (yellow vertices).

Figure 34 demonstrates that aggressions between two individuals did not occur symmetrically. Attacks predominantly went down the hierarchy: *Toba*, the dominant female who was the most frequent aggressor, almost exclusively received aggressions from *Walter* in the context of sexual coercion, but barely from the other females. *Djamuna*, who was the most frequent target of aggressions, was simultaneously the lowest ranking adult female. Most attacks by *Djamuna* were targeted at both immatures, *Tao* and *Eirina*.

2.3.3.2 Prosocial conflict management

As explicated in the Methods section (p. 103), I subdivided the dataset at this point. In the following analyses, a subset of 93 interactions including all cases of aggressive interactions despite those which occurred in the context of male sexual coercion and a second subset of 21 interactions which occurred in the context of male sexual coercion were considered separately.

P3.2 confirmed: Third parties intervened in conflicts of medium and high intensity

(i) The majority of third party interventions was impartial

Overall, interventions by third parties to cease the aggression occurred in 22 of 93 aggressive interactions (24%), in one case it was not determinable whether an intervention took place or not. Usually, one single individual intervened, though on three occasions two individuals interfered.

The majority of third party interventions (*n* = 15, 68%) was *impartial*, i.e. these interventions did include no agonistic behaviour towards any of the opponents. Impartial interventions mainly consisted in *approaching*, *move between/shielding* or *pull victim back*, or in a combination of these behaviours. While the two impartial interventions by Walter did not included any body contact, but consisted in moving between the opponents; impartial interventions by females often included pulling the victim back. All individuals but *Djamuna* performed an impartial intervention at least once: *Toba* and *Suma* intervened six times each, in one of these cases they intervened simultaneously; *Walter* intervened twice, *Tao* and *Eirina* once each.

The remaining seven cases – all occurring in the context of spontaneous aggression – were partial interventions: *Toba* attacked *Djamuna* four times in support of one of her daughters, in a fifth case *Toba* and *Tao* intervened simultaneously in support of *Eirina*; *Suma* attacked *Toba* twice supporting *Djamuna*, in one of these cases, which was the most severe aggressive interaction of the whole observation period, *Suma* intervened simultaneously with *Walter* (see also the description of post-conflict interactions for this case on page 117). There was no case of agonistic support for the aggressor. All interventions but one by *Tao* were successful and ceased the respective aggression.

(ii) Proportion of intervened conflicts with regard to context, aggression intensity and housing condition

The proportion of intervened conflicts varied across the contexts: spontaneous aggressions provoked the highest percentage of interventions by third parties (n = 19, 39%), while no intervention at all occurred in the contexts of weaning and food competition (Fig. 35).

A comparison of the proportions of conflicts with interventions with regard to the intensity of the respective aggression revealed a difference between aggressions of low intensity on the one hand (0%) and of medium or high intensity on the other (28% and 29%, respectively).

When considering the percentage of intervened aggressions with respect to the enclosure, it shows that third parties interfered in 27% of the indoor conflicts but only in 10% of the outdoor conflicts.

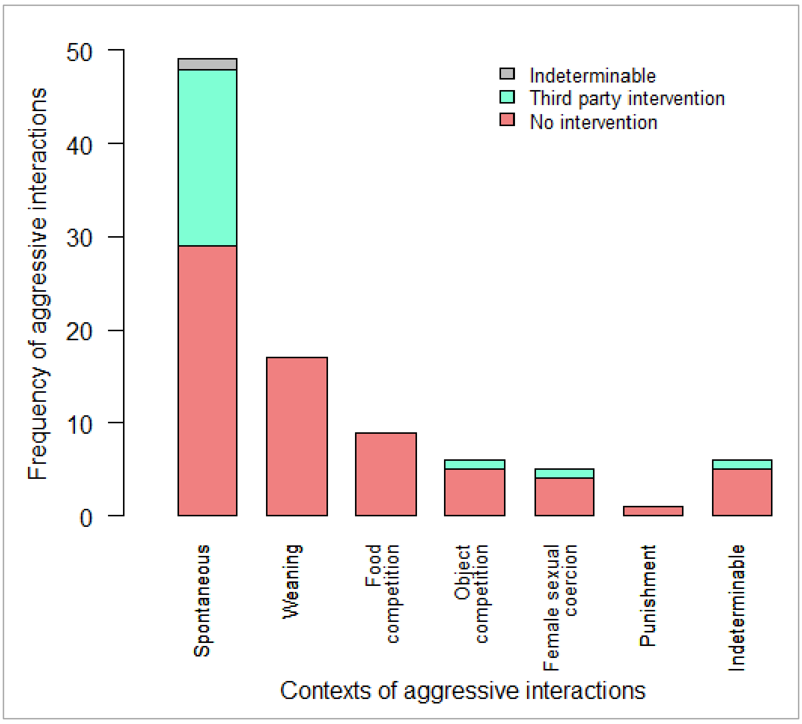

Fig. 35 Proportion of aggressive interactions with and without intervention by a third party for each context

(iii) Particular individuals intervened selectively with regard to the identity of the victim

Regarding the identities of the respective victim and the intervening individual revealed the following patterns: In each case of aggression against the youngest immature *Eirina*, her mother and/or her sister intervened. While no aggression by *Toba* against her older daughter *Tao* in the context of weaning (*n* = 17) was interfered by a third party, 7 of 22 aggressions (32%) against *Tao* in other contexts were ceased by *Toba* (*n* = 5), *Suma* (*n* = 2) and *Eirina* (*n* = 1); on one occasion, both *Toba* and *Suma* intervened. All cases of intervention in aggression against *Djamuna* (*n* = 6) were conducted by *Suma*, on one of these occasions *Walter* interfered too. *Walter* also intervened in two aggressions against *Suma*.

P3.3 confirmed: Immediately following a conflict, opponents engaged more frequently in affiliative interactions compared to control conditions

(i) Both PC-MC method and time rule method confirm the occurrence of reconciliation

Applying the PC-MC method as explicated on page 102, I determined a total of 70 PC-MC pairs of which 31 pairs were *attracted*, 23 pairs *neutral* and 16 pairs *dispersed* (Fig. 36).

I calculated the proportion of attracted, dispersed and neutral PC-MC pairs for each focal individual, i.e. victim (Fig. 37), and conducted an exact Wilcoxon signed rank test (assessed statistical significance at the α-level of 0.05), which revealed that the difference between the proportion of attracted and dispersed PC-MC pairs was statistically significant (*N* = 6, *T* = 21, *p* = 0.031). Thus, according to PC-MC method, reconciliation occurred within this group.

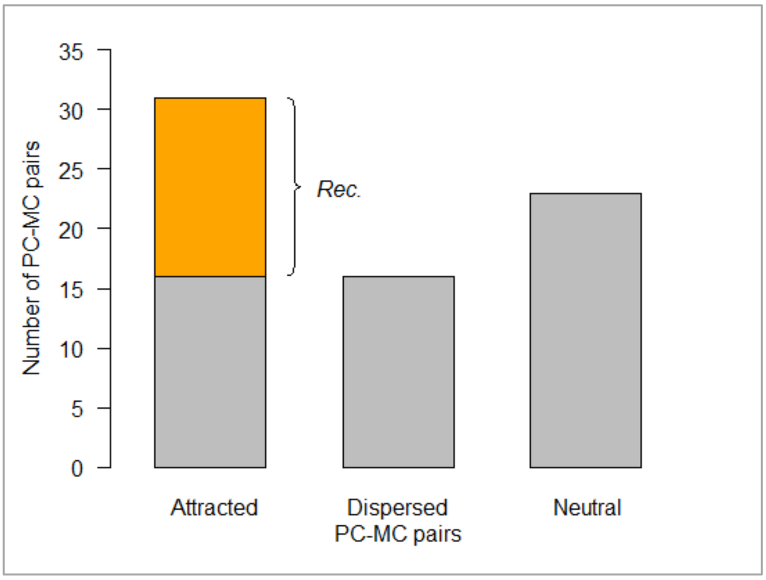

Fig. 36 Absolute frequencies of attracted, dispersed and neutral PC-MC pairs of former opponents across the group. The bracket indicates the proportion of attracted PC-MC pairs (orange) which can be regarded as reconciliation considering a base-line level of affiliative interactions (Aureli et al., 1993)

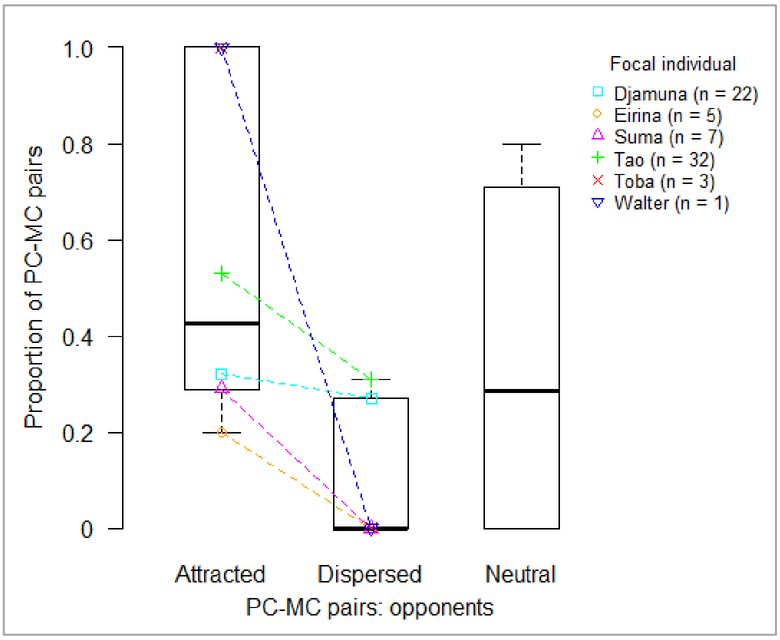

Fig. 37 Proportion of attracted, dispersed and neutral PC-MC pairs across focal individuals (victims). Each coloured symbol indicates a particular individual. Boxplots summarise these data for attracted, dispersed and neutral PC-MC pairs with horizontal lines indicating medians, boxes indicating interquartile ranges and whiskers indicating minima and maxima. Coloured lines connect data points of attracted and dispersed PC-MC pairs for each focal individual. Numbers in brackets following the individuals' names indicate the absolute frequency of PC-MC pairs for each focal individual.

Applying the time rule method as established by Aureli et al. (1989) demonstrated that the majority of first affiliative contacts between the former opponents occurred within the first one-minute interval following the aggressive interaction (Fig. 38)

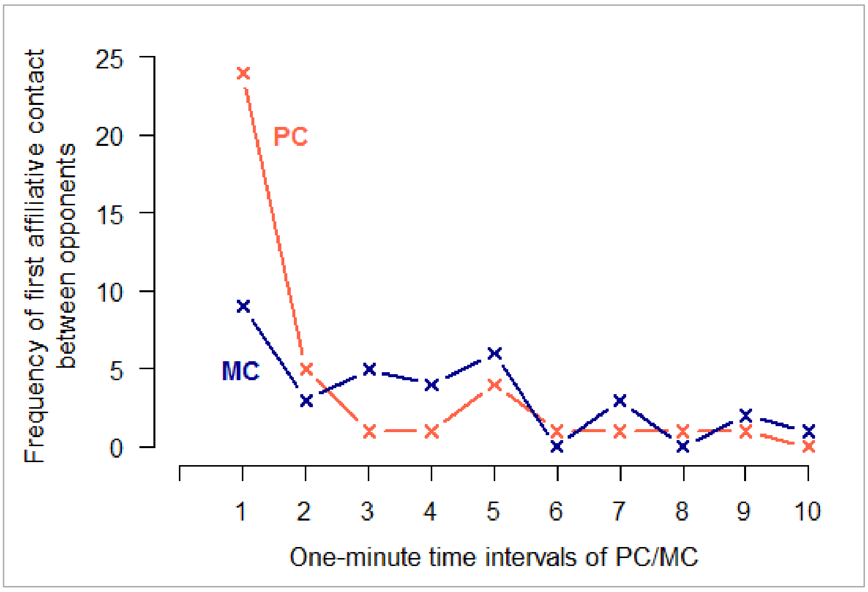

Fig. 38 Number of affiliative contacts between the former opponents per one-minute time interval during the post-conflict observation period (red line) and the matched-control observation period (blue line).

The comparison of the distribution of first affiliative contacts between the former opponents revealed a significant difference between the PC- and the MC-condition (two sample Kolmogorov-Smirnov test, statistical significance assessed at the α-level of 0.05: D^- = 0.545, p = 0.0379). The maximum difference between the cumulative relative frequencies of PC and MC was reached within two minutes after the conflict ($\Delta_{PC\text{-}MC}$ = 0.243). Following Aureli et al. (1989, p. 42), reconciliation

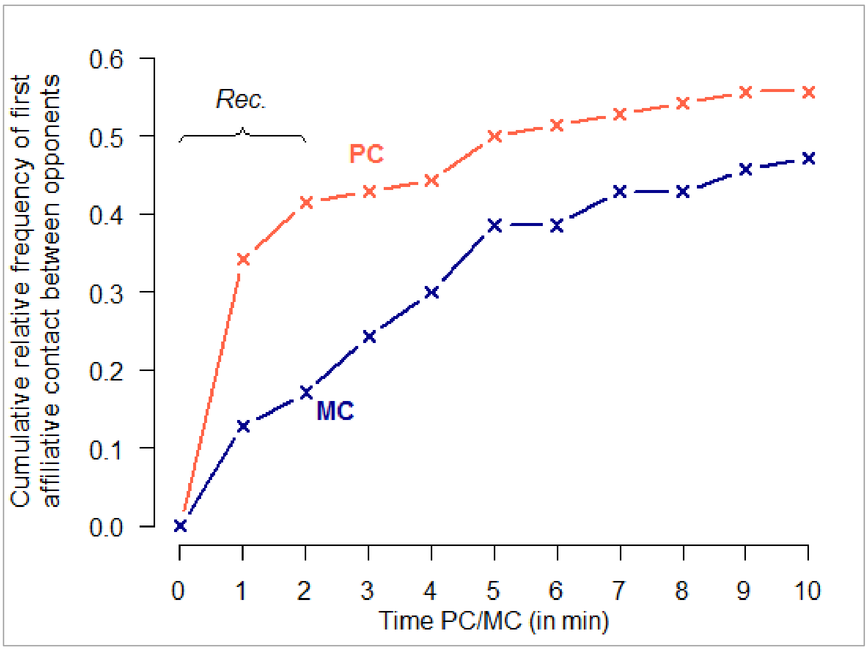

Fig. 39 Cumulative distribution of first affiliative contacts between former opponent for PC (red line) and MC (blue line). The bracket indicates the time window in which each affiliative contact between opponents can regarded as reconciliation (Aureli, van Schaik, & van Hooff, 1989).

can therefore operationally defined as any affiliative contact between the former opponents within the first two minutes subsequent to the end of their conflict (Fig. 39). The conducted exact Wilcoxon signed rank test revealed that the found significant difference was not due to a particular influential dyad ($N = 6$, $T = 21$, $p = 0.031$).

Applying the operational definition of reconciliation, a comparison of the frequency of reconciliations with regard to the housing conditions demonstrates that opponents have proportionally more often reconciled under higher social density (n = 24, i.e. 41% of PC-MC pairs indoors) than under lower social density (n = 5, i.e. 28% of PC-MC pairs outdoors).

Differentiating PC-MC pairs with regard to the contexts of aggression demonstrates differences in the proportion of affiliative post-conflict reunions within two minutes. Reconciliation occurred less frequently after escalated food competition compared to weaning or seemingly spontaneous aggressions (Table 14). However, the data are too few to allow for a reliable extrapolation regarding the effect of contexts.

Table 14 Number and proportion of post-conflict affiliations between opponents within two minutes following the conflict.

Context of aggression	Within 2 min after conflict		All PC-MC pairs
	n	Proportion	n (total)
Spontaneous	13	37%	35
Weaning	7	41%	17
Food competition	1	12%	8
Female sexual coercion	3	100%	3
Object competition	1	50%	2
Punishment	0	0%	1
Indeterminable	4	100%	4
Total:	29	41%	70

In summary, both the PC-MC and the time rule method confirmed the occurrence of reconciliation in the study group.

(ii) Affiliative behaviour during reconciliations have been multifaceted, though often included contact sitting

Across dyads, 29 cases of post-conflict affiliation between opponents may be considered as reconciliation as operationally defined using the time rule method (previous subsection). During reconciliation, either a single affiliative behaviour ($n = 19$) or a combination of two ($n = 9$) or three ($n = 1$) affiliative behaviours have been observed. The most frequent behaviour was *contact sitting* ($n = 12$), followed by *present body part for sucking at fur* ($n = 8$) and *touch body* ($n = 7$). Other behaviours with one to three occurrences were: *object transfer, food transfer, suck at partner's fur*, *nursing, stroke fur, hand on back while walking* and *peering in close proximity.* Most reconciliations occurred after spontaneous aggression (*n* = 13) and in the context of weaning (*n* = 7). Considering the identity of the initiator of the reconciliation, the majority of affiliative contacts (*n* = 21) was initiated by the former victim.

(iii) The only genuine severe aggression was followed by intense, bilateral affiliative interactions between the opponents

Unfortunately, for the most severe aggression by *Toba* against *Djamuna* which resulted in a bite wound on a finger, no PC was possible since – aroused by the commotion and distress screams – *Walter* immediately forced a copulation with *Toba* which lasted for 14 min. Nevertheless, I report the subsequent interactions between *Toba* and *Djamuna* here, because they were extraordinary.

The forced copulation took place near the steel mesh. *Djamuna* sat down in proximity on the other side of the mesh where she was examining and treating her wound, and bedding her probably aching hand on a lump of wood wool. Temporarily she was accompanied by *Suma* who examined and gently touched the injured finger as well. Subsequent to the end of the forced copulation, *Toba* approached *Djamuna* as near as possible and waved wood wool to get *Djamuna's* attention. *Djamuna* ignored her at first. After 7 min, both *Djamuna* and *Toba* left proximity, though 1 min later *Djamuna* approached the mesh again, laid down and leaned against it while treating her hand. Within 3 minutes *Toba* approached *Djamuna* and sat down in closest proximity and leaned towards *Djamuna*. *Djamuna* leaned against her too and held her hand towards *Toba*, whereupon *Toba* gently touched, flexed and stretched the injured finger with her forefinger (Fig. 40). In the aftermath on this day, *Toba* and *Djamuna* often sat in body contact (with mesh between them) and exchanged chewed pompoms of wood wool several times.

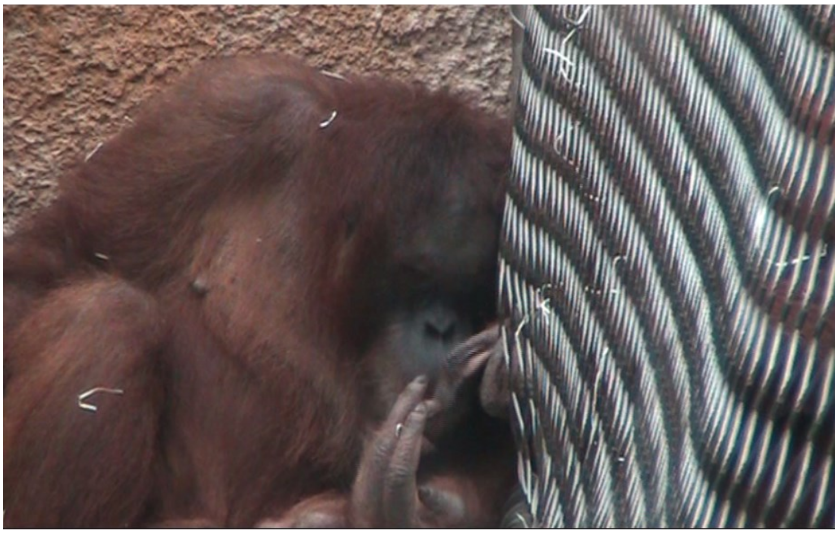

Fig. 40 Video still demonstrating the affiliative interaction between *Toba* (on the right, behind the mesh) and *Djamuna* (on the left). *Toba* carefully examines *Djamuna's* injured finger

(iv) Sample size did not allow for conclusions about a selectivity of conciliatory tendencies

I calculated the corrected conciliatory tendency (*CCT*) for each undirected dyad of opponents (Table 15). Due to the low number of PC-MC pairs for most of the dyads, conclusions about a general selectivity of conciliatory tendencies were not possible. Only for two dyads with a comparably high frequency of PC-MC pairs, a cautious comparison was possible: The *CCT* within the mother-daughter dyad *Toba-Tao* was found to be higher than the *CCT* between the unrelated adult females *Toba* and *Djamuna*. Here, *Toba* seemed to be selective with respect to whom she was going to reconcile with (Table 15). When, alternatively, applying the time-rule method and operationally defining all affiliative post-conflict contacts within a time slot of 2 minutes as reconciliation, 29 affiliative post-conflict contacts out of 76 PC-observations were to be indicated as reconciliation. As demonstrated in figure 41, the proportion of reconciled conflicts differed across dyads.

Table 15 Absolute frequencies of attracted, dispersed and neutral PC-MC pairs for undirected dyads and the respective corrected conciliatory tendencies (*CCT*). Red boxes indicate the *CCT* of those dyads which may allow for a comparison due to a relative high number of PC-MC pairs

Dyad (undirected)	Number of PC-MC pairs				*CCT*
	Attracted	Dispersed	Neutral	Total	
Djamuna-Eirina	1	0	5	6	**0.17**
Djamuna-Tao	5	3	0	8	**0.25**
Djamuna-Toba	8	5	7	20	**0.15**
Suma-Djamuna	1	1	1	3	**0**
Suma-Tao	0	0	1	1	**0**
Suma-Toba	3	0	5	8	**0.38**
Suma-Walter	1	0	0	1	**1**
Toba-Tao	12	7	3	22	**0.23**
Walter-Tao	0	0	1	1	**0**
Total:	31	16	23	70	

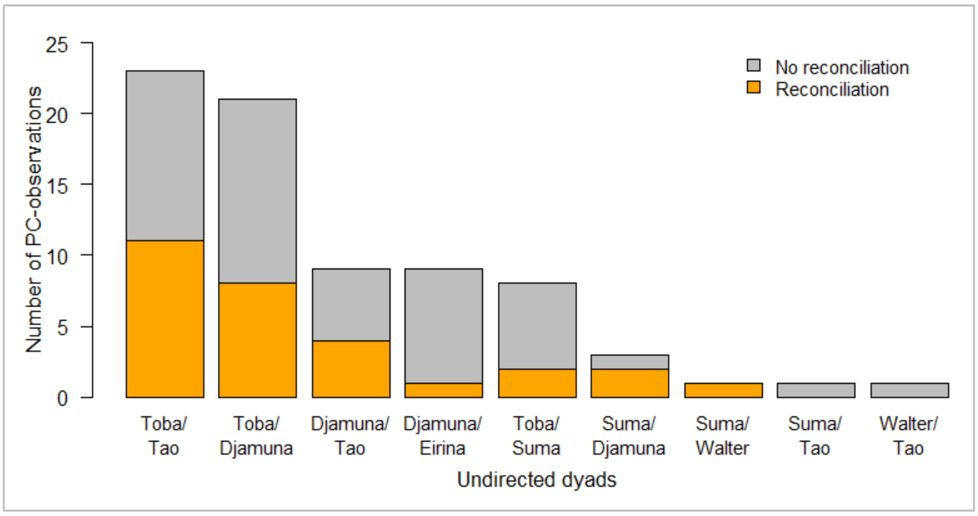

Fig. 41 Absolute frequencies of reconciled aggressions for each undirected dyad. The orange parts of the bars indicate the proportion of reconciled aggressions (PC-affiliations within 2 min)

P3.4 not confirmed: PC-MC method and time-rule method did not demonstrate a significant increase of post-conflict third party affiliations compared to control conditions

(i) Victims of conflicts and bystanders did not engage more frequently in affiliative interactions within the first minutes following a conflict than in non-conflict situations

Applying the PC-MC method for post-conflict third party affiliative contacts resulted in 72 PC-MC pairs of which 29 pairs were attracted, 26 pairs were dispersed and 17 pairs were neutral (Fig. 42). As for reconciliation, I calculated the proportion of attracted, dispersed and neutral PC-MC pairs for each focal individual, i.e. victim, and conducted an exact Wilcoxon signed rank test with assessed statistical significance at the α-level of 0.05, which revealed no statistically significant difference between the proportion of attracted and dispersed PC-MC pairs ($N = 6$, $T = 16$, $p = 0.313$). Thus, the occurrence of increased post-conflict third party affiliation could not be demonstrated for the study group by the PC-MC method.

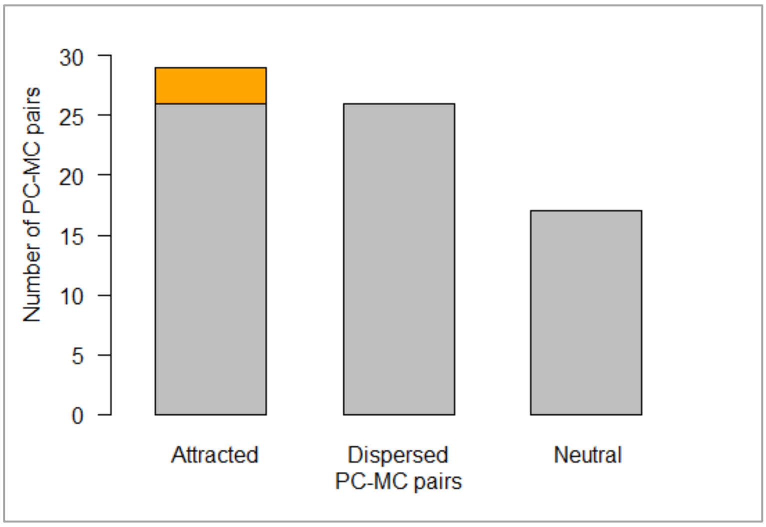

Fig. 42 Absolute frequencies of attracted, dispersed and neutral PC-MC pairs of the former victim and a third party across the group. The orange part of the first bar indicates the non-significant difference of attracted and dispersed PC-MC pairs

However, focal individuals varied with regard to their proportion of attracted and dispersed PC-MC pairs. Especially *Tao* and *Djamuna* who were the most frequent victims demonstrated opposing trends for attracted vs. dispersed PC-MC pairs: *Djamuna* 0.43 vs. 0.22, *Tao* 0.34 vs. 0.5 (Fig. 43)

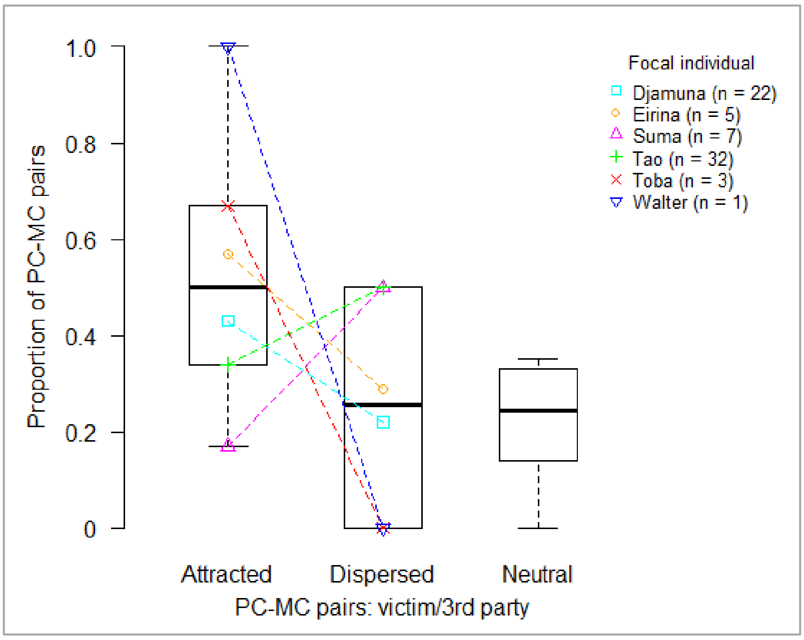

Fig. 43 Proportion of attracted, dispersed and neutral PC-MC pairs for affiliative contacts with third parties across focal individuals (victims). Each coloured symbol indicates a particular individual. Boxplots summarise these data for attracted, dispersed and neutral PC-MC pairs with horizontal lines indicating medians, boxes indicating interquartile ranges and whiskers indicating minima and maxima. Coloured lines connect data points of attracted and dispersed PC-MC pairs for each focal individual. Numbers in brackets following the individuals' names indicate the absolute frequency of PC-MC pairs for each focal individual.

I also applied the time rule method as an alternative instrument to investigate the time distribution of post-conflict third party affiliation. Although the number of first affiliative contacts between victims and bystanders was greater within the first minute following a conflict than in the MC (Fig. 44), the cumulative distribution in the PC did not significantly differ from that in the MC (Fig. 45, two sample Kolmogorov-Smirnov test, statistical significance assessed at the α-level of 0.05: D^- = 0.091, $p = 0.9131$).

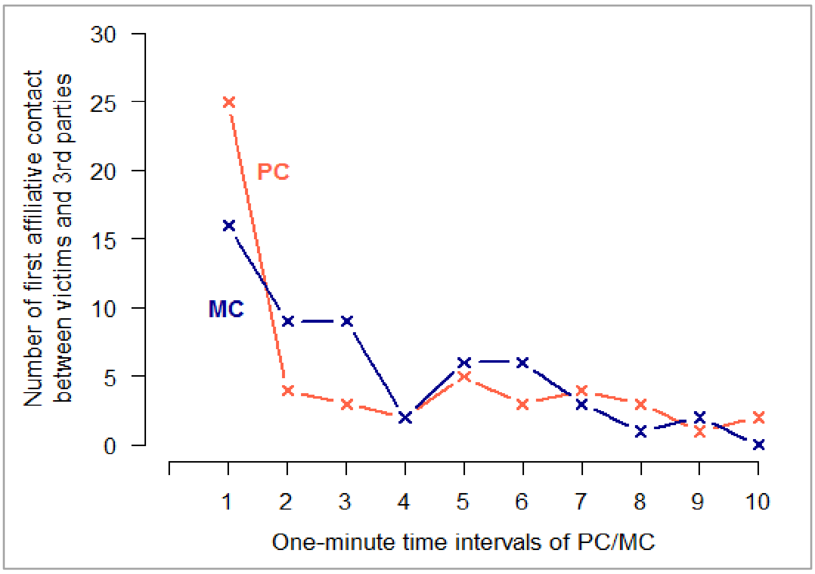

Fig. 44 Number of affiliative contacts between the former victim and a third party per one-minute time interval during the post-conflict observation period (red line) and the matched-control observation period (blue line).

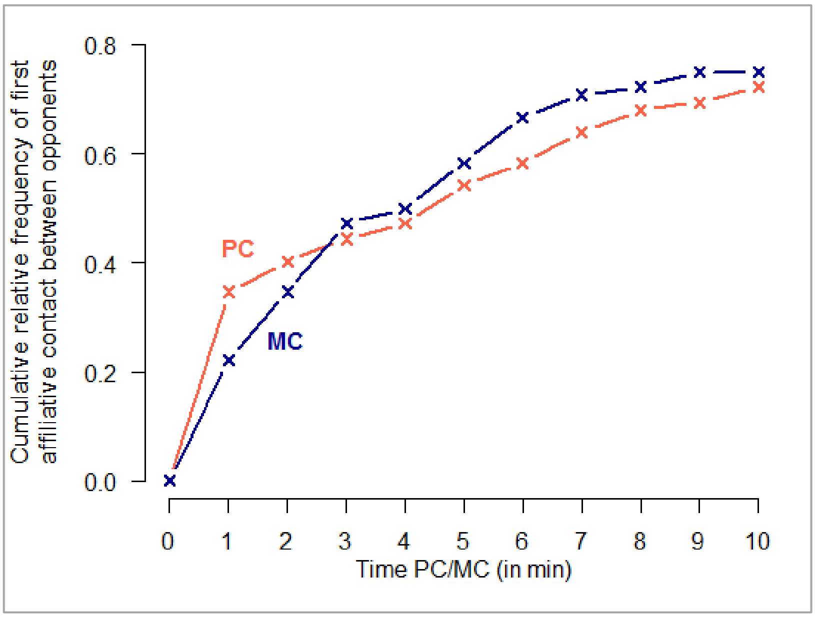

Fig. 45 Cumulative distribution of first affiliative contacts between former victims and third parties for PC (red line) and MC (blue line).

In summary, neither the PC-MC method nor the time-rule method has demonstrated an increase of post-conflict third party affiliations compared to control observations. However, given the small sample size and opposing trends for the two individuals with the most PC-MC pairs, conclusions about the occurrence of conflict-induced third party affiliations in this study group based on these data should be treated with caution.

(ii) Occurrence of PCTA with regard to reconciliation

Considering the 68 PC-MC pairs which were obtainable for both post-conflict opponent- and third-party affiliation, it shows that within the first two minutes which were operationally defined as the time window for reconciliation, 11 reconciliations were accompanied by post-conflict third party affiliations and 14 reconciliations were not. 15 instances of PCTA occurred without previous reconciliation. In total, in 40 out of 68 conflicts the victim was engaged in post-conflict affiliations with the former opponent or with a bystander or with both within two minutes, while 28 conflicts were not followed by any affiliation within this time window.

(iii) The form of affiliative behaviours between victims and third parties following a conflict seems to differ from that in control conditions

Though the frequency of first affiliative contacts between victims and third parties did not significantly differ between the PC and the MC, there was a difference with regard to the types of affiliative behaviour that were performed in either condition (Table 16).

Table 16 Absolute and relative frequencies of affiliative behaviours observed between victims and third parties during PC and MC, respectively. Red boxes indicate the most frequent behaviour for each condition. Proportions refer to the total number of affiliative contacts (*n* = 53 for PC, *n* = 54 for MC), they do not sum to 100% since several affiliative contacts were combinations of two behaviours.

Affiliative Behaviour	PC victim/third party		MC victim/third party	
	number	proportion	number	proportion
Contact sitting	24	45%	8	15%
Touch body	13	25%	14	26%
Embrace	6	11%	2	4%
Play	6	11%	23	43%
Food/object transfer	4	8%	3	6%
Sucking at fur/offer fur	3	6%	7	13%
Nursing	2	4%	0	0%
Grooming	2	4%	0	0%
Sexual interaction	2	4%	0	0%
Cuddling	1	2%	3	6%
Contact walking	1	2%	1	2%
Sit in close proximity	1	2%	0	0%
Begging	1	2%	0	0%
Cofeeding	0	0%	1	2%

During the PC a total of 53 affiliative contacts have been observed, during the MC it was 54 contacts. These affiliative contacts consisted either of single behaviours (*n* = 39 for PC, *n* = 46 for MC) or of a combination of two behaviours (*n* = 14 for PC, *n* = 8 for MC). *Contact sitting* was the most frequent behaviour following a conflict (*n* = 24, 45%), whereas it was much less frequent in the MC (*n* = 8, 15%). In contrast, *play* was the most frequent affiliative behaviour during the control observations ($n = 23$, 43 %), but was less often observed in the PC ($n = 6$, 11%). In both conditions *touch body* was the second frequent behaviour ($n = 13$, 25% for PC, $n = 14$, 26% for MC). Embrace, which is a typical post-conflict third party affiliation in chimpanzees (de Waal & van Roosmalen, 1979), has been performed more often in PC ($n = 6$, 11%) than in MC ($n = 2$, 4%).

The behaviour of *Suma* in the immediate aftermath of the most serious conflict between *Toba* and *Djamuna*, which resulted in an injury (already referred to on p. 117), was extraordinary: *Suma* approached *Djamuna* several times, sat in body contact, touched her gently and examined the injured finger carefully.

2.3.3.3 The context of male sexual coercion

Aggressive interactions in the case of male sexual coercion included 14 forced copulations with *Toba*, 2 forced copulation attempts with *Tao*, 4 counter-aggressions by *Toba* immediately subsequent to a forced copulation, and one attack by *Walter* following a moderate intervention by *Tao*. Each case of forced copulation or copulation attempt provoked at least one intervention either by *Toba*, when *Tao* had been the target, or by one or both of her daughters in case of *Toba* being forced. All of these interventions were physical attacks against *Walter* including mostly a combination of behaviours such as *move between/shielding*, *grab*, *pull*, *hit* and *bite*. While both interventions by *Toba* stopped the sexual aggression against *Tao*, no intervention by the immatures was successful. No intervention occurred in the cases of the 5 other attacks in this context. In sum, in the context of male sexual coercions, partial interventions took place in 16 cases (76%), while in the remaining 5 cases no intervention occurred.

Since only 21 cases of aggression occurred in the context of male sexual coercion and several of these aggressions followed upon each other within 3 min – for example when an attack against *Tao* was intervened by *Toba* whereupon *Walter* forced copulation with *Toba* which finally provoked a counter-attack by *Toba* immediately subsequent to the copulation – only 13 post-conflict observations were possible. This small sample size did not allow for applying either the PC-MC method or the time rule method to demonstrate the occurrence of reconciliation or post-conflict third party affiliation. However, in all cases but one, there was no affiliative contact between the former opponents within 10 min following the conflict. On the other hand, immediately subsequent to each case of forced copulation, there were mutual affiliative interactions between *Toba* and *Eirina* and in some cases also *Tao*, with *Eirina* still clinging at her mother.

2.3.4 Discussion

With this study I provided the first systematic investigation of conflict behaviour and associated conflict management in a group of captive Sumatran orangutans. Generally, open conflicts occurred rarely in the study group, though their frequency and intensity increased with higher social density. Both impartial and partial third party intervention to cease ongoing conflicts were observed. Furthermore, opponents engaged more frequently in affiliative interactions with each other immediately after an aggressive interaction compared to situations without previous conflict. Overall, the results of this study support the hypothesis, that group-living orangutans use prosocial strategies to reduce direct and indirect costs of open conflicts.

Increase of both open conflicts and associated conflict management behaviour under higher social density

Open conflicts were generally rare and of moderate intensity, which concurs with previous reports on captive orangutans (Edwards & Snowdon, 1980; Jantschke, 1972; Poole, 1987), even given the fact that the applied definition of aggression was intended to be sensitive and subsumed also behaviours such as a mother's *bared teeth face* towards her daughter in the context of weaning, *push* or *grab/pull at fur* under this concept. In comparison, Rudolf von Rohr et al. (2012) distinguished in their study on policing in chimpanzees two levels of aggression: low, which meant aggression without body contact, and high, which meant physical attacks that included at least beating the victim. Therefore, some of the determined 114 cases of the present study might probably not count as aggression at all, if a narrower definition would be applied.

In several cases the context of the conflict was obvious, such as sexual coercion, weaning or food competition. However, the majority of female-female aggressions seemed to occur "out of the blue" – i. e. without any recognisable reason for the human observer. This is in line e.g. with reports on aggressions among wild female gorillas (Watts, 1991) and also children in peer conflicts (Boulton, 1993), where the observer was not able to identify a direct cause. Nevertheless, the *lack of identified causes* does not justify the conclusion that there *had been* no direct causes. Boulton's study on playground conflicts in children makes this clear: when interviewed about their reasons for fighting, the opponents reported their reasons for the particular conflicts, which often consisted in disagreement over rules or other aspects of the game that they played, in the wish to settle dominance disputes, and sometimes simply in "disliking" the other child (Boulton, 1993). Unfortunately, revealing the causes by asking the opponents is not a possible option in the case of non-human primates. Judge (2003, p. 60) suggests that many of these seemingly spontaneous conflicts might "[…] result from violations of established patterns of social interactions that human observers may not understand." For future studies, taking the relationship history of the opponents into account including former conflicts might help to understand some "causeless" conflicts, but there will still remain a considerable amount of uncertainty in any case.

Aggressive interactions increased both in frequency and intensity under less spacious conditions, even among females who are kept in adjacent, but separate indoor enclosures. Simultaneously, however, the frequency of prosocial conflict management behaviour, particularly third party interventions to cease ongoing conflicts and reconciliation increased likewise, both within and between the subgroups. These findings are similar to those of a study conducted by Nieuwenhuijsen and de Waal (1982) concerning the effect of differing housing conditions on the social behaviour of captive chimpanzees at the Arnhem zoo (for details on the effect of housing conditions on sharing, cf. subsection 2.1.3, pp. 44-49, 57-63 and 65). Given similar climate conditions in the Netherlands and Germany, the Arnhem chimpanzees spent the warm months in their spacious outdoor enclosure and had to use a smaller indoor enclosure for similar long periods of time. Here, the aggression rate increased indoors as did the rate of affiliative interactions. The authors interpreted this finding as a coping strategy for medium-term crowding. Other studies support this suggested function of increasing affiliations as a coping strategy to reduce the effects of social tension under crowding (Caperos et al., 2011; Judge, 2000; Judge & de Waal, 1997).

In addition to focus at affiliative behaviours per se, as Nieuwenhuijsen and de Waal (1982) did, I investigated prosocial behaviours which are directly related to open conflicts. Therefore, the found proportional increase of bystander-ceased aggressions and of reconciliation-followed conflicts under crowded conditions support my general hypothesis about captive orangutans' prosocial behaviour being a means to cope with the challenges of permanent group life even stronger.

Partial and impartial third party interventions to cease ongoing conflicts

Third party interventions occurred in conflicts of medium or high intensity, but never in those of low intensity. A possible explanation would be that low-level conflicts had been probably unnoticed by other individuals. Furthermore, most of low-level conflicts took place in the context of weaning, which is a typical type of parent-offspring conflicts in mammals, in which an intervention by an uninvolved third party would not to be expected.

In all contexts but that of male sexual coercion, the majority of interventions was impartial and mainly performed by a dominant individual. This finding is in line with those on policing in other primate species (Petit & Thierry, 2000) and also with the few reports on policing in wild and captive orangutans (Marzec et al., 2016; Tajima & Kurotori, 2010; Zucker, 1987). Corresponding to the form of the intervening behaviour reported in these studies, the two observed instances of male policing consisted in ceasing the aggression by mere positioning between the opponents without body contact. However, the observed behaviour of the intervening females was different: Several conflicts have been peacefully terminated by pulling the victim away from the aggressor or shielding her while having body contact. Furthermore, in some of the cases, appeasing behaviour towards the victim followed immediately, e.g. embracing her or putting the hand on her back while guiding her away. Female interveners in the present study were found to be selective with regard to the identity of the victim. While Toba intervened when her daughters had been attacked, all interventions – impartial as well as partial ones – in aggressions against Djamuna were performed by Suma, her closest associate. Taking these results of impartial female intervention together, I suggest that the function of impartial intervention in these cases rather consisted in protecting and comforting close social partners and thereby probably strengthening social bonds. These partner-related functions, however, have been suggested so far only for partial interventions (Petit & Thierry, 2000). On the contrary, it has been claimed that close social bonds should not be an important factor, since arbitrators do not favour any of the opponents (Watts et al., 2000), which seems to be the case e.g. for male policing in gorillas (Watts, 1991) and also orangutans (Zucker, 1987). However, since the observed peaceful female interventions fit the definition of impartial intervention (Rudolf von Rohr et al., 2012), I suggest either to widen the scope of possible functions of impartial interventions, or to revised the concepts of partial and impartial intervention. From my point of view, the latter suggestion would be a more appropriate solution, because a peaceful intervention in order to protect the victim implies some sort of side-taking, while an attack of both opponents to stop a conflict does not.

Taking this argument into account, third party intervention can, for instance, be categorised in one of the following two alternative ways: The first one would consist in sticking with the differentiation between partial and impartial interventions, but define these categories – as the names suggest – by the occurrence of side-taking in the sense of supporting one of the opponents. Each category, then, could be further differentiated with regard to the means of intervention – being aggressive or not. Following this categorisation, the male interventions would be classified as impartial, the female ones as partial, but both as non-aggressive (or peaceful). The second alternative would differentiate with regard to the form of intervention, being aggressive or non-aggressive, first, while each category could be further differentiated regarding the occurrence of side-taking. Following this second approach, the particular male and female interventions of this study would be grouped into the major category non-aggressive (or peaceful) and then indicated as impartial and partial, respectively. Whether the first or the second alternative would be more appropriate, depends on the purpose of the categorisation. The first alternative is a more functional one, since the major category refers to an assumed social relationship. The second alternative, on the other hand, is a descriptive one, since the major categories are clearly located at the behavioural level. For the reason of my studies, I would prefer the second alternative, because peaceful interventions are more unlikely to raise the general aggression level and should therefore be more appropriate as means to reduce the costs of open conflicts, which is the general function, I am interested in.

Occurrence of reconciliation in the study group

Applying established methods such as PC/MC method (de Waal & Yoshihara, 1983) and time rule method (Aureli et al., 1989), I demonstrated an increase of affiliative reunions of the opponents within the first minutes following the conflict. With this, the occurrence of reconciliation in orangutans has been confirmed for the first time. The temporal distribution of post-conflict reunions compared to control conditions was analogue to those found for other primate species in which reconciliation occurs, e.g. human children (Butovskaya & Kozintsev, 1999; Verbeek, 1997), chimpanzees (Fraser & Aureli, 2008; Kutsukake & Castles, 2004), bonobos (Palagi et al., 2004), Japanese macaques (Aureli et al., 1993).

Unfortunately, the general rare occurrence of open conflicts, their unbalanced distribution across dyads and the corresponding small and unevenly distributed number of available PC-MC pairs did not allow for reliable conclusions about whether the orangutans reconciled selectively with particular partners. There were only two pairs of opponents, for which a comparison of the conciliatory tendency would have been appropriate, since they engaged comparably frequently in aggressive interactions: While there were nearly as much conflicts between *Toba* and *Tao* as between *Toba* and *Djamuna*, the conciliatory tendency was higher within the mother-daughter dyad *Toba-Tao* than between *Toba* and *Djamuna* who were unrelated adult females. This difference might reflect selectivity of the conciliatory tendency and would be in conformity to the *Valuable Relationship Hypothesis* (Aureli et al., 1989; de Waal & Aureli, 1997). But, again, the sample size is too small for an extrapolation. However, the primary aim of the present study was to investigate, whether reconciliation occurs in captive orangutans. Further studies including a larger sample of captive orangutan groups should be conducted to test for the different proposed functions of reconciliation systematically. Moreover, in future studies, it would be useful to record also signs of anxiety, such as self-directed behaviour, to test for the effect of tension reduction through reconciliation and/or post-conflict third party affiliation.

Likewise, due to the limited number of PC-MC pairs, a qualified extrapolation regarding whether and how the context of a conflict affected the occurrence of reconciliation was not possible. However, the results seem to be in line with a trend found for macaques (Aureli, 1992; Matsumura, 1996), baboons (Castles & Whiten, 1998a) and capuchin monkeys (Verbeek & de Waal, 1997): reconciliation occurred more often in non-food than in food contexts, especially with regard to highly preferred food (but see Arnold & Whiten, 2001, for chimpanzees).

Sitting in body contact was the predominantly performed affiliative post-conflict behaviour between opponents, often combined with other tactile gestures and actions. However, this is a very common affiliative behaviour among captive orangutans, and it was also the most frequent affiliative behaviour in PC-situations among victims and third parties. Therefore, the results of this study do not suggest any behavioural specificity with regard to reconciliation as it has been claimed e.g. for chimpanzees. However, reported post-conflict behaviour varies considerably across species and even within a species across populations and study groups (Aureli et al., 2002). For example, de Waal and van Roosmalen identified *kissing* as the preferentially performed behaviour by former opponents and *embracing* as predominantly occurring during third party post-conflict affiliations in a group of captive chimpanzees (de Waal & van Roosmalen, 1979). Although some studies in the wild and in captivity confirmed *kissing* and/or *embracing* to occur during post-conflict affiliations, the specific occurrence of one of them either during reconciliation or during third party affiliation has not been replicated yet (Fraser & Aureli, 2008). Furthermore, Kutsukake and Castles (2004) found *gentle touch*, but neither *kissing* nor *embracing* to be the most frequent affiliative behaviour in post-conflict situations in a community of wild chimpanzees in the Mahale Mountains. The question whether and when chimpanzees use specific behaviours for reconciliation is still unsettled. When we keep in mind that also the form of human reconciliations extremely varies, depending e.g. on the particular culture (Fry, 2000) or the context (Ljungberg et al., 2005), then it may be possible that the respective behaviour in chimpanzees (and other primates) also depends on similar – or other – factors. However, the observed rather unspecific post-conflict affiliations of orangutans in this study are also in line with studies on other, less “demonstrative” (Cords, 1993, p. 264) primates, where contact sitting or close proximity are the most frequent affiliative behaviours in the aftermath of a conflict (e.g. Westlund et al., 2000; York & Rowell, 1988).

The occurrence of reconciliation in the study group was demonstrated applying well-established methods to integrate the results in the large corpus of reconciliation studies on other primates. Though well-established, the methods were also conservative. Especially the operational definition of reconciliation by applying the time rule method did probably not cover all affiliative post-conflict interactions that were *functionally* reconciliations. Cords (1993) argued for a more functional definition of reconciliation and suggested the PC/MC method to be more appropriate in this respect compared to the time rule method. However, as suggested e.g. by Veenema (2000), it has become common practise to combine several methods, e.g. Koski et al. (2007); (Mallavarapu, Stoinski, Bloomsmith, & Maple, 2006); Roseth et al. (2011). Logan, Emery, and Clayton (2013), who studied post-conflict behaviour in corvids, pointed out that species-characteristics may require an adaptation of these methods and suggested to consider not only the time of the first affiliative PC-contact but also frequency and duration of affiliative contacts following a conflict in comparison to MC-observations for a given time window. I'd like to bring a further aspect to mind, which has also been recommended by de Waal, Leimgruber, and Greenberg (2008) for the context of prosocial choice tasks. In addition to quantitative data, which are unquestionably essential and of central importance, the qualitative description of post-conflict affiliative interactions between the opponents as well as between bystanders and opponents might help to understand the proximate functions of affiliations in the aftermath of a conflict.

Post-conflict third party affiliations

In contrast to reconciliation, the temporal distribution of post-conflict third party affiliations did not differ from that of the control observations. However, though the quantitative analyses did not confirm an increase of PCTAs, this does not necessarily mean that conflict-induced third party affiliations with the victim did not occur. Considering qualitative observational data of post-conflict behaviour might provide further information (de Waal & Aureli, 1997). For instance, when looking at the particular forms of PCTA, on the one hand, and affiliative behaviour observed under control conditions, on the other, PC and MC seemed to differ: Following a conflict, victims and bystanders were sitting in closest proximity with body contact – often combined with touching or embracing – three times as much than in periods without a previous conflict. On the other hand, the most frequent affiliative behaviour in control conditions was play, which occurred much less frequently after conflicts. Contact sitting, gentle touching and embracing are typical for implicit post-conflict affiliation, especially among closely bonded partners, in several species (Call, 1999; Cords, 1993; Fraser & Aureli, 2008; Verbeek, 2008). The found higher frequency of these behaviours in comparison to baseline data might therefore be a hint for the occurrence of conflict-induced third party affiliation with the victim in the study group. The affiliative behaviour of *Suma*, which had followed the most serious attack by Toba against *Djamuna* and consisted in several events of contact sitting, touching and gently examining the injured finger, was undoubtedly provoked by the conflict, which had also been terminated by Suma's partial intervention.

Furthermore, there were some circumstances which might have potentially confounded the detection of consolation. Given the small sample size, it was not possible to take the effect of different contexts into account (apart from the differentiation between the context of male sexual coercion on the on hand and all others on the other). A considerable proportion of conflicts occurred between *Toba* and her older daughter *Tao* in the context of weaning. In this context, I would not expect an increase of affiliations towards the victim by a third party, since this common parent-offspring conflict is not very likely to affect other group members. Given that, on the one hand, *Tao* was one of the two individuals who were most frequently in the role of the victim; and, on the other, that both individuals demonstrated opposing trends for attracted vs. dispersed PC-MC pairs applying the PC-MC method, might be an indication for a confounding context-effect. Moreover, not every conflict occurred in proximity to a bystander; hence, especially low-level aggressions could have been not obvious to others and therefore failed to provoke PCTAs. The third aspect that might have influenced the results regards the spatial separation of the group when kept indoors. Although the individuals of both subgroups have had the opportunity to interact with each other through the mesh – and they actually did it quite often –, the separation potentially restricted the opportunity to initiate PCTAs for bystanders and victims from different enclosures.

As already outlined for reconciliations, the main objective of this study was to investigate whether conflicts provoke post-conflict affiliations in captive orangutans. For the case of post-conflict third party affiliations this investigation did not lead to clearly positive results. Hence, it is hardly possible to discuss probable functions of PCTA in orangutans. However, assuming, as the differing behaviour types might suggest, that the observed PCTA had been – at least partly – conflict-induced and not mere common affiliative behaviour, some cautious suggestions regarding there functions might be made. There was no single case of redirection of aggression by the victim (Aureli, Cozzolino, Cordischi, & Scucchi, 1992) or of a shift of the focus of aggression from the original victim to a third party by the aggressor. Given these findings and the fact that – at least to my knowledge – redirection has not been reported for orangutans so far, the proposed function of PCTA to protect bystanders against becoming a victim (*Self-Protection Hypothesis*, Koski & Sterck, 2009) seems to be not very likely for orangutans. It has further been proposed that PCTA might repair the relationship between the opponents, especially when the bystander is kin-related to the aggressor (Wittig et al., 2007), or reduce anxiety in the victim (McFarland & Majolo, 2012) as a substitute for absent reconciliation. In the present study, less than half of all instances of post-conflict affiliations between opponents within the first two minutes were accompanied by affiliations between a bystander and the victim. More than half of the PCTA within the first two minutes following a conflict had occurred in the absence of reconciliation. Since there is not necessarily a single function of PCTA in a species, the results might be in accordance with the *Substitute Hypothesis* of one or the other form. Due to the lack of necessary data, no statement is possible with respect to other suggested and discussed hypotheses on the function of post-conflict third party affiliation, namely the *Consolation Hypothesis* (Aureli, 1997), the *Social Bonding Hypothesis* (Koski & Sterck, 2007) and *Victim Protection Hypothesis* (Palagi & Norscia, 2013).

Conflict management regarding forced copulations

Forced copulations – or attempted copulations – are a type of sexual aggression which is absent in the African great apes, but common both in humans and orangutans (Muller, Kahlenberg, &

Wrangham, 2009; Muller & Wrangham, 2009; Wrangham & Muller, 2009). During my observations, both cooperative matings – usually initiated by the female – and coerced copulations occurred. Confirming observations in the wild (Utami Atmoko, Mitra Setia, et al., 2009), forced copulations usually provoked counter-aggressions by the female, which often included struggling, hitting and biting. Furthermore, the extent of force by the male increased with the intensity of the female's resistance; as it has been reported for wild orangutans (Knott, 2009). All forced copulations except one took place indoors, when the male had been aroused by loud noises from visitors or by commotion or distress vocalisations within the orangutan group. All cases of male sexual coercion against Toba, who was the only adult female in the respective subgroup, provoked an immediate intervention by one or both of her immature daughters. These interventions were all physical attacks against Walter; however, none of these interventions had been successful. This is also in line with reports from wild orangutans (Utami Atmoko, Mitra Setia, et al., 2009). Given the small number of PC-MC pairs for coerced copulations, conclusions about the occurrence of reconciliation or PCTA have to be treated with caution. However, the behaviour of the involved individuals was quite consistent. In all but one cases, there was no affiliation between the opponents within ten minutes. On the contrary, Toba sometimes attacked Walter immediately afterwards. Hence, reconciliation seems to be absent in this particular form of conflict. This is not surprising, since the females' resistance against copulation attempts by particular males has been suggested as a selective female mating strategy (Stumpf, Emery Thompson, & Knott, 2008). A friendly post-conflict reunion with a non-preferred male would provide a further opportunity for this male to mate, and would, hence, be counterproductive for the female.

On the other hand, immediately following a forced mating, Toba and one or two of her daughters usually engaged in affiliative interactions among each other. Here, consolation would be the most plausible function (Aureli, 1997). Since not only the adult female, but also her daughters, especially the youngest one, who had been clinging at her mother during each copulation, were affected by the aggressive interactions, a stress alleviating effect of these PCTA would probably be mutually.

Summary

This study was the first systematic investigation of prosocial conflict management in captive orangutans. As expected, conflicts of interest rarely resulted in aggressive interactions. However, when conflicts escalated, they were mostly of moderate intensity and were often accompanied or followed by attempts to resolve the conflict. Uninvolved bystanders have been observed to intervene both impartial and partial in ongoing conflicts to cease them. Opponents, on the other hand, showed a tendency to peacefully join each other within the first minutes following the conflict. The latter finding is the first confirmation of the occurrence of reconciliation in orangutans. Though the occurrence of conflict-induced third party affiliations with the victim could not be demonstrated with the established quantitative methods, behavioural data seem to suggest the possibility of this post-conflict strategy for captive orangutans, nevertheless.

Taken the findings together, they fully support my underlying hypothesis, that, notwithstanding their semi-solitary life in the wild, group-living orangutans use prosocial strategies to manage and resolve conflicts and thereby reduce the potential costs of group life.

While this was a first step in the study of conflict resolution in orangutans, especially the occurrence of post-conflict third party affiliation as well as possible functions of prosocial conflict management in orangutans need to be investigated in more detail. Future studies should include a larger sample of orangutan groups and analyse additional data, especially on social relationships, context and signs of stress-related anxiety to enable tests of influencing factors and of hypotheses about the function of the different conflict management strategies.

3 GENERAL DISCUSSION

Prosociality is an essential building block and an important regulating principle of the social life in all human societies, ranging from traditional small-scale communities to large national states and even international communities. While helping, collaborating, sharing resources, mediating between opponents or saving others from danger are actions we are familiar with in our daily life; the existence of these potentially costly, sometimes self-sacrificing behaviours has puzzled scientists and philosophers for centuries. Attempts to solve the puzzle are manifold and range from religious doctrine and philosophical systems to biological, psychological or economical approaches (Dovidio et al., 2006, pp. 7-32).

In this thesis, I adopted a comparative perspective or – to be more precisely – a cross-species view on prosocial behaviour that generally aims to discover the evolutionary roots of human prosociality by investigating, which prosocial abilities and behaviours humans share with their great ape relatives.

Over the last three decades, a large body of hypotheses and empirical data on prosocial behaviour has emerged from an increasing number of studies on prosocial behaviours, such as cooperation, helping, food sharing, conflict management strategies, and their emotional and socio-cognitive underpinnings, across the primate order. Particularly chimpanzees and bonobos, as our closest great ape relatives, alongside with capuchins, callitrichids and macaques, have been extensively investigated (Aureli & de Waal, 2000b; Burkart et al., 2009; de Waal, 2008; Jaeggi & Gurven, 2013a; Thierry et al., 2008; Tomasello & Vaish, 2013; Yamamoto & Takimoto, 2012).

However, orangutans as our most distant living great ape relatives were so far barely involved in the endeavour to elucidate the evolutionary pathways of human prosocial behaviour.

The aim of this thesis was to fill this gap and examine: (i) whether and in which contexts group-living orangutans behave prosocially, (ii) which prosocial behaviours orangutans share with the other great apes, and (iii) which functions these behaviours might possibly have. Answering these questions would be important for the comparative study of prosociality, because, if orangutans revealed to possess prosocial abilities comparable to chimpanzees, we consequently were able to make more substantial claims about the origins of human prosociality in a common hominid ancestor.

Apart from being the “neglected ape” (Nadler, Galdikas, Sheeran, & Rosen, 1995), which alone would justify a systematic research on prosociality in both species, there are at least two characteristics making orangutans particularly interesting for the comparative perspective on prosociality. First, the sequential analysis of the genomes of both orangutan species and the subsequent comparison with the genomes of humans, bonobos and chimpanzees has revealed that the genetic structure had been evolving much faster in the common lineage of *Pan* and *Homo* than in the *Pongo*-lineage (Locke et al., 2011). This suggests that the orangutan genome would resemble the genome of our common ancestor more than the genome of chimpanzees or bonobos does. Which in turn might suggest also phenotypic similarities, including socio-cognitive abilities and behaviour; but of course, phenotypic resemblance is not a necessary consequence of genetic similarity.

Second, orangutans demonstrate a high flexibility in their social behaviour which enables them to cope with two extremely differing living conditions. Due to ecological constraints, both orangutan species have developed a semi-solitary lifestyle, with Sumatran orangutans being more gregarious than the Bornean species (Delgado & van Schaik, 2000). In zoos, however, orangutans usually live in long-term and stable groups, demonstrating a comparable low rate of aggressions and engage in a variety of social interactions (Jantschke, 1972; Poole, 1987; Zucker, 1987; Zucker et al., 1978). Their successful behavioural adjustment to the challenges of a permanent group life might possibly be based on the usage of prosocial behaviour as a means to mitigate conflicts and regulate social relationships.

Based on these considerations, I conducted three studies on zoo-living Sumatran orangutans, to investigate: (i) whether and how captive orangutans use food sharing and object sharing to mitigate regularly occurring, potential conflict situations caused by the uneven distribution of food or non-food objects (Study 1); (ii) whether the relationship quality influences the probability to share with a particular partner (Study 2); and (iii) whether orangutans use prosocial conflict management strategies to cease aggressive interactions and to reduce the costs of actual conflicts (Study 3).

To summarise the main results:

First, unequal distributions of food or objects rarely led to aggressive competition among possessors and non-possessors. Orangutans throughout the study group frequently communicated their interest in food or objects and shared frequently both in passive and active forms. Sharing frequencies – in particular active transfers among adult females – increased under conditions of higher social tension due to less spacious housing conditions.

Second, food sharing tests using monopolisable food confirmed that orangutans shared food preferentially with close social partners. A comparison with data from similar studies on chimpanzees demonstrated a significantly larger proportion of active sharing for orangutans.

Third, aggressive interactions were generally rare and of moderate intensity. The orangutans performed both partial and impartial intervention to cease ongoing conflicts. Opponents tend to reconcile in the aftermath of conflicts. Post-conflict third-party affiliations as an expected third strategy, however, could not be confirmed. When less space was available, the frequencies both of conflicts and of prosocial conflict management behaviour increased.

Since I have already discussed these findings with regard to the respective hypotheses and derived predictions in detail (cf. subsections 2.1.4, 2.2.4 and 2.3.4), the remaining part of this chapter is dedicated to the interpretation of the main findings with regard to the research questions and some suggestions for future research.

The first research question of this thesis was: *Do socially housed Sumatran orangutans act prosocially; and if they do so, in which contexts?* Given the results outlined above, the direct answer to this question is clearly: *Yes – in all considered contexts!* The results of all studies demonstrated – as expected – that group-living orangutans regularly performed typical prosocial behaviours, both in potential competitive situations regarding food or non-food objects and in actual conflicts.

The second research question addressed similarities and differences of prosocial behaviours observed in orangutans and other great apes: *Which prosocial behaviours do orangutans share with the other great apes, particularly with chimpanzees?* In my studies, I was able to demonstrate almost all types of prosocial behaviour I was interested in and which have been described for chimpanzees (e.g. Boesch & Boesch, 1989; de Waal, 1989c; de Waal & van Roosmalen, 1979; Jaeggi, Stevens, et al., 2010; Jaeggi & van Schaik, 2011) also for orangutans: passive and active food sharing with infants and among adults, partial and impartial third party intervention as well as reconciliation. Post-conflict third party affiliation was the only prosocial behaviour for which the occurrence in the study group could not be empirically grounded. However, as I have already argued in the Discussion of Study 3 (subsection 2.3.4), this does not mean that PCTA does not occur in orangutans.

The third research question asked: *What are possible functions of prosocial behaviour in orangutans?* While specific functions have already been discussed in the respective sections of Chapter 2, the broadest and most general answer that may be derived from the results would be: *Orangutans use prosocial behaviours to cope with the challenges of group life*. The present studies provided empirical evidence for the following two-stage argument resulting in the general answer: (i) Group-living orangutans engaged in prosocial interactions, which are common in more gregarious primates, e.g. in chimpanzees, but uncommon or rare in wild orangutans. In chimpanzees, these prosocial behaviours most likely promote social relationships and reduce anxiety and social tension (Fraser & Aureli, 2008; Fraser et al., 2008; Palagi, Cordoni, et al., 2006; Silk, Brosnan, et al., 2013). The results of my second study strongly suggest an interaction between food sharing and social bonding also for orangutans. (ii) Orangutans intensified their prosocial behaviour under less spacious housing conditions. Chimpanzees also respond to crowded conditions with an increase of affiliative interactions, which has been suggested to be a coping strategy for medium-term crowding (Nieuwenhuijsen & de Waal, 1982). Given these similarities in the behaviour of orangutans and chimpanzees under comparable circumstances, I suggest that orangutans use prosocial behaviour to cope with group life.

Open questions and indications for future research

With this thesis I took only the first step towards a comprehensive understanding of the possible forms and the functions of prosociality in orangutans. I am aware that each of the three studies has – despite its advantages – some limitations, which I have outlined in the respective Discussion sections of Chapter 2 (subsections 2.1.4, 2.2.4 and 2.3.4). Here, I want to summarise open questions about prosociality in captive orangutans and to suggest directions of further research.

Given the small number of individuals in my studies, it is necessary to expand the sample size by including observational and experimental data of other and – if possible – larger groups of orangutans. With regard to food sharing, this would e.g. enable to test for (i) separate effects of close kin- and non-kin bonds on the probability of food sharing or (ii) an effect of the relationship quality on the probability of active transfers. With respect to conflict resolution strategies, expanding the sample size would for instance allow for (i) calculating more reliable indices for conciliatory tendencies and testing for selectivity, (ii) conclusions about the occurrence of post-conflict third party affiliations or (iii) identifying possible influencing factors for conflict resolution behaviour, such as context or relationship quality.

To investigate species differences with regard to active food sharing more directly and without possibly confounding effects due to different food types, food sharing tests using large, compact fruits or vegetables should be conducted also with Bornean orangutans, bonobos, chimpanzees and gorillas.

In my studies, I considered only two of three general social contexts in which prosocial behaviour might be expected. Situations, in which cooperation or help are required, emerge much less frequent in the daily life of zoo-living orangutans than potential conflicts of interest. One feasible way to investigate helping behaviour and cooperation in orangutan groups might consist in appropriate manipulated observations.

Summary

The results of all three studies support the underlying hypothesis that socially housed orangutans use prosocial behaviour to cope with group life, in particular to mitigate potential conflict situations, to cease ongoing conflicts and to reduce the costs of aggressive interactions. The results suggest furthermore, that orangutans use prosocial behaviour in order to establish, maintain and strengthen social bonds. The revealed similarities between orangutans and the other great apes with regard to prosocial abilities and behaviours provide further support for the hypothesis that the socio-cognitive and behavioural basis of human prosocial behaviour has probably evolved in a common ancestor of all extant hominids.

BIBLIOGRAPHY

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 40*, 227-266. doi:10.1163/156853974X00534

Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology, 18*(18), 1415-1419. doi:10.1016/j.cub.2008.08.020

Amrein, M., Heistermann, M., & Weingrill, T. (2014). The effect of fission-fusion zoo housing on hormonal and behavioral indicators of stress in Bornean orangutans (*Pongo pygmaeus*). *International Journal of Primatology, 35*(2), 509-528. doi:10.1007/s10764-014-9765-5

Ancrenaz, M., Marshall, A. J., Goossens, B., van Schaik, C. P., Sugardjito, J., Gumal, M., & Wich, S. (2008). *Pongo pygmaeus*. *The IUCN Red List of Threatened Species., Version 2014.3*. doi:10.1111/j.1365-294X.2008.03793.x

Ancrenaz, M., Sollmann, R., Meijaard, E., Hearn, A. J., Ross, J., Samejima, H., . . . Wilting, A. (2014). Coming down from the trees: Is terrestrial activity in Bornean orangutans natural or disturbance driven? *Scientific Reports, 4*, 4024. doi:10.1038/srep04024

Arnold, K., & Barton, R. A. (2001). Postconflict behavior of spectacled leaf monkeys (*Trachypithecus obscurus*). II. Contact with third parties. *International Journal of Primatology, 22*(2), 267-286. doi:10.1023/A:1005675615723

Arnold, K., & Whiten, A. (2001). Post-conflict behaviour of wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Behaviour, 138*(5), 649-690. doi:10.1163/156853901316924520

Arora, N., van Noordwijk, M. A., Ackermann, C., Willems, E. P., Nater, A., Greminger, M., . . . Pamungkas, J. (2012). Parentage-based pedigree reconstruction reveals female matrilineal clusters and male-biased dispersal in nongregarious Asian great apes, the Bornean orang-utans (*Pongo pygmaeus*). *Molecular Ecology, 21*(13), 3352-3362. doi:10.1111/j.1365-294X.2012.05608.x

Aureli, F. (1992). Post-conflict behavior among wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology, 31*(5), 329-337. doi:10.1007/BF00177773

Aureli, F. (1997). Post-conflict anxiety in nonhuman primates: the mediating role of emotion in conflict resolution. *Aggressive Behavior, 23*, 315-328. doi:10.1002/(SICI)1098-2337(1997)23:5<315::AID-AB2>3.0.CO;2-H

Aureli, F., Cords, M., & van Schaik, C. P. (2002). Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour, 64*, 325-343. doi:10.1006/anbe.2002.3071

Aureli, F., Cozzolino, R., Cordischi, C., & Scucchi, S. (1992). Kin-oriented redirection among Japanese macaques: an expression of a revenge system? *Animal Behaviour, 44*, 283-291. doi:10.1016/0003-3472(92)90034-7

Aureli, F., Das, M., Verleur, D., & van Hooff, J. A. R. A. M. (1994). Postconflict social interactions among Barbary macaques (*Macaca sylvanus*). *International Journal of Primatology, 15*(3), 471-485. doi:10.1007/Bf02696104

Aureli, F., & de Waal, F. B. M. (1997). Inhibition of social behavior in chimpanzees under high-density conditions. *American Journal of Primatology, 41*, 213-228. doi:10.1002/(SICI)1098-2345(1997)41:3<213::AID-AJP4>3.0.CO;2-#

Aureli, F., & de Waal, F. B. M. (2000a). Why natural conflict resolution? In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 3-10). Berkeley, CA, US: University of California Press.

Aureli, F., & de Waal, F. B. M. (Eds.). (2000b). *Natural Conflict Resolution*. Berkeley, Los Angeles, California: University of California Press.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., . . . van Schaik, C. P. (2008). Fission-fusion dynamics: new research frameworks. *Current Anthroplogy, 49*(4), 627-654. doi:10.1086/586708

Aureli, F., & Smucny, D. A. (1998). New directions in conflict resolution research. *Evolutionary Anthropology, 6*(4), 115-119. doi:10.1002/(SICI)1520-6505(1998)6:4<115::AID-EVAN1>3.0.CO;2-C

Aureli, F., van Panthaleon van Eck, C. J., & Veenema, H. C. (1995). Long-tailed macaques avoid conflicts during short-term crowding. *Aggressive Behavior, 21*, 113-122. doi:10.1002/1098-2337(1995)21:2<113::AID-AB2480210204>3.0.CO;2-I

Aureli, F., & van Schaik, C. P. (1991). Post-conflict behavior in long-tailed macaques (*Macaca fascicularis*): I. The social events. *Ethology, 89*(2), 89-100. doi:10.1111/j.1439-0310.1991.tb00296.x

Aureli, F., van Schaik, C. P., & van Hooff, J. A. R. A. M. (1989). Functional aspects of reconciliation among captive long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology, 19*, 39-51. doi:10.1002/ajp.1350190105

Aureli, F., Veenema, H. C., van Panthaleon van Eck, C. J., & van Hooff, J. A. R. A. M. (1993). Reconciliation, consolation, and redirection in Japanese macaques (*Macaca fuscata*). *Behaviour, 124*(1-2), 1-21. doi:10.1163/156853993X00470

Baayen, R. H. (2008). *Analyzing linguistic data. A practical introduction to statistics using R*. Cambridge: Cambridge University Press.

Baillargeon, R. H., Morisset, A., Keenan, K., Normand, C. L., Jeyaganth, S., Boivin, M., & Tremblay, R. E. (2011). The development of prosocial behaviors in young children: a prospective population-based cohort study. *The Journal of Genetic Psychology, 172*(3), 221-251. doi:10.1080/00221325.2010.533719

Baldassarri, D., & Grossman, G. (2013). The effect of group attachment and social position on prosocial behavior. Evidence from lab-in-the-field experiments. *PLoS One, 8*(3). doi:10.1371/journal.pone.0058750

Bard, K. A. (1992). Intentional behavior and intentional communication in young free-ranging orangutans. *Child Development, 63*(5), 1186-1197. doi:10.2307/1131526

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). lme4: linear mixed-effects models using 'Eigen' and S4 (Version R package 1.1-10). Retrieved from http://CRAN.R-project.org/package=lme4

Batson, C. D., & Powell, A. A. (2003). Altruism and prosocial behavior. In T. Millon & M. J. Lerner (Eds.), *Handbook of Psychology* (Vol. 5, pp. 463-484). Hoboken, NJ: John Wiley & Sons, Inc.

Batson, C. D., & Shaw, L. L. (1991). Evidence for altruism: toward a pluralism of prosocial motives. *Psychological Inquiry, 2*(2), 107-122. doi:10.1207/s15327965pli0202_1

Baumard, N., & Sperber, D. (2010). Weird people, yes, but also weird experiments. *Behavioral and Brain Sciences, 33*(2-3), 84-85. doi:10.1017/S0140525X10000038

Berman, C. M., Ionica, C. S., Dorner, M., & Li, J. (2006). Postconflict affiliation between former opponents in *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology, 27*(3), 827-854. doi:10.1007/s10764-006-9039-y

Berman, C. M., Lonica, C., & Li, J. (2007). Supportive and tolerant relationships among male Tibetan macaques at Huangshan, China. *Behaviour, 144*, 631-661. doi:10.1163/156853907781347790

Bliege Bird, R., & Bird, D. W. (1997). Delayed reciprocity and tolerated theft: The behavioral ecology of food-sharing strategies. *Current Anthropology, 38*(1), 49-78. doi:10.1086/204581

Bliege Bird, R., Bird, D. W., Smith, E. A., & Kushnick, G. C. (2002). Risk and reciprocity in Meriam food sharing. *Evolution and Human Behavior, 23*(4), 297-321. doi:10.1016/S1090-5138(02)00098-3

Bliege Bird, R., & Power, E. A. (2015). Prosocial signaling and cooperation among Martu hunters. *Evolution and Human Behavior, 36*(5), 389-397. doi:10.1016/j.evolhumbehav.2015.02.003

Boehm, C. (1994). Pacifying interventions at Arnhem Zoo and Gombe. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), *Chimpanzee Cultures* (pp. 211-226). Cambridge: Harvard University Press.

Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour, 48*(3), 653-667. doi:10.1006/anbe.1994.1285

Boesch, C. (2002). Cooperative hunting roles among Tai chimpanzees. *Human Nature, 13*(1), 27-46. doi:10.1007/s12110-002-1013-6

Boesch, C. (2010). Away from ethnocentrism and anthropocentrism: Towards a scientific understanding of "what makes us human". *Behavioral and Brain Sciences, 33*(2-3), 86-87. doi:10.1017/S0140525x10000051

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai-National-Park. *American Journal of Physical Anthropology, 78*(4), 547-573. doi:10.1002/ajpa.1330780410

Boesch, C., Bole, C., Eckhardt, N., & Boesch, H. (2010). Altruism in forest chimpanzees: the case of adoption. *PLoS One, 5*(1), e8901. doi:10.1371/journal.pone.0008901

Borries, C., Launhardt, K., Epplen, C., Epplen, J. T., & Winkler, P. (1999). Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups - defence pattern, paternity and sexual behaviour. *Behavioral Ecology and Sociobiology, 46*, 350-356. doi:10.1007/s002650050629

Boulton, M. J. (1993). Proximate causes of aggressive fighting in middle school children. *British Journal of Educational Psychology, 63*(2), 231-244. doi:10.1111/j.2044-8279.1993.tb01054.x

Brandon-Jones, D., Eudey, A., Geissmann, T., Groves, C. P., Melnick, D. J., Morales, J. C., . . . Stewart, C.-B. (2004). Asian primate classification. *International Journal of Primatology, 25*(1), 97-164. doi:10.1023/B:IJOP.0000014647.18720.32

Brown, G. R. (2004). Tolerated scrounging in nonhuman primates. *Behavioral and Brain Sciences, 27*(4), 562-563.

Brown, G. R., Almond, R. E. A., & van Bergen, Y. (2004). Begging, stealing and offering: food transfer in non-human primates. *Advances in the Study of Behaviour, 34*, 265-295. doi:10.1016/S0065-3454(04)34007-6

Buchan, J. C., Alberts, S. C., Silk, J. B., & Altmann, J. (2003). True paternal care in a multi-male primate society. *Nature, 425*, 179-181. doi:10.1038/nature01866

Bullinger, A. F., Burkart, J. M., Melis, A. P., & Tomasello, M. (2013). Bonobos, *Pan paniscus*, chimpanzees, *Pan troglodytes*, and marmosets, *Callithrix jacchus*, prefer to feed alone. *Animal Behaviour, 85*(1), 51-60. doi:10.1016/j.anbehav.2012.10.006

Burkart, J. M., Fehr, E., Efferson, C., & van Schaik, C. P. (2007). Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences of the United States of America, 104*(50), 19762-19766. doi:10.1073/pnas.0710310104

Burkart, J. M., Hrdy, S. B., & van Schaik, C. P. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology, 18*(5), 175-186. doi:10.1002/evan.20222

Burkart, J. M., & van Schaik, C. P. (2010). Cognitive consequences of cooperative breeding in primates? *Animal Cognition, 13*(1), 1-19. doi:10.1007/s10071-009-0263-7

Butovskaya, M., & Kozintsev, A. (1999). Aggression, friendship, and reconciliation in Russian primary schoolchildren. *Aggressive Behavior, 25*(2), 125-139. doi:10.1002/(SICI)1098-2337(1999)25:2<125::AID-AB5>3.0.CO;2-X

Calcutt, S. E., Lonsdorf, E. V., Bonnie, K. E., Milstein, M. S., & Ross, S. R. (2014). Captive chimpanzees share diminishing resources. *Behaviour, 151*(14), 1967-1982. doi:10.1163/1568539x-00003225

Call, J. (1999). The effect of inter-opponent distance on the occurrence of reconciliation in stumptail (*Macaca arctoides*) and rhesus macaques (*Macaca mulatta*). *Primates, 40*(3), 515-523. doi:10.1007/BF02557587

Call, J., Aureli, F., & de Waal, F. B. M. (2002). Postconflict third-party affiliation in stumptailed macaques. *Animal Behaviour, 63*, 209-216. doi:10.1006/anbe.2001.1908

Call, J., & Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and human children (*Homo sapiens*). *Journal of Comparative Psychology, 112*(2), 192-206. doi:10.1037/0735-7036.112.2.192

Caperos, J. M., Sánchez, S., Peláez, F., Fidalgo, A., & Morcillo, A. (2011). The effect of crowding on the social behavior of the cooperatively breeding cotton-top tamarins (*Saguinus oedipus*). *International Journal of Primatology, 32*, 1179-1189. doi:10.1007/s10764-011-9534-7

Capitanio, J. P. (1999). Personality dimensions in adult male rhesus macaques: prediction of behaviors across time and situation. *American Journal of Primatology, 47*, 299-320. doi:10.1002/(SICI)1098-2345(1999)47:4<299::AID-AJP3>3.0.CO;2-P

Carter, G. G. (2014). The reciprocity controversy. *Animal Behavior and Cognition, 1*(3), 368-386. doi:10.12966/abc.08.11.2014

Carter, G. G., & Wilkinson, G. S. (2013). Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society B-Biological Sciences, 280*(1753), 20122573. doi:10.1098/rspb.2012.2573

Cassella, C. M., Mills, A., & Lukas, K. E. (2012). Prevalence of regurgitation and reingestion in orangutans housed in North American zoos and an examination of factors influencing its occurrence in a single group of Bornean orangutans. *Zoo Biology, 31*(5), 609-620. doi:10.1002/zoo.21000

Castles, D. L., & Whiten, A. (1998a). Post-conflict behaviour of wild olive baboons. I. Reconciliation, redirection and consolation. *Ethology, 104*(2), 126-147. doi:10.1111/j.1439-0310.1998.tb00057.x

Castles, D. L., & Whiten, A. (1998b). Post-conflict behaviour of wild olive baboons. II. Stress and self-directed behaviour. *Ethology, 104*(2), 148-160. doi:10.1111/j.1439-0310.1998.tb00058.x

Chalmeau, R., & Gallo, A. (1995). Cooperation in primates: Critical analysis of behavioural criteria. *Behavioural Processes, 35*(1–3), 101-111. doi:10.1016/0376-6357(95)00049-6

Chalmeau, R., Lardeux, K., Brandibas, P., & Gallo, A. (1997). Cooperative problem solving by orangutans (*Pongo pygmaeus*). *International Journal of Primatology, 18*(1), 23-32. doi:10.1023/A:1026337006136

Chapais, B. (1992). The role of alliances in the social inheritance of rank among female primates. In A. H. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and Alliances in Humans and Other Animals* (pp. 29-60). Oxford: Oxford University Press.

Chaux, E. (2005). Role of third parties in conflicts among Colombian children and early adolescents. *Aggressive Behavior, 31*(1), 40-55. doi:10.1002/ab.20031

Clarke, P. M. R., Henzi, S. P., & Barrett, L. (2009). Sexual conflict in chacma baboons, *Papio hamadryas ursinus*: absent males select for proactive females. *Animal Behaviour, 77*(5), 1217-1225. doi:10.1016/j.anbehav.2009.02.003

Clutton-Brock, T. H., & Parker, G. A. (1995a). Punishment in animal societies. *Nature, 373*, 209-216. doi:10.1038/373209a0

Clutton-Brock, T. H., & Parker, G. A. (1995b). Sexual coercion in animal societies. *Animal Behaviour, 49*(5), 1345-1365. doi:10.1006/anbe.1995.0166

Cohen, J. (1960). A coefficient of agreement for nominal scales. *Educational and Psychological Measurement, 20*, 37-46. doi:10.1177/001316446002000104

Colman, A. D., Liebold, K. E., & Boren, J. J. (1969). A method for studying altruism in monkeys. *The Psychological Record, 19*(3), 401-404.

Colmenares, F., Hofer, H., & East, M. L. (2000). Greeting ceremonies in baboons and hyenas. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 94-96, Box 95.93). Berkeley, CA, US: University of California Press.

Connor, R. C. (2007). Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society B-Biological Sciences, 362*(1480), 587-602. doi:10.1098/rstb.2006.1997

Cooper, M. A., Aureli, F., & Singh, M. (2007). Sex differences in reconciliation and post-conflict anxiety in bonnet macaques. *Ethology, 113*, 26-38. doi:10.1111/j.1439-0310.2006.01287.x

Cordoni, G., & Palagi, E. (2008). Reconciliation in wolves (*Canis lupus*): new evidence for a comparative perspective. *Ethology, 114*(3), 298-308. doi:10.1111/j.1439-0310.2008.01474.x

Cordoni, G., Palagi, E., & Borgognini Tarli, S. (2006). Reconciliation and consolation in captive western gorillas. *International Journal of Primatology, 27*(5), 1365-1382. doi:10.1007/s10764-006-9078-4

Cords, M. (1993). On operationally defining reconciliation. *American Journal of Primatology, 29*(4), 255-267. doi:10.1002/ajp.1350290403

Cords, M. (1997). Friendships, alliances, reciprocity and repair. In A. Whiten & R. W. Byrne (Eds.), *Machiavellian intelligence II* (pp. 29-49). Cambridge: Cambridge University Press.

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

Cords, M., & Killen, M. (1998). Conflict resolution in human and nonhuman primates. In J. Langer & M. Killen (Eds.), *Piaget, Evolution, and Development* (pp. 193-218). Mahwah, NJ, US: Lawrence Erlbaum Associates Publishers.

Côté, I. M., & Poulinb, R. (1995). Parasitism and group size in social animals: a meta-analysis. *Behavioral Ecology, 6*(2), 159-165. doi:10.1093/beheco/6.2.159

Crawford, M. P. (1937). The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs, 14*, 1-88.

Crick, J., Suchak, M., Eppley, T. M., Campbell, M. W., & de Waal, F. B. M. (2013). The roles of food quality and sex in chimpanzee sharing behavior (*Pan troglodytes*). *Behaviour, 150*(11), 1203-1224. doi:10.1163/1568539x-00003087

Cronin, K. A. (2012). Prosocial behaviour in animals: the influence of social relationships, communication and rewards. *Animal Behaviour, 84*(5), 1085-1093. doi:10.1016/j.anbehav.2012.08.009

Cronin, K. A., Kurian, A. V., & Snowdon, C. T. (2005). Cooperative problem solving in a cooperatively breeding primate (*Saguinus oedipus*). *Animal Behaviour, 69*(1), 133-142. doi:10.1016/j.anbehav.2004.02.024

Darwin, C. (1859). *The Origin of Species by Means of Natural Selection*. London: John Murray.

Das, M., Penke, Z., & van Hooff, J. A. R. A. M. (1998). Postconflict affiliation and stress-related behavior of long-tailed macaque aggressors. *International Journal of Primatology, 19*(1), 53-71. doi:10.1023/A:1020354826422

de Kort, S. R., Emery, N. J., & Clayton, N. S. (2003). Food offering in jackdaws (*Corvus monedula*). *Die Naturwissenschaften, 90*(5), 238-240. doi:10.1007/s00114-003-0419-2

de Waal, F. B. M. (1986). The integration of dominance and social bonding in primates. *The Quarterly Review of Biology, 61*(4), 459-479. doi:10.2307/2827744

de Waal, F. B. M. (1989a). Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution, 18*(5), 433-459. doi:10.1016/0047-2484(89)90074-2

de Waal, F. B. M. (1989b). The myth of a simple relation between space and aggression in captive primates. *Zoo Biology Supplement, 1*, 141-148. doi:10.1002/zoo.1430080514

de Waal, F. B. M. (1989c). *Peacemaking among Primates*. Cambridge, MA, US: Harvard University Press.

de Waal, F. B. M. (1992). Appeasement, celebration, and food sharing in the two *Pan* species. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. B. M. de Waal (Eds.), *Topics in primatology* (Vol. 1: Human Origins, pp. 37-50). Tokyo: University of Tokyo Press.

de Waal, F. B. M. (1996). Conflict as negotiation. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great Ape Societies* (pp. 159-172). Cambridge: Cambridge University Press.

de Waal, F. B. M. (1997a). The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior, 18*, 375-386. doi:10.1016/S1090-5138(97)00085-8

de Waal, F. B. M. (1997b). Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology, 111*(4), 370-378. doi:10.1037/0735-7036.111.4.370

de Waal, F. B. M. (2000). Primates—a natural heritage of conflict resolution. *Science, 289*(5479), 586-590. doi:10.1126/science.289.5479.586

de Waal, F. B. M. (2008). Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology, 59*, 279-300. doi:10.1146/annurev.psych.59.103006.093625

de Waal, F. B. M., & Aureli, F. (1996). Consolation, reconciliation, and a possible cognitive difference between macaques and chimpanzees. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into Thought: The Mind of the Great Apes* (pp. 80-110). Cambridge: Cambridge University Press.

de Waal, F. B. M., & Aureli, F. (1997). Conflict resolution and distress alleviation in monkeys and apes. *Integrative Neurobiology of Affiliation, 807*, 317-328. doi:10.1111/j.1749-6632.1997.tb51929.x de Waal, F. B. M., & Brosnan, S. F. (2006). Simple and complex reciprocity in primates. In P. M. Kappeler & C. P. van Schaik (Eds.), *Cooperation in Primates and Humans: Mechanisms and Evolution* (pp. 85-105). Berlin, Heidelberg: Springer.

de Waal, F. B. M., Leimgruber, K., & Greenberg, A. R. (2008). Giving is self-rewarding for monkeys. *Proceedings of the National Academy of Sciences of the United States of America, 105*(36), 13685-13689. doi:10.1073/pnas.0807060105

de Waal, F. B. M., & Suchak, M. (2010). Prosocial primates: selfish and unselfish motivations. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1553), 2711-2722. doi:10.1098/rstb.2010.0119

de Waal, F. B. M., & van Roosmalen, A. (1979). Reconciliation and consolation among chimpanzees. *Behavioural Ecology and Sociobiology, 5*, 55-66. doi:10.1007/BF00302695

de Waal, F. B. M., & Yoshihara, D. (1983). Reconciliation and redirected affection in rhesus monkeys. *Behaviour, 85*(3/4), 224-241. doi:10.1163/156853983X00237

Delgado, R. A., Jr., & van Schaik, C. P. (2000). The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): a tale of two islands. *Evolutionary Anthropology, 9*(5), 201-218. doi:10.1002/1520-6505(2000)9:5<201::AID-EVAN2>3.0.CO;2-Y

Dovidio, J. F., Piliavin, J. A., Schroeder, D. A., & Penner, L. A. (2006). *The Social Psychology of Prosocial Behavior*. Mahwah, NJ: Lawrence Erlbaum Associates Inc.

Drea, C. M., & Carter, A. N. (2009). Cooperative problem solving in a social carnivore. *Animal Behaviour, 78*, 967-977. doi:10.1016/j.anbehav.2009.06.030

Duboscq, J., Agil, M., Engelhardt, A., & Thierry, B. (2014). The function of postconflict interactions: New prospects from the study of a tolerant species of primate. *Animal Behaviour, 87*, 107-120. doi:10.1016/j.anbehav.2013.10.018

Dufour, V., Pele, M., Neumann, M., Thierry, B., & Call, J. (2009). Calculated reciprocity after all: computation behind token transfers in orang-utans. *Biology Letters, 5*(2), 172-175. doi:10.1098/rsbl.2008.0644

Dunbar, R. I. M. (1988). Evolution of grouping patterns *Primate Social Systems* (pp. 106-150). Boston, MA: Springer US.

Dunbar, R. I. M., & Shultz, S. (2010). Bondedness and sociality. *Behaviour, 147*(7), 775-803. doi:10.1163/000579510x501151

Edwards, S. D., & Snowdon, C. T. (1980). Social behavior of captive, group-living orang-utans. *International Journal of Primatology, 1*(1), 39-62. doi:10.1007/BF02692257

Eisenberg, N., Fabes, R. A., & Spinrad, T. L. (2007). Prosocial development *Handbook of Child Psychology* (Vol. 3, pp. 646-718): John Wiley & Sons, Inc.

Eisenberg, N., & Mussen, P. H. (1989). *The Roots of Prosocial Behavior in Children*. Cambridge: Cambridge University Press.

Emery Thompson, M. (2009). Human rape: revising evolutionary perspectives. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual Coercion in Primates and Humans. An Evolutionary Perspective on Male Aggression Against Females* (pp. 346-376). Boston: Harvard University Press.

Eppley, T. M., Suchak, M., Crick, J., & de Waal, F. B. M. (2013). Perseverance and food sharing among closely affiliated female chimpanzees. *Primates, 54*(4), 319-324. doi:10.1007/s10329-013-0374-2

Fehr, E., Bernhard, H., & Rockenbach, B. (2008). Egalitarianism in young children. *Nature, 454*(7208), 1079-1083. doi:10.1038/nature07155

Feistner, A. T. C., & McGrew, W. C. (1989). Food-sharing in primates: a critical review. In P. K. Seth & S. Seth (Eds.), *Perspectives in Primate Biology* (Vol. 3, pp. 21-36). New Delhi: Today's and Tomorrow's Printers & Publishers.

Flack, J. C., Girvan, M., de Waal, F. B. M., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature, 439*. doi:10.1038/nature04326

Fletcher, G. E., Warneken, F., & Tomasello, M. (2012). Differences in cognitive processes underlying the collaborative activities of children and chimpanzees. *Cognitive Development, 27*(2), 136-153. doi:10.1016/j.cogdev.2012.02.003

Fox, E. A. (2002). Female tactics to reduce sexual harassment in the Sumatran orangutan (*Pongo pygmaeus abelii*). *Behavioral Ecology and Sociobiology, 52*(2), 93-101. doi:10.1007/s00265-002-0495-x

Fox, J., & Weisberg, S. (2011). *An {R} companion to applied regression* Retrieved from http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Fraser, O. N., & Aureli, F. (2008). Reconciliation, consolation and postconflict behavioral specificity in chimpanzees. *American Journal of Primatology, 70*(12), 1114-1123. doi:10.1002/ajp.20608

Fraser, O. N., & Bugnyar, T. (2011). Ravens reconcile after aggressive conflicts with valuable partners. *PLoS One, 6*(3). doi:10.1371/journal.pone.0018118

Fraser, O. N., Stahl, D., & Aureli, F. (2008). Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America, 105*(25), 8557-8562. doi:10.1073/pnas.0804141105

Fraser, O. N., Stahl, D., & Aureli, F. (2010). The function and determinants of reconciliation in *Pan troglodytes*. *International Journal of Primatology, 31*(1), 39-57. doi:10.1007/s10764-009-9377-7

Freidin, E., Carballo, F., & Bentosela, M. (2015). Direct reciprocity in animals: the roles of bonding and affective processes. *International Journal of Psychology*. doi:10.1002/ijop.12215

Fruth, B., & Hohmann, G. (2002). How bonobos handle hunts and harvests: why share food? In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural Diversity in Chimpanzees and Bonobos* (pp. 231-243). New York: Cambridge University Press.

Fry, D. P. (2000). Conflict management in cross-cultural perspective. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 334-351). Berkeley, CA, US: University of California Press.

Fujisawa, K. K., Kutsukake, N., & Hasegawa, T. (2005). Reconciliation pattern after aggression among Japanese preschool children. *Aggressive Behavior, 31*(2), 138-152. doi:10.1002/ab.20076

Furuichi, T., & Ihobe, H. (1994). Variation in male relationships in bonobos and chimpanzees. *Behaviour, 130*(3/4), 211-228. doi:10.1163/156853994X00532

Gamer, M., Lemon, J., Fellows, I., & Puspendra, S. (2012). irr: various coefficients to interrater reliability and agreement (Version R package 0.84). Retrieved from http://www.r-project.org

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Animal Behaviour, 71*(4), 953-963. doi:10.1016/j.anbehav.2005.09.009

Gomes, C. M., & Boesch, C. (2009). Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS One, 4*(4), e5116. doi:10.1371/journal.pone.0005116

Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B-Biological Sciences, 276*(1657), 699-706. doi:10.1098/rspb.2008.1324

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge: Harvard University Press.

Goossens, B., Chikhi, L., Jalil, M. F., James, S., Ancrenaz, M., Lackman-Ancrenaz, I., & Bruford, M. W. (2009). Taxonomy, geographic variation and population genetics of Bornean and Sumatran orangutans. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 1-13). New York: Oxford University Press.

Grammer, K. (1992). Intervention in conflicts among children: contexts and consequences. In A. H. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and Alliances in Humans and Other Animals* (pp. 258-283). Oxford: Oxford University Press.

Groves, C. P. (2001). *Primate Taxonomy*. Washington DC: Smithsonian Institution Press.

Günsoy, C., Cross, S. E., Uskul, A. K., Adams, G., & Gercek-Swing, B. (2015). Avoid or fight back? Cultural differences in responses to conflict and the role of collectivism, honor, and enemy perception. *Journal of Cross-Cultural Psychology, 46*(8), 1081-1102. doi:10.1177/0022022115594252

Gurven, M. (2004). To give and to give not: The behavioral ecology of human food transfers. *Behavioral and Brain Sciences, 27*, 543-589. doi:10.1017/S0140525X04000123

Gurven, M. (2006). The evolution of contingent cooperation. *Current Anthropology, 47*(1), 185-192. doi:10.1086/499552

Gurven, M., & Hill, K. (2009). Why do men hunt? A reevaluation of "man the hunter" and the sexual division of labor. *Current Anthropology, 50*(1), 51-74. doi:10.1086/595620

Gurven, M., & Jaeggi, A. V. (2015). Food sharing. In R. Scott & S. Kosslyn (Eds.), *Emerging Trends in the Social and Behavioral Sciences* (pp. 1-12). Hoboken, NJ: John Wiley & Sons Inc.

Hall, K., & Brosnan, S. F. (2016). A comparative perspective on the evolution of moral behavior. In T. K. S. R. D. Hansen (Ed.), *The Evolution of Morality* (pp. 157-176). Cham, Switzerland: Springer International Publishing.

Hamburg, M. E., Finkenauer, C., & Schuengel, C. (2014). Food for love: the role of food offering in empathic emotion regulation. *Frontiers in Psychology, 5*. doi:10.3389/fpsyg.2014.00032

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I & II. *Journal of Theoretical Biology, 7*(1), 1-52. doi:10.1016/0022-5193(64)90038-4 and 10.1016/0022-5193(64)90039-6

Harcourt, A. H., & de Waal, F. B. M. (1992). *Coalitions and Alliances in Humans and Other Animals*. Oxford: Oxford University Press.

Hardus, M. E., Lameira, A. R., Zulfa, A., Atmoko, S. S. U., de Vries, H., & Wich, S. A. (2012). Behavioral, ecological, and evolutionary aspects of meat-eating by Sumatran orangutans (*Pongo abelii*). *International Journal of Primatology, 33*(2), 287-304. doi:10.1007/s10764-011-9574-z

Hare, B., & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology, 20*(5), R230-R231. doi:10.1016/j.cub.2009.12.038

Hausfater, G. (1976). Predatory behavior of yellow baboons. *Behaviour, 56*(1), 44-67. doi:10.1163/156853976X00299

Hawkes, K. (1991). Showing off: Tests of an hypothesis about men's foraging goals. *Ethology & Sociobiology, 12*(1), 29-54. doi:10.1016/0162-3095(91)90011-E

Hay, D. F. (1994). Prosocial development. *Journal of Child Psychology and Psychiatry and Allied Disciplines, 35*(1), 29-71. doi:10.1111/j.1469-7610.1994.tb01132.x

Hector, D. P. (1986). Cooperative hunting and its relationship to foraging success and prey size in an avian predator. *Ethology, 73*(3), 247-257. doi:10.1111/j.1439-0310.1986.tb00915.x

Heesen, M., Rogahn, S., Macdonald, S., Ostner, J., & Schuelke, O. (2014). Predictors of food-related aggression in wild Assamese macaques and the role of conflict avoidance. *Behavioral Ecology and Sociobiology, 68*(11), 1829-1841. doi:10.1007/s00265-014-1792-x

Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences, 33*, 61-135. doi:10.1017/S0140525X0999152X

Hill, K., & Gurven, M. (2004). Economic experiments to examine fairness and cooperation among the Ache Indians of Paraguay. In J. Henrich, R. Boyd, S. Bowles, C. Camerer, E. Fehr, & H. Gintis (Eds.), *Foundations of Human Sociality* (pp. 382-412). New York, NY, US: Oxford University Press.

Hill, K., & Hurtado, A. M. (2009). Cooperative breeding in South American hunter-gatherers. *Proceedings of the Royal Society B: Biological Sciences, 276*(1674), 3863-3870. doi:10.1098/rspb.2009.1061

Hirata, S., & Celli, M. L. (2003). Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. *Animal Cognition, 6*(4), 235-244. doi:10.1007/s10071-003-0187-6

Hockings, K. J., Humle, T., Anderson, J. R., Biro, D., Sousa, C., Ohashi, G., & Matsuzawa, T. (2007). Chimpanzees share forbidden fruit. *PLoS One, 2*(9), e886. doi:10.1371/journal.pone.0000886

Hoelzel, A. R. (1991). Killer whale predation on marine mammals at Punta Norte, Argentina; food sharing, provisioning and foraging strategy. *Behavioral Ecology and Sociobiology, 29*(3), 197-204. doi:10.1007/bf00166401

Hohmann, G., & Fruth, B. (2008). New records on prey capture and meat eating by bonobos at Lui Kotale, Salonga National Park, Democratic Republic of Congo. *Folia Primatologica, 79*(2), 103-110. doi:10.1159/000110679

Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. M. (2011). Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America, 108*(33), 13847-13851. doi:10.1073/pnas.1111088108

Hothorn, T., & Hornik, K. (2015). exactRankTests: exact distributions for rank and permutation tests (Version R package 0.8-28). Retrieved from https://CRAN.R-project.org/package=exactRankTests

Husson, S. J., Wich, S. A., Marshall, A. J., Dennis, R. D., Ancrenaz, M., Brassey, R., . . . Simorangkir, T. (2009). Orangutan distribution, density, abundance and impacts of disturbance. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 77-96). New York: Oxford University Press.

The IUCN Red List of Threatened Species. Version 2016-2. Retrieved from www.iucnredlist.org. Downloaded on 22 July 2016

Jaeggi, A. V., Burkart, J. M., & van Schaik, C. P. (2010). On the psychology of cooperation in humans and other primates: combining the natural history and experimental evidence of prosociality. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1553), 2723-2735. doi:10.1098/rstb.2010.0118

Jaeggi, A. V., de Groot, E., Stevens, J. M. G., & van Schaik, C. P. (2013). Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior, 34*(2), 69-77. doi:10.1016/j.evolhumbehav.2012.09.005

Jaeggi, A. V., Dunkel, L. P., van Noordwijk, M. A., Wich, S. A., Sura, A. A. L., & van Schaik, C. P. (2010a). Social learning of diet and foraging skills among wild immature Bornean orangutans (*Pongo pygmaeus wurmbii*): implications for culture. *American Journal of Primatology, 72*, 62-71. doi:10.1002/ajp.20752

Jaeggi, A. V., Dunkel, L. P., van Noordwijk, M. A., Wich, S. A., Sura, A. A. L., & van Schaik, C. P. (2010b). Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *American Journal of Primatology, 72*(1), 62-71. doi:10.1002/Ajp.20752

Jaeggi, A. V., & Gurven, M. (2013a). Natural cooperators: food sharing in humans and other primates. *Evolutionary Anthropology, 22*(4), 186-195. doi:10.1002/evan.21364

Jaeggi, A. V., & Gurven, M. (2013b). Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: a phylogenetic meta-analysis. *Proceedings of the Royal Society B-Biological Sciences, 280*(1768), 20131615. doi:10.1098/rspb.2013.1615

Jaeggi, A. V., Stevens, J. M. G., & van Schaik, C. P. (2010). Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. *American Journal of Physical Anthropology, 143*(1), 41-51. doi:10.1002/ajpa.21288

Jaeggi, A. V., van Noordwijk, M. A., & van Schaik, C. P. (2008). Begging for information: mother-offspring food sharing among wild Bornean orangutans. *American Journal of Primatology, 70*(6), 533-541. doi:10.1002/ajp.20525

Jaeggi, A. V., & van Schaik, C. P. (2011). The evolution of food sharing in primates. *Behavioral Ecology and Sociobiology, 65*(11), 2125-2140. doi:10.1007/s00265-011-1221-3

Janson, C. H. (1988). Intra-specific food competition and primate social structure: a synthesis. *Behaviour, 105*(1/2), 1-17. doi:10.1163/156853988X00412

Jantschke, F. (1972). *Orang-Utans in Zoologischen Gärten*. München: R. Piper & Co. Verlag.

Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are rational maximizers in an ultimatum game. *Science, 318*(5847), 107-109. doi:10.1126/science.1145850

Johnson-Pynn, J., Fragaszy, D. M., & Cummins-Sebree, S. (2003). Common territories in comparative and developmental psychology: Quest for shared means and meaning in behavioral investigations. *International Journal of Comparative Psychology, 16*, 1-27.

Judge, P. G. (2000). Coping with crowded conditions. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 129-154). Berkeley, CA, US: University of California Press.

Judge, P. G. (2003). Conflict resolution. In D. Maestripieri (Ed.), *Primate Psychology* (pp. 41-68). Cambridge, MA, US: Harvard University Press.

Judge, P. G., & de Waal, F. B. M. (1993). Conflict avoidance among rhesus monkeys: Coping with short-term crowding. *Animal Behaviour, 46*, 221-232. doi:10.1006/anbe.1993.1184

Judge, P. G., & de Waal, F. B. M. (1997). Rhesus monkey behaviour under diverse population densities: coping with long-term crowding. *Animal Behaviour, 54*(3), 643-662. doi:10.1006/anbe.1997.0469

Kaplan, H., & Gurven, M. (2005). The natural history of human food sharing and cooperation: A review and a new multi-individual approach ot the negotiation of norms. In H. Gintis, S. Bowles, R. Boyd, & E. Fehr (Eds.), *Moral Sentiments and Material Interests: The Foundations of Cooperation in Economic Life* (pp. 75-113). Cambridge, Massachusetts: MIT Press.

Kaplan, H. S., Hooper, P. L., & Gurven, M. (2009). The evolutionary and ecological roots of human social organization. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1533), 3289-3299. doi:10.1098/rstb.2009.0115

Kappeler, P. M., & van Schaik, C. P. (1992). Methodological and evolutionary aspects of reconciliation among primates. *Ethology, 92*, 51-69. doi:10.1111/j.1439-0310.1992.tb00948.x

Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology, 23*(4), 707-740. doi:10.1023/A:1015520830318

Kawanaka, K. (1982). Further studies on predation by chimpanzees of the Mahale Mountains. *Primates, 23*(3), 364-384. doi:10.1007/BF02381320

Kim, Y., Martinez, L., Choe, J. C., Lee, D.-J., & Tomonaga, M. (2015). Orangutans (*Pongo* spp.) do not spontaneously share benefits with familiar conspecifics in a choice paradigm. *Primates, 56*(2), 193-200. doi:10.1007/s10329-015-0460-8

Knott, C. D. (2009). Orangutans: Sexual coercion without sexual violence. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual Coercion in Primates and Humans. An Evolutionary Perspective on Male Aggression Against Females* (pp. 81-111). Boston: Harvard University Press.

Kopp, K. S., & Liebal, K. (2016). Here you are!—Selective and active food sharing within and between groups in captive Sumatran orangutans (*Pongo abelii*). *Behavioral Ecology and Sociobiology, 70*(8), 1219-1233. doi:10.1007/s00265-016-2130-2

Koski, S. E., Koops, K., & Sterck, E. H. M. (2007). Reconciliation, relationship quality, and postconflict anxiety: Testing the integrated hypothesis in captive chimpanzees. *American Journal of Primatology, 69*(2), 158-172. doi:10.1002/ajp.20338

Koski, S. E., & Sterck, E. H. M. (2007). Triadic postconflict affiliation in captive chimpanzees: does consolation console? *Animal Behaviour, 73*(1), 133-142. doi:10.1016/j.anbehav.2006.04.009

Koski, S. E., & Sterck, E. H. M. (2009). Post-conflict third-party affiliation in chimpanzees: What's in it for the third party? *American Journal of Primatology, 71*(5), 409-418. doi:10.1002/ajp.20668

Koyama, N. F., Caws, C., & Aureli, F. (2006). Interchange of grooming and agonistic support in chimpanzees. *International Journal of Primatology, 27*(5). doi:10.1007/s10764-006-9074-8

Kramer, K. L. (2011). The evolution of human parental care and recruitment of juvenile help. *Trends in Ecology & Evolution, 26*(10), 533-540. doi:10.1016/j.tree.2011.06.002

Krueger, K., Schneider, G., Flauger, B., & Heinze, J. (2015). Context-dependent third-party intervention in agonistic encounters of male Przewalski horses. *Behavioural Processes, 121*, 54-62. doi:10.1016/j.beproc.2015.10.009

Kummer, H. (1978). On the value of social relationships in nonhuman primates: A heuristic scheme. *Social Science Information, 17*, 687-705. doi:10.1177/053901847801700418

Kuroda, S. (1984). Interaction over food among pygmy chimpanzees. In R. Susman (Ed.), *The Pygmy Chimpanzee* (pp. 301-324): Springer US.

Kuroda, S., Suzuki, S., & Nishihara, T. (1996). Preliminary report on predatory behavior and meat sharing in Tschego chimpanzees (*Pan troglodytes troglodytes*) in the Ndoki Forest, northern Congo. *Primates, 37*(3), 253-259. doi:10.1007/bf02381857

Kutsukake, N., & Castles, D. L. (2004). Reconciliation and post-conflict third-party affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates, 45*(3), 157-165. doi:10.1007/s10329-004-0082-z

Lakshminarayanan, V. R., & Santos, L. R. (2008). Capuchin monkeys are sensitive to others' welfare. *Current Biology, 18*(21), R999-R1000. doi:10.1016/j.cub.2008.08.057

Lamprecht, J. (1978). Diet, foraging behavior and interspecific food competition of jackals in Serengeti-National-Park, East-Africa. *Zeitschrift für Säugetierkunde, 43*(4), 210-223.

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology, 71*(10), 840-851. doi:10.1002/ajp.20711

Leone, A., & Palagi, E. (2010). Reconciling conflicts in a one-male society: the case of geladas (*Theropithecus gelada*). *Primates, 51*, 203-212. doi:10.1007/s10329-010-0188-4

Liebal, K., & Haun, D. B. M. (2012). The importance of comparative psychology for developmental science. *International Journal of Developmental Science, 6*, 21-23. doi:10.3233/DEV-2012-11088

Liebal, K., Pika, S., & Tomasello, M. (2006). Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture, 6*(1), 1-38. doi:10.1075/gest.6.1.02lie

Liebal, K., Vaish, A., Haun, D. B. M., & Tomasello, M. (2014). Does sympathy motivate prosocial behaviour in great apes? *PLoS One, 9*(1), e84299. doi:10.1371/journal.pone.0084299

Ljungberg, T., Horowitz, L., Jansson, L., Westlund, K., & Clarke, C. (2005). Communicative factors, conflict progression, and use of reconciliatory strategies in pre-school boys: A series of random events or a sequential process? *Aggressive Behavior, 31*(4), 303-323. doi:10.1002/ab.20068

Locke, D. P., Hillier, L. W., Warren, W. C., Worley, K. C., Nazareth, L. V., Muzny, D. M., . . . Wilson, R. K. (2011). Comparative and demographic analysis of orang-utan genomes. *Nature, 469*(7331), 529-533. doi:10.1038/nature09687

Logan, C. J., Emery, N. J., & Clayton, N. S. (2013). Alternative behavioral measures of postconflict affiliation. *Behavioral Ecology, 24*(1), 98-112. doi:10.1093/beheco/ars140

Lonsdorf, E. V. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition, 9*(1), 36-46. doi:10.1007/s10071-005-0002-7|ISSN 1435-9448

Lorenz, K. (1963). *Das sogenannte Böse. Zur Naturgeschichte der Aggression*. Wien: Dr. G. Borotha-Schoeler Verlag.

MacKinnon, J. (1974). The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Animal Behaviour, 22*, 3-74. doi:10.1016/S0003-3472(74)80054-0

Maechler et al. (2016). sfsmisc: Utilities from "Seminar fuer Statistik" ETH Zurich (Version R package version 1.1-0). Retrieved from https://CRAN.R-project.org/package=sfsmisc

Maestripieri, D. (2002). Parent-offspring conflict in primates. *International Journal of Primatology, 23*(4), 923-951. doi:10.1023/A:1015537201184

Mallavarapu, S., Stoinski, T. S., Bloomsmith, M. A., & Maple, T. L. (2006). Postconflict behavior in captive western lowland gorillas (*Gorilla gorilla gorilla*). *American Journal of Primatology, 68*(8), 789-801. doi:10.1002/ajp.20279

Manson, J. H., Perry, S., & Stahl, D. (2005). Reconciliation in wild white-faced capuchins (*Cebus capucinus*). *American Journal of Primatology, 65*(3), 205-219. doi:10.1002/ajp.20110

Maple, T. L. (1980). *Orangutan Behavior*. New York: Van Nostrand-Reinhold.

Marlowe, F. W., Berbesque, J. C., Barrett, C., Bolyanatz, A., Gurven, M., & Tracer, D. (2011). The 'spiteful' origins of human cooperation. *Proceedings of the Royal Society B: Biological Sciences, 278*(1715), 2159-2164. doi:10.1098/rspb.2010.2342

Marshall-Pescini, S., Dale, R., Quervel-Chaumette, M., & Range, F. (2016). Critical issues in experimental studies of prosociality in non-human species. *Animal Cognition*. doi:10.1007/s10071-016-0973-6

Marshall, A. J., Lacy, R. C., Ancrenaz, M., Byers, O., Husson, S. J., Leighton, M., . . . Stephens, S. (2009). Orangutan population biology, life history, and conservation. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 311-326). New York: Oxford University Press.

Martin, A., & Olson, K. R. (2015). Beyond good and evil: What motivations underlie children's prosocial behavior? *Perspectives on Psychological Science, 10*(2), 159-175. doi:10.1177/1745691615568998

Martin, P., & Bateson, P. (2007). *Measuring Behaviour. An Introductory Guide*. Cambridge: Cambridge University Press.

Marzec, A. M., Kunz, J. A., Falkner, S., Atmoko, S. S. U., Alavi, S. E., Moldawer, A. M., . . . van Noordwijk, M. A. (2016). The dark side of the red ape: male-mediated lethal female competition in Bornean orangutans. *Behavioral Ecology and Sociobiology, 70*(4), 459-466. doi:10.1007/s00265-015-2053-3

Massen, J. J. M., Luyten, I. J. A. F., Spruijt, B. M., & Sterck, E. H. M. (2011). Benefiting friends or dominants: prosocial choices mainly depend on rank position in long-tailed macaques (*Macaca fascicularis*). *Primates, 52*, 237-247. doi:10.1007/s10329-011-0244-8

Matsumura, S. (1996). Postconflict affiliative contacts between former opponents among wild moor macaques (*Macaca maurus*). *American Journal of Primatology, 38*(3), 211-219. doi:10.1002/(SICI)1098-2345(1996)38:3<211::AID-AJP2>3.0.CO;2-1

Maynard Smith, J. (1964). Group selection and kin selection. *Nature, 201*(4924), 1145-1147. doi:10.1038/2011145a0

McFarland, R., & Majolo, B. (2012). The occurrence and benefits of postconflict bystander affiliation in wild Barbary macaques, *Macaca sylvanus*. *Animal Behaviour, 84*(3), 583-591. doi:10.1016/j.anbehav.2012.06.010

McGrew, W. C. (1975). Patterns of plant food sharing by wild chimpanzees. In S. Kondo, M. Kawai, & A. Ehara (Eds.), *Contemporary Primatology, Proceedings of the Fifth International Congress of Primatology* (pp. 304-309). Basel: S. Karger.

Melis, A. P., & Semmann, D. (2010). How is human cooperation different? *Philosophical Transactions of the Royal Society B-Biological Sciences, 365*(1553), 2663-2674. doi:10.1098/rstb.2010.0157

Melis, A. P., Warneken, F., Jensen, K., Schneider, A.-C., Call, J., & Tomasello, M. (2011). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society B-Biological Sciences, 278*(1710), 1405-1413. doi:10.1098/rspb.2010.1735

Mills, M. G. L. (1985). Related spotted hyaenas forage together but do not cooperate in rearing young. *Nature*. doi:10.1038/316061a0

Mitani, J. C. (2006). Reciprocal exchange in chimpanzees and other primates. In P. M. Kappeler & C. P. van Schaik (Eds.), *Cooperation in Primates and Humans: Mechanisms and Evolution* (pp. 107-119). New York: Springer.

Mitani, J. C. (2009a). Cooperation and competition in chimpanzees: current understanding and future challenges. *Evolutionary Anthropology, 18*(5), 215-227. doi:10.1002/evan.20229

Mitani, J. C. (2009b). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour, 77*(3), 633-640. doi:10.1016/j.anbehav.2008.11.021

Mitani, J. C., Grether, G. F., Rodman, P. S., & Priatna, D. (1991). Associations among wild orangutans - sociality, passive aggregations or chance. *Animal Behaviour, 42*, 33-46. doi:10.1016/S0003-3472(05)80603-7

Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour, 61*(5), 915-924. doi:10.1006/anbe.2000.1681

Mitani, J. C., & Watts, D. P. (2005). Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Animal Behaviour, 70*, 1079-1086. doi:10.1016/j.anbehav.2005.02.012

Mitra Setia, T., Delgado, R. A., Utami Atmoko, S. S., Singleton, I., & van Schaik, C. P. (2009). Social organization and male-female relationships. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 245-253). New York: Oxford University Press.

Muller, M. N., Kahlenberg, S. M., Thompson, M. E., & Wrangham, R. W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society B-Biological Sciences, 274*(1612), 1009-1014. doi:10.1098/rspb.2006.0206

Muller, M. N., Kahlenberg, S. M., & Wrangham, R. W. (2009). Male Aggression and Sexual Coercion of Females in Primates. In N. Muller Martin & W. Wrangham Richard (Eds.), *Sexual Coercion in Primates and Humans. An Evolutionary Perspective on Male Aggression Against Females* (pp. 3-22). Boston: Harvard University Press.

Muller, M. N., Thompson, M. E., Kahlenberg, S. M., & Wrangham, R. W. (2011). Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behavioral Ecology and Sociobiology, 65*(5), 921-933. doi:10.1007/s00265-010-1093-y

Muller, M. N., & Wrangham, R. W. (Eds.). (2009). *Sexual Coercion in Primates and Humans, An Evolutionary Perspective on Male Aggression Against Females*. Boston: Harvard University Press.

Nadler, R. D., Galdikas, B. F. M., Sheeran, L. K., & Rosen, N. (Eds.). (1995). *The Neglected Ape*. New York: Plenum Press.

Nakamura, M., & Itoh, N. (2002). Plant food sharing among wild chimpanzees: two cases from Mahale, Tanzania. *Anthropological Science, 110*(1), 90.

Newton-Fisher, N. E. (2006). Female coalitions against male aggression in wild chimpanzees of the Budongo forest. *International Journal of Primatology, 27*(6), 1589-1599. doi:10.1007/s10764-006-9087-3

Nieuwenhuijsen, K., & de Waal, F. B. M. (1982). Effects of spatial crowding on social behavior in a chimpanzee colony. *Zoo Biology, 1*(1), 5-28. doi:10.1002/zoo.1430010103

Nieuwenhuis, R., te Grotenhuis, M., & Pelzer, B. (2012). Influence.ME: tools for detecting influential data in mixed effects models. *R Journal, 4*(2), 38-47. http://hdl.handle.net/2066/103101

Nishida, T. (1970). Social behavior and relationship among wild chimpanzees of the Mahali mountains. *Primates, 11*, 47-87. doi:10.1007/BF01730675

Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y., & Uehara, S. (1992). Meat-sharing as a coalition strategy by an alpha male chimpanzee. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. B. M. de Waal (Eds.), *Topics in primatology* (Vol. 1.: Human Origins, pp. 159-174). Tokyo: Tokyo University Press.

Nishida, T., Uehara, S., & Nyundo, R. (1979). Predatory behavior among wild chimpanzees of the Mahale Mountains. *Primates, 20*, 1-20. doi:10.1007/BF02373826

Nolin, D. A. (2012). Food-sharing networks in Lamalera, Indonesia: Status, sharing, and signaling. *Evolution and Human Behavior, 33*(4), 334-345. doi:10.1016/j.evolhumbehav.2011.11.003

Novak, M. A., Oneill, P., & Suomi, S. J. (1992). Adjustments and adaptations to indoor and outdoor environments: Continuity and change in young adult rhesus monkeys. *American Journal of Primatology, 28*(2), 125-138. doi:10.1002/ajp.1350280205

Ohbuchi, K.-I., Fukushima, O., & Tedeschi, J. T. (1999). Cultural values in conflict management: goal orientation, goal attainment, and tactical decision. *Journal of Cross-Cultural Psychology, 30*(1), 51-71. doi:10.1177/0022022199030001003

Opsahl, T. (2009). *Structure and Evolution of Weighted Networks.* University of London (Queen Mary College), London, UK. Retrieved from http://toreopsahl.com/publications/thesis/

Packer, C., & Pusey, A. E. (1982). Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature, 296*, 740-742. doi:10.1038/296740a0

Packer, C., & Ruttan, L. (1988). The evolution of cooperative hunting. *The American Naturalist, 132*, 159-198. doi:10.1086/284844

Palagi, E., Cordoni, G., & Borgognini Tarli, S. (2006). Possible roles of consolation in captive chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology, 129*(1), 105-111. doi:10.1002/ajpa.20242

Palagi, E., & Norscia, I. (2013). Bonobos protect and console friends and kin. *PLoS One, 8*(11). doi:10.1371/journal.pone.0079290

Palagi, E., Paoli, T., & Borgognini Tarli, S. (2004). Reconciliation and consolation in captive bonobos (*Pan paniscus*). *American Journal of Primatology, 62*(1), 15-30. doi:10.1002/ajp.20000

Palagi, E., Paoli, T., & Borgognini Tarli, S. (2006). Short-term benefits of play behavior and conflict prevention in *Pan paniscus*. *International Journal of Primatology, 27*(5), 1257-1270. doi:10.1007/s10764-006-9071-y

Pelé, M., Dufour, V., Thierry, B., & Call, J. (2009). Token transfers among great apes (*Gorilla gorilla*, *Pongo pygmaeus*, *Pan paniscus*, and *Pan troglodytes*): species differences, gestural requests, and reciprocal exchange. *Journal of Comparative Psychology, 123*(4), 375-384. doi:10.1037/a0017253

Penate, L., Pelaez, F., & Sanchez, S. (2009). Reconciliation in captive cotton-top tamarins (*Saguinus oedipus*), a cooperative breeding primate. *American Journal of Primatology, 71*(11), 895-900. doi:10.1002/ajp.20721

Penner, L. A., Dovidio, J. F., Piliavin, J. A., & Schroeder, D. A. (2005). Prosocial behavior: multilevel perspectives. *Annual Review of Psychology, 56*, 365-392. doi:10.1146/annurev.psych.56.091103.070141

Penner, L. A., & Finkelstein, M. A. (1998). Dispositional and structural determinants of volunteerism. *J Pers Soc Psychol, 74*(2), 525.

Pereira, M. E., & Kappeler, P. M. (2000). Divergent social patterns in two primitive primates. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 318-320, Box 315.312). Berkeley, CA, US: University of California Press.

Petit, O., & Thierry, B. (1994). Aggressive and peaceful interventions in conflicts in Tonkean macaques. *Animal Behaviour, 48*, 1427-1436. doi:10.1006/anbe.1994.1378

Petit, O., & Thierry, B. (2000). Do impartial interventions in conflicts occur in monkeys and apes? In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 267-269, Box 213.261). Berkeley, CA, US: University of California Press.

Pika, S., Liebal, K., Call, J., & Tomasello, M. (2005). The gestural communication of apes. *Gesture, 5*(1-2), 41-56. doi:10.1075/gest.5.1.05pik

Poole, T. B. (1987). Social behavior of a group of orangutans (*Pongo pygmaeus*) on an artificial island in Singapore Zoological Gardens. *Zoo Biology, 6*, 315-330. doi:10.1002/zoo.1430060406

Preuschoft, S., & van Schaik, C. P. (2000). Dominance and communication: conflict management in various social settings. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 77-105). Berkeley, CA, US: University of California Press.

Preuschoft, S., Wang, X., Aureli, F., & de Waal, F. B. M. (2002). Reconciliation in captive chimpanzees: A reevaluation with controlled methods. *International Journal of Primatology, 23*(1), 29-50. doi:10.1023/A:1013293623158

Proctor, D., Williamson, R. A., de Waal, F. B. M., & Brosnan, S. F. (2013). Chimpanzees play the ultimatum game. *Proceedings of the National Academy of Sciences of the United States of America, 110*(6), 2070-2075. doi:10.1073/pnas.1220806110

Prüfer, K., Munch, K., Hellmann, I., Akagi, K., Miller, J. R., Walenz, B., . . . Paabo, S. (2012). The bonobo genome compared with the chimpanzee and human genomes. *Nature, 486*(7404), 527-531. doi:10.1038/nature11128

R Core Team. (2015). R: a language and environment for statistical computing (Version 3.2.2). Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

R Core Team. (2016). R: a language and environment for statistical computing (Version 3.2.4). Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rao, N., & Stewart, S. M. (1999). Cultural influences on sharer and recipient behavior: Sharing in Chinese and Indian preschool children. *Journal of Cross-Cultural Psychology, 30*(2), 219-241. doi:10.1177/0022022199030002005

Rapaport, L. G. (2001). Food transfer among adult lion tamarins: mutualism, reciprocity or one-sided relationships? *International Journal of Primatology, 22*(4), 611-629. doi:10.1023/A:1010789618761

Rekers, Y., Haun, D. B. M., & Tomasello, M. (2011). Children, but not chimpanzees, prefer to collaborate. *Current Biology, 21*(20), 1756-1758. doi:10.1016/j.cub.2011.08.066

Ren, R. M., Yan, K. H., Su, Y. J., Qi, H. J., Liang, B., Bao, W. Y., & de Waal, F. B. M. (1991). The reconciliation behavior of golden monkeys (*Rhinopithecus roxellanae roxellanae*) in small breeding groups. *Primates, 32*(3), 321-327. doi:Doi 10.1007/Bf02382673

Reynolds, V. (2005). *The Chimpanzees of the Budongo Forest: Ecology, Behaviour and Conservation*. New York: Oxford Univ Press.

Rijksen, H. D. (1978). *A Field Study on Sumatran Orang Utans (Pongo pygmaeus abelii, Lesson 1827). Ecology, Behaviour and Conservation*. Wageningen: H. Veenman & Zonen B.V.

Robbins, M. M. (2008). Feeding competition and agonistic relationships among Bwindi *Gorilla beringei*. *International Journal of Primatology, 29*, 999-1018. doi:10.1007/s10764-008-9275-4

Rochat, P., Dias, M. D. G., Liping, G., Broesch, T., Passos-Ferreira, C., Winning, A., & Berg, B. (2009). Fairness in distributive justice by 3- and 5-year-olds across seven cultures. *Journal of Cross-Cultural Psychology, 40*(3), 416-442. doi:10.1177/0022022109332844

Romero, T., & Aureli, F. (2008). Reciprocity of support in coatis (*Nasua nasua*). *Journal of Comparative Psychology, 122*(1), 19-25. doi:10.1037/0735-7036.122.1.19

Romero, T., Colmenares, F., & Aureli, F. (2008). Postconflict affiliation of aggressors in *Papio hamadryas*. *International Journal of Primatology, 29*, 1591–1606. doi:10.1007/s10764-008-9315-0

Romero, T., & de Waal, F. B. M. (2010). Chimpanzee (*Pan troglodytes*) consolation: third-party identity as a window on possible function. *Journal of Comparative Psychology, 124*(3), 278-286. doi:10.1037/a0019144

Rose, L. M. (1997). Vertebrate predation and food-sharing in *Cebus* and *Pan*. *International Journal of Primatology, 18*(5), 727-765. doi:10.1023/A:1026343812980

Roseth, C. J., Pellegrini, A. D., Dupuis, D. N., Bohn, C. M., Hickey, M. C., Hilk, C. L., & Peshkam, A. (2011). Preschoolers' bistrategic resource control, reconciliation, and peer regard. *Social Development, 20*(1), 185-211. doi:10.1111/j.1467-9507.2010.00579.x

Rossano, F., & Liebal, K. (2014). "Requests" and "offers" in orangutans and human infants. In P. Drew & E. Couper-Kuhlen (Eds.), *Requesting in Social Interaction* (pp. 335-364): John Benjamins Publishing Company.

Rudolf von Rohr, C., Burkart, J. M., & van Schaik, C. P. (2011). Evolutionary precursors of social norms in chimpanzees: a new approach. *Biology & Philosophy, 26*(1), 1-30. doi:10.1007/s10539-010-9240-4

Rudolf von Rohr, C., Koski, S. E., Burkart, J. M., Caws, C., Fraser, O. N., Ziltener, A., & van Schaik, C. P. (2012). Impartial third-party interventions in captive chimpanzees: A reflection of community concern. *PLoS One, 7*(3). doi:10.1371/journal.pone.0032494

Sabbatini, G., Vizioli, A. D., Visalberghi, E., & Schino, G. (2012). Food transfers in capuchin monkeys: an experiment on partner choice. *Biology Letters, 8*(5), 757-759. doi:10.1098/rsbl.2012.0534

Schaller, G. B. (1972). *The Serengeti lion*. Chicago: University of Chicago Press.

Schino, G., & Aureli, F. (2008). Grooming reciprocation among female primates: a meta-analysis. *Biology Letters, 4*(1), 9-11. doi:10.1098/rsbl.2007.0506

Schino, G., & Aureli, F. (2009). Reciprocal altruism in primates: partner choice, cognition, and emotions. *Advances in the Study of Behavior, 39*, 45-69. doi:10.1016/S0065-3454(09)39002-6

Schino, G., & Aureli, F. (2010). A few misunderstandings about reciprocal altruism. *Communicative & Integrative Biology, 3*(6), 561-563. doi:10.4161/cib.3.6.12977

Schino, G., & Aureli, F. (2016). Reciprocity in group-living animals: partner control versus partner choice. *Biological Reviews*, n/a-n/a. doi:10.1111/brv.12248

Schino, G., Tiddi, B., & di Sorrentino, E. P. (2007). Agonistic support in juvenile Japanese macaques: Cognitive and functional implications. *Ethology, 113*(12), 1151-1157. doi:10.1111/j.1439-0310.2007.01426.x

Scott, J., & Lockard, J. S. (2007). Competition coalitions and conflict interventions among captive female gorillas. *International Journal of Primatology, 28*, 761–781. doi:10.1007/s10764-007-9161-5

Seyfarth, R. M., & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature, 308*, 541-543. doi:10.1038/308541a0

Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. In S. T. Fiske, D. L. Schacter, & S. E. Taylor (Eds.), *Annual Review of Psychology* (Vol. 63, pp. 153-177).

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour, 28*(4), 1070-1094. doi:10.1016/S0003-3472(80)80097-2

Shumaker, R. W., Palkovich, A. M., Beck, B. B., Guagnano, G. A., & Morowitz, H. (2001). Spontaneous use of magnitude discrimination and ordination by the orangutan (*Pongo pygmaeus*). *Journal of Comparative Psychology, 115*(4), 385-391. doi:10.1037/0735-7036.115.4.385

Silk, J. B. (1978). Patterns of food sharing among mother and infant chimpanzees at Gombe national park, Tanzania. *Folia Primatologica, 29*(2), 129-141. doi:10.1159/000155835

Silk, J. B. (1979). Feeding, foraging, and food sharing behavior of immature chimpanzees. *Folia Primatologica, 31*(1-2), 123-142. doi:10.1159/000155876

Silk, J. B. (1996). Why do primates reconcile? *Evolutionary Anthropology, 5*, 39-42. doi:10.1002/(SICI)1520-6505(1996)5:2<39::AID-EVAN2>3.0.CO;2-R

Silk, J. B. (1997). The function of peaceful post-conflict contacts among primates. *Primates, 38*(3), 265-279. doi:10.1007/BF02381614

Silk, J. B. (1998). Making amends: Adaptive perspectives on conflict remediation in monkeys, apes, and humans. *Human Nature, 9*(4), 341-368. doi:10.1007/s12110-998-1014-1

Silk, J. B. (2000). The function of peaceful post-conflict interactions. An alternative view. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 179-181, Box 179.171). Berkeley, CA, US: University of California Press.

Silk, J. B. (2002a). The form and function of reconciliation in primates. *Annual Review of Anthropology, 31*, 21-44. doi:10.1146/annurev.anthro.31.032902.101743

Silk, J. B. (2002b). Kin selection in primate groups. *International Journal of Primatology, 23*(4), 849-875. doi:10.1023/a:1015581016205

Silk, J. B. (2002c). Using the 'f'-word in primatology. *Behaviour, 139*(2/3), 421-446. doi:10.1163/156853902760102735

Silk, J. B. (2007a). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B-Biological Sciences, 362*(1480), 539-559. doi:10.1098/rstb.2006.1994

Silk, J. B. (2007b). Social components of fitness in primate groups. *Science, 317*(5843), 1347-1351. doi:10.1126/science.1140734

Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology, 61*(2), 183-195. doi:10.1007/s00265-006-0249-2

Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P., & Shapiro, S. (2013). Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour, 85*(5), 941-947. doi:10.1016/j.anbehav.2013.02.014

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., . . . Schapiro, S. J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature, 437*(7063), 1357-1359. doi:10.1038/nature04243

Silk, J. B., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology, 22*(5), 213-225. doi:10.1002/evan.21367

Silk, J. B., & House, B. R. (2011). Evolutionary foundations of human prosocial sentiments. *Proceedings of the National Academy of Sciences of the United States of America, 108 (Suppl 2)*, 10910-10917. doi:10.1073/pnas.1100305108

Singleton, I., Knott, C. D., Morrogh-Bernard, H. C., Wich, S. A., & van Schaik, C. P. (2009). Ranging behavior of orangutan females and social organization. In S. A. Wich, S. S. Utami-Atmoko, T. M. Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 205-213). New York: Oxford University Press.

Singleton, I., & van Schaik, C. P. (2002). The social organisation of a population of Sumatran orang-utans. *Folia Primatologica, 73*(1), 1-20. doi:10.1159/000060415

Skerry, A. E., Sheskin, M., & Santos, L. R. (2011). Capuchin monkeys are not prosocial in an instrumental helping task. *Animal Cognition, 14*(5), 647-654. doi:10.1007/s10071-011-0399-0

Slocombe, K. E., & Newton-Fisher, N. E. (2005). Fruit sharing between wild adult chimpanzees (*Pan troglodytes schweinfurthii*): a socially significant event? *American Journal of Primatology, 65*(4), 385-391. doi:10.1002/ajp.20123

Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior, 22*(1763), 60404-60400.

Spehar, S. N., Mathewson, P. D., Nuzuar, Wich, S. A., Marshall, A. J., Kuhl, H., . . . Meijaard, E. (2010). Estimating orangutan densities using the standing crop and marked nest count methods: Lessons learned for conservation. *Biotropica, 42*(6), 748-757. doi:10.1111/j.1744-7429.2010.00651.x

Stanford, C. B. (1992). Costs and benefits of allomothering in wild capped langurs (*Presbytis pileata*). *Behavioral Ecology and Sociobiology, 30*(1), 29-34. doi:10.1007/BF00168591

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology, 41*(5), 291-309. doi:10.1007/s002650050390

Stevens, J. R. (2004). The selfish nature of generosity: harassment and food sharing in primates. *Proceedings of the Royal Society B-Biological Sciences, 271*(1538), 451-456. doi:10.1098/rspb.2003.2625

Stevens, J. R., & Gilby, I. C. (2004). A conceptual framework for nonkin food sharing: timing and currency of benefits. *Animal Behaviour, 67*(4), 603-614. doi:10.1016/j.anbehav.2003.04.012

Stevens, J. R., & Stephens, D. W. (2002). Food sharing: a model of manipulation by harassment. *Behavioral Ecology, 13*(3), 393-400. doi:10.1093/beheco/13.3.393

Stewart, S. M., & McBride-Chang, C. (2000). Influences on children's sharing in a multicultural setting. *Journal of Cross-Cultural Psychology, 31*(3), 333-348. doi:10.1177/0022022100031003003

Stiner, M. C., Gopher, A., & Barkai, R. (2011). Hearth-side socioeconomics, hunting and paleoecology during the late Lower Paleolithic at Qesem Cave, Israel. *Journal of Human Evolution, 60*(2), 213-233. doi:10.1016/j.jhevol.2010.10.006

Strubin, C., Steinegger, M., & Bshary, R. (2011). On group living and collaborative hunting in the yellow saddle goatfish (*Parupeneus cyclostomus*). *Ethology, 117*(11), 961-969. doi:10.1111/j.1439-0310.2011.01966.x

Stumpf, R. M., Emery Thompson, M., & Knott, C. D. (2008). A comparison of female mating strategies in *Pan troglodytes* and *Pongo* spp. *International Journal of Primatology, 29*(4), 865-884. doi:10.1007/s10764-008-9284-3

Stumpf, R. M., Martinez-Mota, R., Milich, K. M., Righini, N., & Shattuck, M. R. (2011). Sexual conflict in primates. *Evolutionary Anthropology, 20*(2), 62-75. doi:10.1002/evan.20297

Sugardjito, J., & Nurhuda, N. (1981). Meat-eating behaviour in wild orang utans, *Pongo pygmaeus*. *Primates, 22*(3), 414-416. doi:10.1007/BF02381583

Tajima, T., & Kurotori, H. (2010). Nonaggressive interventions by third parties in conflicts among captive Bornean orangutans (*Pongo pygmaeus*). *Primates, 51*, 179-182. doi:10.1007/s10329-009-0180-z

Takahata, Y., Hasegawa, T., & Nishida, T. (1984). Chimpanzee predation in the Mahale mountains from August 1979 to May 1982. *International Journal of Primatology, 5*, 213-233. doi:10.1007/BF02735758

Takimoto, A., Kuroshima, H., & Fujita, K. (2010). Capuchin monkeys (*Cebus apella*) are sensitive to others' reward: an experimental analysis of food-choice for conspecifics. *Animal Cognition, 13*(2), 249-261. doi:10.1007/s10071-009-0262-8

Tan, J., & Hare, B. (2013). Bonobos share with strangers. *PLoS One, 8*(1), e51922. doi:10.1371/journal.pone.0051922

Teleki, G. (1973). *The Predatory Behavior of Wild Chimpanzees*. Lewisburg, Pennsylvania: Bucknell University Press.

Thierry, B., & Anderson, J. R. (1986). Adoption in anthropoid primates. *International Journal of Primatology, 7*(2), 191-216. doi:10.1007/BF02692318

Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C., & de Waal, F. B. M. (2008). A comparative study of conflict resolution in macaques: insights into the nature of trait covariation. *Animal Behaviour, 75*(3), 847-860. doi:10.1016/j.anbehav.2007.07.006

Thomas, E. M. (1994). Management of violence among the Ju/wasi of Nyae Nyae: the old way and the new way. In S. P. Reyna & R. E. Downs (Eds.), *Studying War: Anthropological Perspectives* (pp. 69-84). New York: Gordon & Breach.

Thorpe, S. K. S., & Crompton, R. H. (2006). Orangutan positional behavior and the nature of arboreal locomotion in Hominoidea. *American Journal of Physical Anthropology, 131*(3), 384-401. doi:10.1002/ajpa.20422

Thorpe, S. K. S., & Crompton, R. H. (2009). Orangutan positional behavior: interspecific variation and ecological correlates. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 33-47). New York: Oxford University Press.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie, 20*, 410-433. doi:10.1111/j.1439-0310.1963.tb01161.x

Tomasello, M., & Call, J. (1997). *Primate Cognition*. New York: Oxford University Press.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences, 28*(5), 675-735. doi:10.1017/S0140525X05000129

Tomasello, M., & Vaish, A. (2013). Origins of human cooperation and morality. *Annual Review of Psychology, 64*, 231-255. doi:10.1146/annurev-psych-113011-143812

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology, 46*(1), 35-57. doi:10.2307/2822435

Ueno, A., & Matsuzawa, T. (2004). Food transfer between chimpanzee mothers and their infants. *Primates, 45*(4), 231-239. doi:10.1007/s10329-004-0085-9

Utami Atmoko, S. S., Mitra Setia, T., Goossens, B., James, S. S., Knott, C. D., Morrogh-Bernard, H. C., . . . van Noordwijk, M. A. (2009). Orangutan mating behavior and strategies. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 235-244). New York: Oxford University Press.

Utami Atmoko, S. S., Singleton, I., van Noordwijk, M. A., van Schaik, C. P., & Mitra Setia, T. (2009). Male-male relationships in orangutans. In S. A. Wich, S. S. Utami-Atmoko, T. M. Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 225-234): Oxford University Press.

Utami, S. S., Goossens, B., Bruford, M. W., de Ruiter, J. R., & van Hooff, J. A. R. A. M. (2002). Male bimaturism and reproductive success in Sumatran orang-utans. *Behavioral Ecology, 13*(5), 643-652. doi:10.1093/beheco/13.5.643

Utami, S. S., & van Hooff, J. A. R. A. M. (1997). Meat-eating by adult female Sumatran orangutans (*Pongo pygmaeus abelii*). *American Journal of Primatology, 43*, 159-165. doi:10.1007/BF02381583

van Hooff, J. A. R. A. M., & van Schaik, C. P. (1994). Male bonds - affiliative relationships among nonhuman primate males. *Behaviour, 130*, 309-337. doi:10.1163/156853994x00587

van Noordwijk, M. A., Arora, N., Willems, E. P., Dunkel, L. P., Amda, R. N., Mardianah, N., . . . van Schaik, C. P. (2012). Female philopatry and its social benefits among Bornean orangutans. *Behavioral Ecology and Sociobiology, 66*(6), 823-834. doi:10.1007/s00265-012-1330-7 van Noordwijk, M. A., Sauren, S. E. B., Abulani Ahbam, N., Morrogh-Bernard, H. C., Utami Atmoko, S. S., & van Schaik, C. P. (2009). Development of independence: Sumatran and Bornean orangutans compared. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 189-203). New York: Oxford University Press.

van Noordwijk, M. A., & van Schaik, C. P. (2005). Development of ecological competence in Sumatran orangutans. *American Journal of Physical Anthropology, 127*(1), 79-94. doi:10.1002/ajpa.10426

van Noordwijk, M. A., & van Schaik, C. P. (2009). Intersexual food transfer among orangutans: do females test males for coercive tendency? *Behavioral Ecology and Sociobiology, 63*, 883-890. doi:10.1007/s00265-009-0728-3

van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in orangutans. *Primates, 40*(1), 69-86. doi:10.1007/BF02557703

van Schaik, C. P., & Burkart, J. M. (2011). Social learning and evolution: the cultural intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 1008-1016. doi:10.1098/rstb.2010.0304

van Schaik, C. P., & Kappeler, P. M. (1997). Infanticide risk and the evolution of male–female association in primates. *Proceedings of the Royal Society of London B: Biological Sciences, 264*(1388), 1687-1694. doi:10.1098/rspb.1997.0234

van Schaik, C. P., Marshall, A. J., & Wich, S. A. (2009). Geographic variation in orangutan behavior and biology. Its functional interpretations and its mechanistic basis. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 351-361). New York: Oxford University Press.

van Schaik, C. P., & van Hooff, J. A. R. A. M. (1996). Toward an understanding of the orangutan's social system. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great Ape Societies* (pp. 3-15). Cambridge: Cambridge University Press.

van Schaik, C. P., & van Noordwijk, M. A. (1986). The hidden costs of sociality: intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). *Behaviour, 99*(3), 296-314. doi:10.1163/156853986X00595

van Wolkenten, M. L., Davis, J. M., Lee Gong, M., & de Waal, F. B. M. (2006). Coping with acute crowding by *Cebus apella*. *International Journal of Primatology, 27*(5), 1241-1256. doi:10.1007/s10764-006-9070-z

Veenema, H. C. (2000). Methodological progress in post-conflict research. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 21-23, Box 22.21). Berkeley, CA, US: University of California Press.

Veenema, H. C., Das, M., & Aureli, F. (1994). Methodological improvements for the study of reconciliation. *Behavioural Processes, 31*(1), 29-37. doi:10.1016/0376-6357(94)90035-3

Verbeek, P. (1997). *Peacemaking of young children.* (57), ProQuest Information & Learning, US.

Verbeek, P. (2008). Peace ethology. *Behaviour, 145*(11), 1497-1524. doi:10.1163/156853908786131270

Verbeek, P., & de Waal, F. B. M. (1997). Postconflict behavior of captive brown capuchins in the presence and absence of attractive food. *International Journal of Primatology, 18*(5), 703-725. doi:10.1023/A:1026391728909

Verbeek, P., Hartup, W. W., & Collins, A. (2000). Conflict management in children and adolescents. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 34-53). Berkeley, CA, US: University of California Press.

Vlamings, P. H. J. M., Uher, J., & Call, J. (2006). How the great apes (*Pan troglodytes*, *Pongo pygmaeus*, *Pan paniscus* and *Gorilla gorilla*) perform on the reversed contingency task: the effects of food quantity and food visibility. *Journal of Experimental Psychology: Animal Behavior Processes, 32*(1), 60-70. doi:10.1037/0097-7403.32.1.60

Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S. P., . . . Povinelli, D. J. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour, 75*, 1757-1770. doi:10.1016/j.anbehav.2007.09.036

Vuchinich, S., Emery, R. E., & Cassidy, J. (1988). Family members as third parties in dyadic family conflict: strategies, alliances, and outcomes. *Child Development, 59*, 1293-1302. doi:10.2307/1130492

Ward, P. I., & Enders, M. M. (1985). Conflict and cooperation in the group feeding of the social spider *Stegodyphus mimosarum*. *Behaviour, 94*(1), 167-182. doi:10.1163/156853985X00325

Warneken, F., Chen, F., & Tomasello, M. (2006). Cooperative activities in young children and chimpanzees. *Child Development, 77*(3), 640-663. doi:10.1111/j.1467-8624.2006.00895.x

Warneken, F., Hare, B., Melis, A. P., Hanus, D., & Tomasello, M. (2007). Spontaneous altruism by chimpanzees and young children. *Plos Biology, 5*(7), 1414-1420. doi:10.1371/journal.pbio.0050184

Warneken, F., & Tomasello, M. (2007). Helping and cooperation at 14 months of age. *Infancy, 11*(3), 271-294. doi:10.1111/j.1532-7078.2007.tb00227.x

Warneken, F., & Tomasello, M. (2009). Varieties of altruism in children and chimpanzees. *Trends in Cognitive Sciences, 13*(9), 397-402. doi:10.1016/j.tics.2009.06.008

Watts, D. P. (1991). Harassment of immigrant female mountain gorillas by resident females. *Ethology, 89*, 135-153. doi:10.1111/j.1439-0310.1991.tb00300.x

Watts, D. P. (1995a). Post-conflict social events in wild mountain gorillas (Mammalia, Hominoidea). I. Social interactions between opponents. *Ethology, 100*(2), 139-157. doi:10.1111/j.1439-0310.1995.tb00321.x

Watts, D. P. (1995b). Post-conflict social events in wild mountain gorillas. II. Redirection, side direction, and consolation. *Ethology, 100*(2), 158-174. doi:10.1111/j.1439-0310.1995.tb00322.x

Watts, D. P. (1997). Agonistic interventions in wild mountain gorilla groups. *Behaviour, 134*, 23-57. doi:10.1163/156853997X00269

Watts, D. P. (2004). Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology, 25*(3), 507-521. doi:10.1023/B:IJOP.0000023573.56625.59

Watts, D. P. (2006). Conflict resolution in chimpanzees and the valuable-relationships hypothesis. *International Journal of Primatology, 27*(5), 1337-1364. doi:10.1007/s10764-006-9081-9

Watts, D. P., Colmenares, F., & Arnold, K. (2000). Redirection, consolation, and male policing: how targets of aggression interact with bystanders. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 281-301). Berkeley, CA, US: University of California Press.

Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour, 138*, 299-327. doi:10.1163/15685390152032488

Weingrill, T., Willems, E. P., Zimmermann, N., Steinmetz, H., & Heistermann, M. (2011). Species-specific patterns in fecal glucocorticoid and androgen levels in zoo-living orangutans (*Pongo* spp.). *General and Comparative Endocrinology, 172*(3), 446-457. doi:10.1016/j.ygcen.2011.04.008

Westlund, K., Ljungberg, T., Borefelt, U., & Abrahamsson, C. (2000). Post-conflict affiliation in common marmosets (*Callithrix jacchus jacchus*). *American Journal of Primatology, 52*(1), 31-46. doi:10.1002/1098-2345(200009)52:1<31::AID-AJP3>3.0.CO;2-Z

Wich, S. A., de Vries, H., Ancrenaz, M., Perkins, L., Shumaker, R. W., Suzuki, A., & van Schaik, C. P. (2009). Orangutan life history variation. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 65-75). New York: Oxford University Press.

Wich, S. A., Singleton, I., Nowak, M. G., Utami Atmoko, S. S., Nisam, G., Arif, S. M., . . . Kühl, H. S. (2016). Land-cover changes predict steep declines for the Sumatran orangutan (*Pongo abelii*). *Science Advances, 2*(3). doi:10.1126/sciadv.1500789

Wiessner, P. (2002). Hunting, healing, and hxaro exchange: A long-term perspective on !Kung (Ju/'hoansi) large-game hunting. *Evolution and Human Behavior, 23*(6), 407-436. doi:10.1016/S1090-5138(02)00096-X

Wittig, R. M., & Boesch, C. (2003). The choice of post-conflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour, 140*(11-12), 1527-1559. doi:10.1163/156853903771980701

Wittig, R. M., & Boesch, C. (2010). Receiving post-conflict affiliation from the enemy's friend reconciles former opponents. *PLoS One, 5*(11), e13995. doi:10.1371/journal.pone.0013995

Wittig, R. M., Crockford, C., Deschner, T., Langergraber, K. E., Ziegler, T. E., & Zuberbühler, K. (2014). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B-Biological Sciences, 281*(1778), 20133096. doi:10.1098/rspb.2013.3096

Wittig, R. M., Crockford, C., Wilkberg, E., Seyfarth, R. M., & Cheney, D. L. (2007). Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proceedings of the Royal Society B: Biological Sciences, 274*, 1109-1115. doi:10.1098/rspb.2006.0203

Wrangham, R. W., & Muller, M. N. (2009). Sexual coercion in humans and other primates: The road ahead. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual Coercion in Primates and Humans. An Evolutionary Perspective on Male Aggression Against Females* (pp. 451-468). Boston: Harvard University Press.

Yamamoto, S. (2015). Non-reciprocal but peaceful fruit sharing in wild bonobos in Wamba. *Behaviour, 152*(3-4), 335-357. doi:10.1163/1568539X-00003257

Yamamoto, S., Humle, T., & Tanaka, M. (2009). Chimpanzees help each other upon request. *PLoS One, 4*(10), e7416. doi:10.1371/journal.pone.0007416

Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. *Proceedings of the National Academy of Sciences of the United States of America, 109*(9), 3588-3592. doi:10.1073/pnas.1108517109

Yamamoto, S., & Takimoto, A. (2012). Empathy and fairness: psychological mechanisms for eliciting and maintaining prosociality and cooperation in primates. *Social Justice Research, 25*(3), 233-255. doi:10.1007/s11211-012-0160-0

Yamamoto, S., & Tanaka, M. (2009). How did altruism and reciprocity evolve in humans? Perspectives from experiments on chimpanzees (*Pan troglodytes*). *Interaction Studies, 10*(2), 150-182. doi:10.1075/is.10.2.04yam

York, A. D., & Rowell, T. E. (1988). Reconciliation following aggression in patas monkeys, *Erythrocebus patas*. *Animal Behaviour, 36*, 502-509. doi:10.1016/S0003-3472(88)80021-6

Zahavi, A. (1995). Altruism as a handicap: the limitations of kin selection and reciprocity. *Journal of Avian Biology, 26*(1), 1-3. doi:10.2307/3677205

Zahn-Waxler, C., Radke-Yarrow, M., & King, R. A. (1979). Child rearing and children's prosocial initiations toward victims of distress. *Child Development, 50*(2), 319-330. doi:10.2307/1129406

Zahn-Waxler, C., Radke-Yarrow, M., Wagner, E., & Chapman, M. (1992). Development of concern for others. *Developmental Psychology, 28*(1), 126-136. doi:10.1037/0012-1649.28.1.126

Zucker, E. L. (1987). Control of intragroup aggression by a captive male orangutan. *Zoo Biology, 6*(3), 219-223. doi:10.1002/zoo.1430060304

Zucker, E. L., Dennon, M. B., Puleo, S. G., & Maple, T. L. (1986). Play profiles of captive adult orangutans: a developmental perspective. *Developmental psychobiology, 19*(4), 315-326. doi:10.1002/dev.420190404

Zucker, E. L., Mitchell, G., & Maple, T. L. (1978). Adult male-offspring play interactions within a captive group of orang-utans (*Pongo pygmaeus*). *Primates, 19*(2), 379-384. doi:10.1007/BF02382806

LIST OF FIGURES

LIST OF TABLES

APPENDIX

The tables provided in the Appendix were already included in the prior publication of Study 2 (Kopp & Liebal, 2016, Electronic Supplementary Material ESM1).

Due to copy right reasons, the pages 166-172 are not available in the online version of this dissertation. Please see the original article at http://dx.doi.org/10.1007/s00265-016-2130-2. You may also contact the author for a copy of the manuscript at kathrin.kopp@fu-berlin.de.

SUMMARY

Prosociality - the faculty to act in favour of others - is highly developed in humans across cultures. The prosocial repertoire of humans is manifold ranging from sharing of food and other resources, collaborating, teaching children, mediating between opponents up to donating money, blood and organs to others, sometimes even to strangers.

As humans, we are as much cultural beings as we are biological beings, and as the latter, we are also a part and a result of an evolutionary history which we largely share with other animals, especially other primates. Taking a comparative perspective on human prosociality basically means to account for this fact and to investigate how much of our prosocial behaviour and its emotional and socio-cognitive prerequisites we share with other species and what might be specifically human.

Over the past three decades, extensive research on prosocial behaviour across the primate order has already deepened our insight into its evolutionary origins. A large part of this knowledge relates to studies with chimpanzees who are, alongside with bonobos, our closest great ape relatives. However, there is much less known on prosocial behaviour in orangutans, who are our most distant great ape cousins. In contrast to all other great apes, wild orangutans dot not live in groups, but seem to cope with group life in zoos quite well. This raises the questions whether orangutans share prosocial abilities and behaviours with the other great apes and whether they use them to cope with group life.

The objective of this thesis is, therefore, to provide the first systematic investigation on prosocial behaviour in socially housed orangutans in order to answer these questions.

I conducted two observational studies and one study with a quasi-experimental design on groups of zoo-living Sumatran orangutans.

The aim of the first study (Section 2.1) was to investigate, whether orangutans share food and non-food objects to mitigate potential conflict situations caused by the uneven distribution of food or non-food objects. I observed a group of orangutans in their large outdoor enclosure in the summer and in two smaller adjacent indoor enclosures in the winter (80 hours each) and recorded all interaction over food and non-food objects.

The main finding was that conflicts of interest regarding food and non-food objects only very rarely led to open conflicts, but were usually communicated by non-aggressive interactions which frequently resulted in sharing. These results support the proposed function of prosocial behaviour as a means to mitigate potential conflict situations and thereby to cope with the challenges of permanent group life.

As a second result, the sharing of food and objects turned out to be selectively with regard to particular group mates. Especially adult females engaged increasingly in food interactions and active sharing under less spacious housing conditions during the winter.

The aim of the second study (Section 2.2) was to investigate systematically whether the relationship quality affected the readiness of an individual to share with a particular partner, as the second result of the first study suggested. I conducted food sharing tests using monopolisable food in order to induce food interactions in three orangutan groups. To assess the relationship quality for each dyad, I calculated a proximity-based sociality index. The results of this study demonstrated that orangutans preferentially shared food with close social partners. Moreover, a comparison with data from similar studies on chimpanzees demonstrated a significantly larger proportion of active sharing for orangutans.

With the third study (Section 2.3), I addressed the question whether orangutans use prosocial conflict management strategies to cease aggressive interactions and to reduce the costs of actual conflicts. Analyses of the behaviour of opponents and bystanders in open conflict situations, in the immediate aftermath of conflicts and under control conditions demonstrated both partial and impartial third party interventions to cease ongoing conflicts and reconciliation. While there are few reports on policing in captive orangutans, the results of this study provide the first evidence for the occurrence of reconciliation in orangutans so far.

The results of all three studies fully support the hypothesis that socially housed orangutans use prosocial behaviour to cope with group life, in particular to mitigate potential conflict situations, to cease ongoing conflicts and to reduce the costs of aggressive interactions. Moreover, the results suggest, that orangutans use prosocial behaviour in order to establish, maintain and strengthen social bonds. The revealed similarities between orangutans and the other great apes with regard to prosocial abilities and behaviours provide further support for the hypothesis that the socio-cognitive and behavioural basis of human prosociality has probably evolved in a common ancestor of all extant hominids.

ZUSAMMENFASSUNG

Prosozialität, d.h. die Fähigkeit, zugunsten anderer zu handeln, ist ein kulturübergreifender wesentlicher Aspekt des menschlichen sozialen Lebens. Prosoziale Handlungen kommen, auch in Abhängigkeit von der jeweiligen Kultur, in unterschiedlichsten Facetten vor und reichen vom Teilen von Nahrung über Kooperation, Unterrichten von Kindern oder Streitschlichten bis hin zum Spenden von Geld, Blut oder Organen, unter Umständen sogar für Unbekannte.

Dennoch sind wir als Menschen nicht nur Kultur-, sondern auch Naturwesen und als letztere Teil und Ergebnis einer Evolutionsgeschichte, deren größten Teil wir mit anderen Tieren, insbesondere anderen Primaten, teilen. Eine vergleichende Perspektive auf Prosozialität einzunehmen, bedeutet im Wesentlichen, dieser letztgenannten Tatsache Rechnung zu tragen und zu untersuchen, wieviel der menschlichen Prosozialität wir mit anderen Arten teilen und welche Teile spezifisch menschlich sind.

Innerhalb der letzten drei Jahrzehnte ist eine Vielzahl von Studien zu prosozialem Verhalten in den unterschiedlichsten Primatenarten durchgeführt worden, was zu zahlreichen Erkenntnissen hinsichtlich möglicher evolutionärer Wurzeln menschlicher Prosozialität geführt hat.

Ein wesentlicher Teil unseres heutigen Wissens stammt aus Untersuchungen mit Schimpansen, die neben den Bonobos die dem Menschen phylogenetisch nächste Spezies sind. Im Gegensatz dazu wissen wir bisher kaum etwas über prosoziales Verhalten von Orang-Utans, die von allen heute lebenden Menschenaffen phylogenetisch am weitesten vom Menschen entfernt sind. Orang-Utans unterscheiden sich in vielen Aspekten von den afrikanischen Menschenaffen, besonders jedoch dadurch, dass sie in ihrem natürlichen Lebensraum nicht in Gruppen leben. In Zoos hingegen leben sie gewöhnlich in über lange Zeit stabilen Gruppen und scheinen sich gut daran anpassen zu können. Dies wirft die Frage auf, ob Orang-Utans über ähnliche prosoziale Verhaltensweisen wie die anderen Menschenaffen verfügen und wenn, ob sie diese benutzen, um mit dem Gruppenleben zurechtzukommen. Diese Fragen liegen auch meiner Dissertation zugrunde.

Ziel meiner Arbeit war es, diese Fragen erstmalig im Rahmen einer systematischen Untersuchung des prosozialen Verhaltensrepertoires von in Gruppen lebenden Orang-Utans zu stellen, zu untersuchen und zu beantworten.

Vor diesem Hintergrund habe ich zwei Beobachtungsstudien und eine Studie mit einem quasi-experimentellen Design mit Orang-Utan-Gruppen in Zoologischen Gärten durchgeführt.

Ziel der ersten Studie (Kapitel 2.1) war es zu untersuchen, ob Orang-Utans in potentiellen Konkurrenzsituationen hinsichtlich des Besitzes von Futter oder Objekten diese dadurch entschärfen, indem sie Futter oder Objekte teilen. Ich führte hierzu Beobachtungen einer Orang-Utan-Gruppe sowohl im Sommer, als sie ein weitläufiges Außengehege bewohnten, als auch im

Winter, den sie in zwei kleineren benachbarten Innengehegen verbrachten, durch und nahm sämtliche Interaktionen bezüglich Futter oder Objekten auf. Die Dauer der Beobachtungen betrug pro Gehege insgesamt 80 Stunden. Die zentralen Ergebnisse dieser Studie waren, dass potentielle Konfliktsituationen nur selten eskalierten und Nicht-Besitzer stattdessen ihr Interesse am Futter oder am Objekt signalisierten, was auch häufig zum Futtertransfer führte. Dieses Ergebnis spricht dafür, dass Futterteilen Orang-Utans als Mittel zur Entschärfung von potentiellen Konflikten dient. Darüber hinaus zeigte sich, dass insbesondere erwachsene Weibchen auf die beengten Verhältnisse im Winter mit einer erhöhten Rate an Futter- und Objektinteraktionen untereinander reagierten und auch mehr Bereitschaft zeigten, Futter zu teilen. Da dies ein Hinweis darauf sein könnte, dass Orang-Utans, wie z.B. auch Schimpansen, Futterteilen zum Pflegen sozialer Beziehungen einsetzen, habe ich mit genau dieser Fragestellung eine zweite Studie speziell zum Futterteilen durchgeführt (Kapitel 2.2). Um Futterinteraktionen zu induzieren, wurden drei Orang-Utan-Gruppen jeweils an mehreren Testtagen mit einer monopolisierbaren Futterquelle in Form einer großen hartschaligen Frucht versorgt und alle Interaktionen in diesem Zusammenhang aufgezeichnet. Anhand von Beobachtungsdaten wurde die Beziehungsqualität aller Dyaden bestimmt und in einem auf Nähe basierenden Index kodiert. Die anschließende Analyse zeigte, dass Orang-Utans vorrangig mit denjenigen Gruppenmitgliedern Futter teilten, mit denen sie eine enge Beziehung hatten. Ein weiteres Ergebnis war, dass im Vergleich mit ähnlichen Studien mit Schimpansen Orang-Utans deutlich häufiger aktiv geteilt haben.

Die dritte Studie (Kapitel 2.3) war eine Beobachtungstudie analog zur ersten. Hier ging es allerdings um prosoziales Verhalten bei aggressiven Interaktionen. Aggressive Auseinandersetzungen waren insgesamt selten. Wenn es jedoch zu einem offenen Konflikt zwischen zwei Individuen gekommen war, griffen in einem Teil der Fälle unbeteiligte Dritte ein und trennten die Gegner, meistens auf friedliche Weise. Unmittelbar nach dem Ende einer Auseinandersetzung kam es verstärkt zu affiliativen Interaktionen zwischen den beiden Opponenten. Dieses Ergebnis der Studie ist der erste empirische Beleg für das Vorkommen von Versöhnung bei Orang-Utans.

Zusammenfassend kann gesagt werden, dass die Ergebnisse der Studien die Hypothese stützen, dass Orang-Utans prosoziales Verhalten nutzen, um sowohl potentielle Konflikte zu entschärfen als auch die Kosten aggressiver Auseinandersetzungen zu mindern. Die Resultate weisen außerdem darauf hin, dass prosoziales Verhalten für soziale Bindungen eine Rolle spielt. Das prosoziale Verhalten von Orang-Utans ähnelt dem der anderen großen Menschenaffen, was die Hypothese stützt, dass die sozio-kognitive und die behaviorale Basis menschlicher Prosozialität bei einem gemeinsamen Vorfahren aller heute lebenden Hominiden entstanden sind.

PRIOR PRINTED PUBLICATION

Kopp, K. S., & Liebal, K. (2016). Here you are! – Selective and active food sharing within and between groups in captive Sumatran orangutans (*Pongo abelii*). *Behavioral Ecology and Sociobiology, 70*(8), 1219-1233. doi:10.1007/s00265-016-2130-2

ACKNOWLEDGEMENTS

This is all about prosociality in apes. The very last section, however, refers to prosocial acts in favour of only one particular beneficiary – me. On the long way leading to these final sentences, I have received great support, have experienced remarkable cooperation, have been re- and proactively provided with ideas, questions, food, coffee and wine, and have been consoled, encouraged and comforted in those times of doubts, I'm sure everyone who ever wrote a dissertation is familiar with. In short: I have witnessed prosocial acts of all types considered in this thesis. Furthermore, I am convinced that most of them were voluntary and genuinely altruistic.

Here and now are the place and the time to thank all the people without whom this work would not have come into existence. I am quite sure to fail in the attempt to name all of them. Therefore, before starting this attempt nevertheless, I want to express my gratitude to all of you: my dear friends and colleagues, family members, discussion partners and students!

In the first place, I want to most sincerely thank my supervisor Katja Liebal for many things: Thank you, Katja, for being open minded for my ideas from the very outset and giving me the opportunity to start with this project at all – though others thought it a rather unpromising subject to study. Thank you for your professional mentoring, your never diminishing encouragement and your enthusiastic, optimistic and really prosocial way to lead our group through uncertain times.

Next, I'd like to thank all the people in the zoos who made this dissertation possible. I am most grateful to the curators Ilona Schappert and André Schüle who not only granted me the permission to conduct my observations in the zoos of Dortmund and Berlin, respectively, but also supported my work throughout the studies. Most cordially, however, I want to thank all keepers at the Rainforest House *Rumah hutan* in Dortmund and the Ape House in Berlin for the time they devoted to me despite their tight working schedules, their interest, humour and patience when being confronted with my countless questions and suggestions. Thank you all – it was incredible to work with you and to experience your daily dedication to the welfare of the orangutans and the other wild animals in your care! My special thanks go to Eddy Laudert, Natascha Kurt, Sonja Borchers, Andreas Krause and Jörg Woitzik in Dortmund for letting me being part of the team. Thank you for sharing your knowledge and experience, for constant help and friendship! Every time I reoccupied my room at *Westermann*, it was like coming home. In Berlin, I'd like to say most heartily thank you to Ruben Gralki and Christian Aust for making the impossible not only possible, but real. Ruben, thank you in particular, for so many chats after hours at the orangutans' enclosure, for exchanging information and opinions on orangutans and other apes, for taking my – sometimes probably weird – ideas seriously and for your exceptional commitment to the apes in your care and their last relatives in the wild. Furthermore, I want to thank Robert Eisenberg from Leipzig Zoo for his jolly friendship and for introducing me to the zookeepers' world.

I want to thank Anja Kopper, Laura Thomsen, Sonja Ebel, Suska Nolte, Paula Mahlke, Bruno Suski and Luisa Hetmann for helping me with such boring, but necessary things as the reliability coding or proximity scans. Thank you all for your precise work and your enthusiasm for the orangutans! Special thanks go to Martin Schultze for his straightforward, though nonetheless creative statistical support. Furthermore, I want to thank Adrian Jaeggi and Maria van Noordwijk for their extremely valuable and thought-provoking comments regarding the manuscript of the prior published article on food sharing, and for sharing insider-information on wild orangutans.

Now, it's about time to thank my dearest colleagues Manuela Lembeck, Linda Scheider, Julia Keil and Robert Ullrich as well as my former colleagues Cordelia Mühlenbeck, Sonja Ebel, Carla Pritsch, Laura Damerius, Leander Steinkopf, Eva Luëf, Paul Kuchenbuch and Eiko Fried for their scientific and mental support, coffee breaks, enjoyable meetings in the country side and conference trips. It is a great pleasure being part of the best and most prosocial working team I know. Dear Manu, you deserve very special thanks for backing me up at work during the last months.

There are many people who were not directly connected with my work, but – being essential parts of my life – enabled me to start, to go on with and to finish this thesis. Marcel, I don't know how to put my gratitude into words. Thank you for being by my side, for reassuring and encouraging me, and especially for standing my moods during the past months. Furthermore, I want to thank my family, particularly my parents and siblings, for all their love and support throughout my life. Thank you, dad, for your confidence and patience, especially when my way turned out to be more winding than you would have wished it to be. *In memoriam*, thank you, mum, for everything – you were the most altruistic person I had the luck to know. Most cordial thanks also go to you, Gisela, for your affection, your generosity and for simply being the best mother-in-law in the world.

I want to most heartily thank all my dearest friends who were extraordinary lenient with me given my unusual unsociability during the process of writing this thesis. Dana and Inka, thank you in particular! My deepest thanks go also to my friends and neighbours in Mildenberg. In particular, thank you, Steffen, for lending an ear, for chatting and laughing the sorrows away and for being there whenever I needed a friend. Thank you, Kerstin, for the continuous supply with friendship, gummy bears and hot soup.

Finally and sincerely, I want to thank Andreas Elepfandt, both academic mentor and friend, who promoted me on my way through biology and philosophy. Thank you, Andreas, for teaching me to look and think outside the boundaries of scientific disciplines and for showing me that being a natural scientist not only means to be curious, but also to be one's own sharpest critic, to cooperate, to be honest and – most importantly – to be human.

For reasons of data protection, the CV is not included in the online-version of this dissertation.

Eidesstattliche Erklärung

Hiermit versichere ich, die vorliegende Dissertation selbständig und nur unter Verwendung der angegebenen Quellen und Hilfsmittel erarbeitet und verfasst zu haben.
Diese Arbeit ist in keinem früheren Promotionsverfahren angenommen oder abgelehnt worden.

Berlin, den 30.09.2016 Kathrin Susanne Kopp