

## **Chimpanzees, Conflicts, and Cognition.**

Functions and mechanisms of chimpanzee conflict resolution.

Sonja Elena Koski

Koski, Sonja Elena

Chimpanzees, conflicts and cognition. Functions and mechanisms of chimpanzee conflict resolution.

PhD Dissertation, Utrecht University 2007

Cover photos: Kathelijne Koops

Cover design: Femke Bulten/ Beeldwerking & Vormgeving, Utrecht University

Printing: PrintPartners Ipskamp, Enchede, NL

ISBN: 978-90-393-4475-0

© Copyright Sonja E. Koski 2007

**Chimpanzees, Conflicts, and Cognition.**

Functions and mechanisms of chimpanzee conflict resolution.

**Chimpansees, Conflicten en Cognitie.**

De functies en mechanismen van chimpansee conflictoplossing.  
(met een samenvatting in het Nederlands)

**Simpanssit, Konfliktit ja Kognitio.**

Simpanssien konfliktinratkaisun syyt ja mekanismit.  
(sisältää suomenkielisen tiivistelmän)

**PROEFSCHRIFT**

ter verkrijging van de graad van doctor aan de Universiteit Utrecht op  
gezag van de rector magnificus, prof. dr. W.H. Gispen, ingevolge het  
besluit van het college voor promoties in het openbaar te verdedigen op  
woensdag 14 maart 2007 des middags te 12.45 uur

door

**Sonja Elena Koski**

geboren op 14 december 1973  
te Helsinki, Finland

Promotoren: Prof. Dr. J.A.R.A.M. van Hooff

Prof. Dr. J.J. Bolhuis

Co- promotor: Dr. E.H.M. Sterck

This thesis was accomplished with financial support from Lucie Burgers  
Foundation for Comparative Behaviour Research and University of Utrecht.

To my father,  
Who taught me to Read

Isälle,  
joka opetti minut Lukemaan



## Contents

<b>CHAPTER 1.</b> Chimpanzees: 98% human or just another primate species? A general introduction to chimpanzee social behaviour and cognition.	<b>9</b>
<b>CHAPTER 2.</b> Reconciliation, relationship quality, and postconflict anxiety: testing the integrated hypothesis in captive chimpanzees. S.E.Koski, K. Koops and E.H.M. Sterck 2007. <i>Am. J. Primatol.</i> , 69, 158-172.	<b>37</b>
<b>CHAPTER 3.</b> What to do after a fight? The determinants and inter- dependency of post-conflict interactions in chimpanzees. S.E.Koski, H. de Vries, S. van den Tweel and E.H.M. Sterck. Subm. <i>Behaviour</i>	<b>57</b>
<b>CHAPTER 4.</b> Triadic postconflict affiliation in captive chimpanzees: does consolation console? S.E.Koski and E.H.M. Sterck 2007. <i>Anim. Behav.</i> 73, 133-142.	<b>81</b>
<b>CHAPTER 5.</b> Selfish 'consolers' – bystander chimpanzees protect themselves from further aggression. S.E.Koski and E.H.M. Sterck. Subm. <i>Proc. R. Soc. B</i>	<b>103</b>
<b>CHAPTER 6.</b> Chimpanzee consolation – spinning the empathy wheel. S.E.Koski and E.H.M. Sterck. Unpublished manuscript.	<b>115</b>
<b>CHAPTER 7.</b> Functions, cognition, and emotions – cross-sectioning chimpanzee conflict resolution. Summary, discussion and conclusions.	<b>129</b>
<b>Appendix</b>	<b>145</b>

<b>Samenvatting</b> (Summary in Dutch)	<b>149</b>
<b>Tiivistelmä</b> (Summary in Finnish)	<b>161</b>
<b>References</b>	<b>173</b>
<b>Acknowledgements</b>	<b>189</b>
<b>Curriculum Vitae</b>	<b>191</b>

# *CHAPTER 1*

---

---

CHIMPANZEES: 98% HUMAN OR  
JUST ANOTHER PRIMATE SPECIES?

A General Introduction to Chimpanzee  
Social Behaviour and Cognition

---

---



## **CHIMPANZEES: 98% HUMAN OR JUST ANOTHER PRIMATE SPECIES?**

### **General introduction to chimpanzee social behaviour and cognition**

Primates are our closest living relatives and have many features in common with us, the hairless apes. Like us, they live in social groups and squabble with their group members about who gains most benefits. And like humans, they resolve their conflicts afterwards. In particular chimpanzees have served as mirrors of human social behaviour, being attributed with cognitively advanced social strategies like consolation, morals and even politics. Appealing as this picture is, the scientific ground underneath these statements is rather thin. In this thesis, I aim to delve into one lauded, but not thoroughly investigated aspect of chimpanzee social behaviour, namely the conflict and post-conflict interactions. In particular, I address the occurrence, function and mechanisms of post-conflict behaviour of captive chimpanzees.

### **The evolution of intelligence – Why are we and other primates so smart?**

Humans are by far the most intelligent species of all, whichever criteria or measure we take for intelligence. We have sophisticated communication systems extending to virtual networks of information exchange, cultural variation unparalleled in nature, astro- and nanotechnology, written history, philosophy and religions, law-governed social systems; one can come up with endless examples. Although the level of these achievements is unparalleled in nature, this does not necessitate that these phenomena were completely unique to humans. The current research efforts concentrate on the extent to which these phenomena are present in non-human animals. This is connected to the quest of assessing how we humans got where we are now.

For a long while science (and religions) emphasised the difference in the cognitive capacities between humans and other species. Animals were seen as machines that acted on a stimulus-reaction basis with little flexibility. The picture has drastically changed, and the last 30 years have seen an increased interest in animal intelligence. Building on the work of Robert Yerkes and Wolfgang Köhler,

research on animal cognition was kicked off by the seminal paper of Premack and Woodruff (1978) that asked 'does the chimpanzee have a theory of mind?'. The paper with its peer commentary spurred a vivid research interest in primate cognition. Since then, an extensive battery of experimental and observational research has tried to unravel the depths of animal cognition, and the field remains hotly debated.

A large part of these studies have focused on primates (e.g., Byrne and Whiten 1988; Cheney and Seyfarth 1990; Whiten and Byrne 1997; Tomasello and Call 1997; Matsuzawa 2001; Matsuzawa et al. 2006) although in recent years attention has been extended to birds, dogs, cetaceans and elephants (e.g., Clayton and Dickinson 1998; Lefebvre et al. 2003; Hare and Tomasello 2005; Miklosi et al. 2004; Marino 2004; Plotnik et al. 2006; Dally et al. 2006). Primates are an obvious clade to study when the interest concerns the evolution of human (-primate) cognition, due to our shared evolutionary history. Primates' general cognitive abilities are advanced compared to many other taxa (Deaner et al. 2006; see for comparisons of domain-specific abilities e.g. Shettleworth 1998) and they have large brains relative to their body size (Harvey and Krebs 1990; Barton and Dunbar 1997; Barton and Harvey 2000; Striedter 2006). Large brain size (or relatively enlarged neocortex) and advanced cognitive capacities are assumed to be connected (e.g., Byrne and Whiten 1988; 1997; Deacon 1990). Indeed, evidence for this notion was found using innovation, social learning and tool use as proxies for 'intelligence' (Reader and Laland 2002). Within the primate order, however, there is considerable variation in cognitive abilities as well as in ecological conditions, social structures, and life histories. The cognitive abilities range from the fairly basic capacities of Lemuridae, via more advanced skills of monkeys, to the rather sophisticated great apes (Cheney and Seyfarth 1990; Heyes 1993; Tomasello and Call 1997; Matsuzawa 2001, Matsuzawa et al. 2006; Deaner et al. 2000, 2006). Most primates are social, while the group size ranges from one (i.e., individuals forage solitary but do know identity of the neighbouring individuals) to hundreds of individuals (Smuts et al. 1987). The social structures consist of solitary living, monogamy, polygamy and polygynandry with larger and smaller groups with one or several males (Dunbar

1988; Smuts et al. 1987). The groups are stable, consisting of adults of both sexes, and can be coherent or present structural flexibility (i.e., have fission-fusion dynamics).

Such variation in cognitive abilities and social behaviour is a prerequisite for comparative studies that aim at developing and testing hypotheses on evolution of cognition. A number of theories have been put forward to explain the evolutionary leap in the cognitive capacities in primates. The theories roughly categorise the selection pressures for increased cognitive abilities as ecological, social, or, recently, life-history associated. Ecological hypotheses emphasise the importance of species' environment and/or diet in the cognitive evolution. The spatiotemporal structure of the environment can be complex, demanding advanced mapping skills and memory of availability and location of resources. Frugivores face more challenges in this respect than folivores due to the patchy distribution and fluctuating fruit availability (Clutton-Brock and Harvey 1980; Milton 1988). On the other hand, complexity of extracting the consumable food items has been suggested to require sophisticated manipulation skills and, in some cases, lead to the development of tool use (Byrne 1995; 2002; van Schaik 2004).

Life-history has been shown to correlate with relative brain size in primates (Deaner et al. 2003), which indicates that brain size enlargement and slow life history have coevolved. This evoked the hypothesis that slow life history has allowed the evolution of primates' enhanced cognitive skills. According to this hypothesis, life history acts as a 'filter' between the selective pressures to advanced cognition (were they ecological, social or both) and the enlarged brain size, and thus, only species that can 'afford' slow development can increase their cognitive capacities (van Schaik and Deaner 2003; Deaner et al. 2003). This hypothesis also encompasses the view that the development of cognitively complex skills requires long maturation time, and therefore a slow life history facilitates learning cognitively demanding tasks.

The theory of social life prompting the evolution of cognitive skills is perhaps the most popular view today. There are some variations to the theme, but the general doctrine of the social (or Machiavellian) intelligence hypothesis

stipulates that living in large, individualised, complex social groups has selected for enhanced cognitive capacities (Humphrey 1976; Jolly 1966; Whiten and Byrne 1988). Social groups contain networks of different kinds of relationships (e.g., kinship, co-operative, and dominance relationships), which require computationally complex processes to manage successfully. Individuals who can strategise flexibly their own actions in this network gain benefits over others incapable of strategising. Thus, the need for effective cooperation and competition with group mates has supposedly formed the selective pressure for cognitive capacities. The social intelligence hypothesis has gained support by a positive correlation between the relative neocortex size and social network of group size within primates (Dunbar 1992, 1995; Kudo and Dunbar 2001). Recently, direct evidence for benefits of social skills was provided by a study showing that the ability to establish and maintain social relationships increases an individual's fitness (Silk et al. 2003). Although the theory has been criticised for using questionable measures of social complexity and 'intelligence', and not explaining particular cases (e.g., van Schaik and Deaner 2003; van Schaik 2004), many agree that the selective pressures of social life are probably one of the contributors to the primate intelligence (e.g., Cosmides 1989; Byrne and Whiten 1997; Tomasello and Call 1997; Dunbar 2000; Reader and Laland 2002; van Schaik 2004; Kamil 2004; Zuberbühler and Byrne 2006).

### **What's the use of social intelligence?**

The Machiavellian version of the social intelligence hypothesis (Byrne and Whiten 1988; Whiten and Byrne 1997) contains the idea that it is beneficial to be able to predict another's future behaviour, to deceive and to manipulate others. Such 'Machiavellian' behaviour requires an ability to form mental representations of others' mental states. Mental state attribution is the key ability in the cognitive concept Theory of Mind (ToM). ToM is a term for an ability to make mental representations of other's mental states, that is, to be able to understand that the other has goals, intentions, beliefs, and perspective that differ from those of self (Premack and Woodruff 1978).

In humans, the development of ToM is gradual (see Box 1). Children reach the levels of mental state attribution gradually, and the understanding of own mental states occurs before an understanding of others' mental states. The gradual development of cognitive capacities required for ToM demonstrates that

**BOX 1.** The developmental levels of Theory of Mind

A fully developed, adult-human-like ToM requires cognitive capacities that develop gradually. Dennett (1983) has formulated a scale of the development of mental state attribution. At the simplest level, called 'the zero-order intentionality', an individual has no understanding of self or of own mental states. At the next level, a subject presents 'the first-order intentionality', which means an ability to represent own goals and beliefs, but having no understanding of other's mental states. Individual with 'the second-order intentionality' can in addition represent other's representations, i.e., to understand that others have their beliefs and mental states. Adult humans reach yet higher levels (X understands that Y believes that Z thinks, etc.). The full ToM is assumed to require second-order intentionality, as a subject needs to understand that another's mind is different from its own mind (Leslie 1987).

Perner (1991) has formulated a scale of representation development with slightly differently defined levels. Perner's primary representational level corresponds roughly to the first-level intentionality of Dennett. The secondary representational level, however, describes a level between the first- and second order intentionality. On the secondary representation level individual can understand that own representations may differ from reality but not necessarily that other's representations may also be false. At the level of meta-representations (corresponding to the second-order intentionality) individuals can formulate an understanding of representations as representations and thus, can understand other's beliefs as separate entities.

The secondary representational level is achieved during the second year of life. At this stage children understand the for instance the representational nature of pictures, and show abilities for mirror self-recognition, pretence and some understanding of other's emotions (Zahn-Waxler et al. 1992; Bart and Hayne 1999; Suddendorf and Whiten 2001). The meta-representational -or second-order intentional - level is achieved at about four years of age, when children can understand false beliefs, have imaginary object pretence (Suddendorf et al. 1999), and possess episodic memory (Wimmer and Perner 1983; Perner and Lang 1999; see further in Flavell 2000, 2004).

ToM is not a dichotomous monolith, which you either fully possess or not at all (reviewed in Flavell 2000, 2004; see for discussions on ToM domain specificity vs. –generality e.g. Apperly et al. 2005; Stone and Gerrans 2006). Instead, ToM appears to consist of a number of cognitive capacities, some of which may be present in non-human primates, even if they did not reach the adult-human level of ToM. Furthermore, it is possible that some species present abilities that reach further in the scale of cognitive abilities than others.

Myriads of studies have investigated cognitive capacities in primates (reviews in e.g. Byrne and Whiten 1988; Call and Tomasello 1997; Whiten and Byrne 1997; Heyes and Huber 2000; Matsuzawa et al. 2006). Monkeys appear to be capable of knowing quite a bit of their social environment, while there are no indications that they are able to represent other's mental states (Cheney and Seyfarth 1990). On the other hand, apes seem able to attribute at least some mental states to others (Tomasello et al. 2003 a,b; Call 2003; but see Povinelli and Bering 2002; Povinelli and Vonk 2003, 2004). Thus, it appears that apes possess more of the capacities associated with ToM than monkeys do.

How does mind reading benefit an individual, in which context would it be especially beneficial, and is there evidence for employment of social intelligence? The social usage of cognitive capacities has received less attention than their existence. Studies on an ability to deceive others are one of the notable exceptions (see below); many species are described to behave deceptively to gain additional benefits (Whiten and Byrne 1988; Byrne 1995). Also, monkeys are shown to understand not just their own rank in relation to others, but also the relative ranks among group members, and to be able to classify individuals according to kinship and rank position (Seyfarth 1981; Cheney and Seyfarth 1990; 2003; Tomasello 2000; Bergman et al. 2003). Information of the relative dominance and kinship relationships among group mates can be used to choose the most beneficial interaction partners. Further, studies on the exchange of commodities in the group depending on their relative market value have shown that primates are capable of flexible social decision-making (e.g. Barret et al. 2003).

To generalise, flexible strategising in behavioural decisions, i.e., selective choice of interaction partners according to multiple, changing variables such as partner value, partner's probable further actions and costs associated with interactions, can tilt the cost/benefit ratio of social life to individual's advantage. We might therefore expect species whose social life places demands for social manoeuvring to be 'socially intelligent' and to show behavioural adjusting to contexts, to interaction partners and to their behaviour.

The paradigm outlined above – studying the benefit of cognitive skills in a social environment— essentially investigates the function (and thus, ultimately the fitness consequences) of social behaviours. In addition, it is crucial to understand what cognitive processes are associated with social interactions. Moreover, behavioural studies should to be supplemented by experimental research that can target the extent of cognitive skills of a species with the necessary rigor. These approaches, preferably when used together, can inform us about the selection pressures that have led to the development and maintenance of particular social strategies and their required cognitive capacities.

This thesis aims to incorporate the functional and the mechanistic sides of chimpanzee behaviour in combination with our current knowledge of chimpanzee cognitive capacities. Below, I first summarize the framework in which I have studied social cognition, namely aggressive conflicts and their resolution. Thereafter, I introduce chimpanzees as the study species. Finally, I outline the steps I have taken in this research by introducing the chapters of this thesis.

### **Conflicts and their resolution**

Competition over limited resources is an inevitable consequence of social life. Competition leads to conflicts of interest among group members, which have the potential to escalate to aggressive encounters. Aggressive conflicts can be costly in terms of lost energy, wounds and an increased predation risk, as well as of damaged relationships with group members (and therefore, loss of benefits, such as tolerance near resources, support and aid from interaction partners). Without

mechanisms to prevent escalation, costs of group living may exceed the benefits, which would lead to group's disintegration, being detrimental for all the individuals in the group. Therefore, for the group and the relationships therein to prevail, conflicts should be prevented when possible (Aureli and de Waal 2000).

Prevention of aggression can occur via several mechanisms. A dominance hierarchy is one of the most common ways to manage escalation, as upon knowing their status relative to one another individuals can avoid escalation of conflicts and settle the dispute according to the hierarchy (Preuschoft and Aureli 2000). Avoidance can also function as a conflict prevention strategy in species where fission carries relatively low costs (Schaffner and Aureli 2004). Additional conflict avoidance mechanisms include respect of possession, increased frequency of affiliative activities (such as grooming, sex and playing), and rituals (de Waal 1992a; Aureli and de Waal 1997; Cords and Killen 1998; Judge 2000; Koyama 2000; Palagi 2006).

When conflicts nevertheless do occur, their detrimental effects need to be mitigated. This can be done by means of affiliative behaviour between the combatants, known as reconciliation (de Waal and van Roosmalen 1979; Aureli and de Waal 2000). Reconciliation provides many benefits; short-term effects include reducing the likelihood of receiving further aggression from other group members and stress alleviation (Aureli and van Schaik 1991a,b; Castles and Whiten 1998b; Kutsukake and Castles 2001). Functionally the most important benefit is repair of the damaged relationship between opponents to the pre-conflict level (Kappeler and van Schaik 1992; Cords 1992; Koyama 2001; Wittig and Boesch 2005; Watts 2006). Besides the original opponents, previously uninvolved group members can participate in conflict resolution, for instance by mediating reconciliation or affiliating with one or both of the opponents (de Waal 1982; Aureli and van Schaik 1991a; de Waal and Aureli 1996; Das et al 1998). Conflict resolution is predicted to occur in species that have individualised relationships and within-group contest competition that leads to aggression, and in which aggression damages the relationships leading to a loss of benefits to one or both conflict opponents (Aureli et al. 2002; Schaffner et al. 2005). As predicted, conflict resolution is common in social species that meet these criteria,

including most primates, domestic goats, dolphins, and spotted hyenas (Schino 1998; Hofer and East 2000; Samuels and Flaherty 2000; Aureli et al. 2002; Wahaj and Holekamp 2003). Unfortunately, many species that could be expected to exhibit conflict resolving behaviours (e.g., African wild dogs, wolves, elephants, whales, and corvids) have not yet been studied in this respect.

### **Social cognition in conflict resolution**

The patterns of conflict resolution are determined by the types of relationships in the group. Groups contain relationships of differing qualities, kinship and dominance being the most apparent relationship attributes. In addition, 'friendship' is an often used attribute to describe social relationships. Friendship describes close, affiliative relationships among non-kin (Noë and Sluifster 1995; Cords 1997; Tomasello and Call 1997; Silk 2002). Friendships are characterised by frequent participation in affiliative interactions (e.g., grooming), high rates of association, exchange of beneficial acts (e.g. coalitional support, food sharing) and low levels of stress when together (Dunbar 1991; Cords 1997; Silk et al. 1999; Silk 2002). Finally, relationships can be characterised according to three dimensions, namely value (referring to direct fitness gained from the relationship: Kummer 1978), compatibility (referring to the general tenor, 'friendliness', of the relationship) and security (referring to the consistency of interactions), all of which influence the relationship's quality and importance for the partners (Cords and Aureli 2000).

Relationship quality determines the necessity of maintaining the benefits of the relationship. The more important the relationship is for the interaction partners, the more acutely it needs to be repaired after damage (Aureli et al. 2002). Relationships of the highest quality (i.e., kin, friends, allies) are more often repaired than relationships of less value (Kappeler and van Schaik 1992; Cords and Thurnheer 1993; Aureli et al. 1997; van Hooff 2001; Aureli et al 2002; Watts 2006)

The network of social relationships of various qualities, contextually changing variables of conflicts and the influence of other individuals' behaviour on own behaviour makes conflicts and their aftermath complex and cognitively

demanding. Each individual needs to make 'decisions' (the term does not imply a conscious decision-making process) on whether and how to get involved in the conflict, and to assess the consequences of involvement for its relationships. For example, during a conflict the group members can choose to join the conflict by supporting one of the opponents or by intervening neutrally, or they can try to avoid the aggression (de Waal and van Hooff 1981; Petit and Thierry 1994, 2000). After a conflict the group members can choose to get involved and accept a risk of receiving further aggression, or to stay aside. All of these options carry their own risks to the individual and consequences to the relationships among all the individuals involved.

This makes conflicts complex systems, in which flexibility in an individual's behaviour could be assumed to be advantageous. Therefore, conflicts can provide a window on how individuals employ social intelligence in their 'decision-making'. Peri- and post-conflict events have the potential to provide information on social cognition and its relevance both on the proximate level, i.e. which cognitive processes are employed in interactions, and on the functional level, i.e. how social cognition benefits an individual. For that reason, conflicts and their resolution in relation to social cognition in chimpanzees was chosen as the realm of my study.

### **The study species**

Chimpanzees, as a highly social and intelligent species (see below), are an interesting subject for a study on the employment of social intelligence. Fortunately, chimpanzees have been studied for decades and information of their social system, behaviour and cognitive capacities is abundant. There are numerous anecdotal indications that chimpanzees are indeed rather Machiavellian; their social dynamics is exceedingly co-operative and yet competitive, and described as 'politics' (de Waal 1982). Their advanced cognitive skills and complex social life make chimpanzees an intriguing species for investigating how they use their social intelligence in their everyday life.

### ***Chimpanzee ecology and socioecology***

As in all species, behaviour of chimpanzees is inseparably bound to their ecology and socio-ecology. Below I introduce the basics of chimpanzee ecology and social structure.

Chimpanzee, *Pan troglodytes*, is one of the two closest living relatives of human. The evolutionary lineage split into Pan and Homo 4 to 6 million years ago (Groves 2001). Chimpanzees share over 98% of their genome with humans. Consequently, chimpanzee physiology, morphology and, to some extent, behaviour show considerable overlap with humans (e.g. Tomasello 1999; de Waal 2005; Hauser 2005).

Chimpanzees live across equatorial Africa. Currently, four subspecies are recognised: *P. t. verus* in Western Africa, *P. t. vellerosus* in Nigeria, *P. t. troglodytes* in Central Africa, and *P. t. schweinfurthii* in Eastern Africa.

As in all great apes, the life-history of chimpanzees is slow. Their average lifespan is 40 to 50 years (Nishida et al. 1990; Boesch and Boesch-Achermann 2000), although in captivity they can live longer. The age of first reproduction is 13-15 years and inter-birth interval is 5-6 years (Nishida et al 1990; Sugiyama 1994; Boesch and Boesch-Achermann 2000). Mating occurs throughout the year with no distinct birth season. Females mate promiscuously, which males try to counter by mate guarding and consortships (Tutin 1979; Watts 1998). Males are philopatric while females emigrate to other communities during adolescence (Pusey 1979, Boesch and Boesch-Achermann 2000).

Chimpanzees live in multimale-multifemale groups that have a fission-fusion structure (Goodall 1986; Nishida 1990; Boesch 1991). A whole community consists of 20 up to more than a hundred individuals that associate and travel in smaller parties in a fluid manner. Party size varies between communities: in Taï, Ivory Coast, the average party size is 8.3 individuals, in Bossou, Guinea, it is small at 4.0 individuals, in Kibale, Uganda, the average party size is 10 but can increase to 47 individuals, and in the Tanzanian sites the average party size is 5.6 (Gombe) and 6.1 (Mahale) individuals (Boesch 1996; Boesch and Boesch-Achermann 2000; Mitani et al. 2002). In general, females are more solitary than males, mostly associating with their dependent offspring (e.g., Goodall 1986;

Hasegawa 1990; Pepper et al. 1999). Males, in turn, spend the majority of their time associating with each other. The party composition, however, also varies between the communities; Western chimpanzee females are more gregarious than the Eastern ones (Sugiyama and Koman 1979; Goodall 1986; Pusey et al 1997; Boesch and Boesch-Ackermann 2000). Consequently, the Western chimpanzees are labelled 'bisexually bonded' (Boesch and Boesch-Achermann 2000). Of the Eastern chimpanzees, the females of Kibale associate with each other more often than their Tanzanian counterparts (Wrangham et al. 1992).

Males form close bonds with each other in all populations, which are manifested in and maintained by time spent together, grooming, coalitions, territorial defence and meat sharing (e.g., van Hooff and van Schaik 1994; Watts 2002; rev. Mitani et al. 2002). Male bonding is important for co-operation in territorial defence and hunting, but equally important in intra-group competition. Males form coalitions with each other and the allies aid each other in agonistic encounters (e.g. de Waal 1982; Watts 2002). These highly opportunistic 'political' networks play a key role in the dominance struggles (de Waal 1982). The dominance structure of male chimpanzees is clearly defined and linear, in which the dominant male enjoys mating and feeding privileges. The alpha position is maintained with the support of allies, and is frequently challenged by lower ranking males. As a result, male relationships are highly valuable but instable.

In contrast, the female dominance hierarchy is less strict and defined (although it, too, varies between communities: Wrangham et al. 1992; Baker and Smuts 1994; Pusey et al. 1997; Wittig and Boesch 2003c). The pay-off difference between high and low ranking females, although existing, is not very large (Baker and Smuts 1994; Pusey et al. 1997). Female relationships are relatively stable over time, especially in captivity (de Waal 1992). This leads to tolerant, stable but low value relationships among (unrelated) females.

Submission to the dominant is signalled by unidirectional pant-grunts (Noë et al. 1980) combined with a crouching body position, and a dominant individual uses dominance displays, a hunchbacked body position with piloerection, bipedal swaggering, hunch-overs, etc. to strengthen the dominance (Goodall 1986, van

Hooff 1973; Noë et al. 1980). The displays are very loud and impressive show-outs of physical strength, and are often combined with drumming of buttresses (or anything that makes a loud noise) producing a sound that carries far in the forest. In spite of the clear dominance structure of males, the general social dynamics of chimpanzees is relatively egalitarian, meaning that there is high tolerance to proximity and possession and a high prevalence of counter-aggression in conflicts (de Waal and Luttrell 1989, Sterck et al. 1997; Hemelrijk 1999; Thierry 2000).

### ***Chimpanzee cognitive skills***

Cognitive skills involved in mental state attribution (and thus in ToM) can be studied experimentally by paradigms, which target specific aspects of mental state attribution. Below, I will review what is known about chimpanzee cognition according to particular paradigms, all of which relate to the chimpanzees' ability to represent the minds of (self and) others. The list is not all-encompassing, as I have included mainly the paradigms that have a special relevance to emotional state understanding. The chosen paradigms are all interrelated and the (occasionally) arbitrary division is based on the experimental set-ups.

#### *Mirror self-recognition*

Mirror self-recognition has become the main paradigm to test for animal's awareness of self (e.g. Anderson 1984; Povinelli 1987). The rationale is that if an animal recognises itself in the mirror, it will respond by self-directed behaviour, whereas if it does not recognise itself, it responds by other-directed behaviour. Thus, self-directed behaviour employing the mirror is a sign of self-recognition. The classic test for mirror self-recognition by Gallup (1970) has become the yard stick of animal self-recognition. The test involves an application of an odourless paint mark on subject's face in a spot that is invisible to the subject without the assistance of a mirror. The test measures the frequency of selective touching of the marked spot, assuming that touching the mark implies the animal's awareness of self. Some extensions and modifications of the standard test have been done, for instance testing self-recognition with distorting mirrors, which

controls for recognition based on movement contingency (Kitchen et al. 1996). Chimpanzees pass the mirror self recognition test (on a species level, but not necessarily every individual) whereas monkeys do not (Anderson 1984; Gallup 1998; de Waal et al. 2005). Chimpanzees may also explore with the aid of a mirror body parts that are invisible to them, such as their back, genital swelling, teeth, etc. (reviewed by Inoue-Nakamura 2001). Criticism of the test claims that the mark-touching may be a consequence of the anaesthesia used in the procedure and, thus, that passing the mark test is not a proof for self recognition or –awareness (Heyes 1998). Furthermore, it is not agreed upon which level of self-awareness mirror self recognition is connected to; mere body awareness and movement contingency or a mental concept of ‘self’ (Povinelli 1987; Heyes 1995, 1998; Sterelny 2000). On the other hand, it has been pointed out that failing the test does not mean complete absence of self-awareness (de Waal et al. 2005), and that self-awareness is likely not a discrete on/off capacity (Itakura 2001). Nevertheless, chimpanzees seem to have a capacity to recognize themselves in a mirror and to possess (a level of) self-awareness insofar as we can judge by mirror self-recognition.

#### *Visual perspective taking*

Visual perspective taking means the ability to take another’s visual point of view and to assess what others do and do not see. It consists of several, cognitively differently demanding aspects: understanding the necessity of certain physical properties of a visual trajectory (e.g. that face and/or eyes must be directed towards the object, there are no barriers on the trajectory etc.), understanding that the other forms a representation of the object, and understanding that the other sees something else than the subject sees (distinction of representation of self and other) (e.g., Bräuer et al. 2005). One of the paradigms to study visual perspective taking is ‘gaze following’ i.e. whether a subject follows the conspecific’s or human’s gaze towards an object (which either is or is not there) (Tomasello et al. 1998; Call et al. 1998). This paradigm is built upon the assumption that the subject understands that the other sees something the subject does not see and to gain information the subject follows the other’s gaze

toward the object. However, passing the test does not necessarily mean that the subject understands the other's mental state ('seeing'), but merely acts on a learned association between 'other looking somewhere, self searching randomly in the same direction until the object is found' and a reward. Therefore, some tests have increased the level of complicatedness by adding a visual barrier between the subject's visual trajectory so that the subject has to move to gain a view on the object (Tomasello et al. 1999). Chimpanzees pass these tests and frequently perform 'check looks' back at the experimenter to confirm the direction of gaze if there was nothing to see (Call et al. 1998).

Another set of experiments known as the Guesser-Knower paradigm taps into the connection between seeing and knowing, or attributing knowledge to other. The basic version of the test involves two experimenters facing a chimpanzee, one who is knowledgeable ('knower') and one who is not ('guesser'). Hidden from the chimpanzee, but visible for the two experimenters a bait is placed to a container (one of several containers on a table). The guesser's information of the baiting is blocked by a visual occluder (eyes covered, bucket over the head, etc.). Both experimenters point to one of the buckets and the chimpanzee has to understand which of the experimenters knows where the bait is (Povinelli and Eddy 1996). Chimpanzees consistently failed the tests, or require a large amount of training before they succeed, and were concluded not to understand visual perspectives (Povinelli et al. 1990; Povinelli and Eddy 1996). However, these tests have been criticized for lacking ecological validity (Tomasello and Call 1997; Hare 2001). Therefore, a new paradigm, which relied on the naturally competitive tendency of chimpanzees, was developed by Hare et al. (2000). The basic setting involves two animals, the subject and the chimpanzee competitor who is dominant over the subject. Two food items are placed in the middle, one of which is visible to both individuals and the other being visible only to the subordinate subject. This setting aimed tests whether a chimpanzee is able to judge if the competitor has visual access to the food rewards, and if a chimpanzee can use this information to get a reward. Several variations of the same theme were ran along with many controls (e.g. the similar set up but the original competitor absent or delayed in the setting to rule out

subject reading the competitor's behaviour (Hare et al. 2001; Hirata and Matsuzawa 2001). Chimpanzees passed the tests. The combined results of these competitive visual perspective taking tests suggest that chimpanzees do understand what others can and cannot see, remember what the competitor saw in immediate past, and can use this information to direct their behaviour to their own benefit (Tomasello et al. 2003a,b, Call 2003).

### *False belief*

Understanding false beliefs relates to one of the core aspects of ToM, as it demands the capacity to form a representation of the other's belief and yet to understand that other's belief (or representation) is different from the belief or knowledge of self and from the reality. Traditionally, false belief is taken as the yard stick for a full blown, adult human-like ToM (Wimmer and Perner 1983). The classic false belief test is known as the "Sally-Anne test" (a.k.a. Location Change test), in which the subject sees (or hears a story of) Sally putting a toy in a basket and going out of the room. In Sally's absence, Anne moves the toy from the basket into a box. When Sally returns, the subject is asked where Sally will look for her toy. A correct prediction indicating the understanding of false belief is that Sally will look for the toy in the basket and not in the box where it is now hidden. Human children pass the test at around 4 years of age (Baron-Cohen et al. 1985; Perner 1991; Wellman et al. 2001). Younger children tend to predict that Sally looks for the toy in the box, because they cannot distinguish their own knowledge from Sally's belief (Wellman et al. 2001). Some researchers, however, claim the test to be unsuitable for testing children at the early stages of false belief understanding due to its demand for developed linguistic skills and the difficulty of suppressing interference of own knowledge of the truth (Call and Tomasello 1999; Apperly et al. 2005; Onishi and Baillargeon 2005). With non-verbal paradigms children as young as 15 months may understand false beliefs (Onishi and Baillargeon 2005; but see Ruffman and Perner 2005), although in another non-verbal test even some four-year-olds failed the test (Call and Tomasello 1999). Obviously, chimpanzees cannot be tested with the original, verbal paradigm. A few attempts have been made to test chimpanzees with a

non-verbal version of the Sally-Anne test or a modification of it (Premack 1988; Call and Tomasello 1999) and chimpanzees fail these tests (Call and Tomasello 1999; review in Whiten 1997). The Guesser-Knower paradigm described above also taps into the ability of understanding 'knowledge versus belief' and, as noted above, chimpanzees have failed those tests as well (Povinelli et al. 1990). To conclude, thus far there is no evidence for chimpanzees' understanding others' beliefs and/or the difference between other's beliefs and own representation of the 'truth'.

### *Intentionality*

Intentionality (indicating behaviour's 'aboutness' of an object and/or indicating 'on purpose': see Flavell 2000; Tomasello and Rakoczy 2003) can be approached via addressing intentionality in own communication or via attribution of intentionality to others. Chimpanzees appear to understand something about intentions in other's actions, as they distinguish between unwillingness and inability to reach a particular goal (Call et al. 2004). Also, anecdotes on joint goal-oriented action lend support to a chimpanzee understanding of intentionality in action (see e.g. de Waal 1982 on joint mounting to trees). In contrast, chimpanzees appear unable to understand intentions prior to an action (Tomasello et al. 2003a). Intentionality in chimpanzees' own communication is supported more strongly. Chimpanzees understand the need of attentive audience for successful gestural communication, they alter their gaze between the desired object and the target of communication, and they persist and elaborate their signalling in the absence of the positive response (Leavens and Hopkins 1998; Leavens et al. 2004; Leavens et al 2005). Thus, chimpanzees appear to be able to signal intentionally and interpret other's behaviour as intentional but there is no evidence of understanding intentionality in others' communication or prior intentions (Call 2003).

### *Intentional Deception*

A particular case of intentional behaviour is deception. To deceive others intentionally, the subject must understand that the beliefs of the other are

separate from those of self, and can be manipulated to own benefit. Non-intentional deception, sending inaccurate signals, is common in primate and non-primate animal species (Krebs and Dawkins 1984; Cheney and Seyfarth 1991). At the simplest level deception is non-cognitive, inflexible cheating in signalling, which is a strategy acquired by all or certain individuals of the population (e.g. camouflage, Batesian mimicry, etc.; Krebs and Dawkins 1984). More computationally demanding is deception that is flexible to contexts and situations. Many primates have been observed to occasionally deceive their group mates to receive a benefit for self (Whiten and Byrne 1988; Cheney and Seyfarth 1990; Byrne and Whiten 1992; Byrne 1995). Refraining from giving a food call in a proximity of monopolisable food and snatching a piece of preferred food from a higher ranking individual while grooming him are examples of deceptive behaviour (Byrne and Whiten 1990). Although the behaviours often appear as intentionally deceptive, most of them are likely to result from non-mentalistic processes. An animal can be exploiting the unexpected opportunity that was not planned at all, or it may have learned after a few similar occasions that a particular action leads to a reward. The latter option is indeed deceptive, but it does not require any understanding of the other's state of mind. Deceptive behaviour that does not require attribution of mental states has been labelled 'tactical deception' (Whiten and Byrne 1988; Byrne and Whiten 1992) or 'functional deception' (Hauser 1997). Most of the reported cases of deception in chimpanzees can be classified as tactical deception and thus, to be non-mentalistic. Therefore, most researchers agree that currently there is no evidence for chimpanzees' capacity for intentional deception (Whiten and Byrne 1988; Heyes 1998; Cheney and Seyfarth 1991; Tomasello and Call 1997; but see Hare et al. 2006).

#### *Recognition of emotions – empathising*

Chimpanzees' ability to understand other's emotions has received less attention than the aforementioned aspects of mental state attribution. In fact, very few experiments have addressed the topic at all. The ability to understand other's emotions, to empathise, is suggested to be a multilayered process of cognitively

different components (Preston and de Waal 2002a,b). The empathic process includes the ontogenetically early emotion matching (a.k.a. vicarious empathy, affective resonance: Hatfield et al. 1993), in which a subject is not able to make a distinction between self and other and copies the other's emotion (Brownell and Carriger 1990; Hatfield et al. 1993). Gradually emotional contagion becomes more cognitively processed until empathy reaches the cognitive levels of adult humans (Hoffman 2000). In cognitive empathy the distinction between self and other is maintained and the subject understands that the emotional state of the other is separate from the state of self (Preston and de Waal 2002a). Hence, the cognitive level of empathy relates to an understanding of other's perspective and maintaining the difference between own representation and those of the others.

The few experiments on recognition of emotions suggest that chimpanzees master at least some levels of the empathic process. Chimpanzees show emotional contagion on emotionally charged videotapes (Parr 2001). Chimpanzees also show contagious yawning (Anderson et al. 2004; Anderson and Matsuzawa 2006), which may be based motor contagion with no mental state assessment, paralleling the process with emotion matching. However, in humans contagious yawning is connected to (cognitively) empathic abilities (Lehmann 1979; Platek et al. 2003). Finally, chimpanzees are shown to understand the emotional meaning of facial expressions, which could mean they understand the other's emotional state (Parr 2001).

Empathy in humans extends to sympathetic, other-regarding (a.k.a. pro-social) behaviour. The first helping efforts emerge together with the mirror self-recognition at around two years of age (Bertenthal and Fischer 1978; Zahn-Waxler et al. 1992), and other-regarding behaviour increases in frequency and level of complexity when the child develops a full distinction of self and others (Brownell et al. 2002). Again, only a few experiments have been conducted on chimpanzees' other-regarding behaviour. A few juvenile chimpanzees were tested on their spontaneous helping tendency and they indeed helped the human experimenter struggling to achieve a goal (Warneken and Tomasello 2006). However, in food related tasks chimpanzees have failed to show other-regarding

behaviour, even when 'helping' (i.e. giving food) involved incurred no costs to self (Silk et al. 2005; Jensen et al. 2005).

Regardless of the scarce evidence, chimpanzees have long been assumed to be empathic. This is largely due to a particular post-conflict behaviour named consolation (de Waal and Aureli 1996). Consolation, in brief, is affiliative behaviour by a group member given to a participant of an aggressive conflict (see Chapters 3, 4, and 5). These interactions involve often hugging, patting and gentle touching (de Waal and Aureli 1996; Koski unpublished data) and certainly appear very 'sympathetic'. After its initial description (de Waal and van Roosmalen 1979), consolation has been used as evidence for chimpanzees' empathic tendencies (O'Connell 1995; de Waal 1996, 2005; Flack and de Waal 2000; Preston and de Waal 2002a,b; de Waal et al. 2005, Palagi et al. 2006). However, no attempts have been made to determine the cognitive capacities involved in consolation. Furthermore, it is unclear on which cognitive level of empathy consolation may operate.

In conclusion, experimental evidence on chimpanzee's empathic skills is weak. Considering the cognitive skills chimpanzees have (perspective taking, self-recognition, intentionality in action) and their ability to attach an emotional meaning to facial expressions, it is possible that chimpanzees do understand something about other's emotions. However, currently it is unclear on which cognitive level this would occur.

#### *Criticism, an explanation of a third kind, and conclusions*

The paradigms summarised above show that chimpanzees pass some ToM related tasks, while they fail others. Yet, the topic of chimpanzee cognitive skills remains controversial. All of the above evidence on chimpanzee cognitive skills has been criticised as non-conclusive. Most notably, Povinelli and colleagues have claimed that the paradigms used to date do not allow us to separate between skilful behaviour/cue reading and the formation of mental abstractions (e.g., Povinelli and Vonk 2003, 2004). This 'low-level' explanation opposes the mentalistic explanations on chimpanzee performance (see also Heyes 1998). Also, problematically enough, humans are masters of attaching mental states to

other animals and for that reason prone to read animal performance as mentalistic, especially if the task performance appears similar between humans and non-human primates (Hauser 2000; Povinelli and Vonk 2003).

In an effort to find a fruitful outcome, it has been suggested that we should 'turn up the microscope'; instead of debating on a yes/no level on chimpanzees' cognitive abilities, we should see beyond the dichotomous monolith on ToM (Tomasello et al. 2003a,b; Call 2003). The view advocated by Tomasello, Call, and Hare is that chimpanzees are neither 'behaviourists' nor 'meta-representational' creatures, but something in between. Their approach parallels with that of Suddendorf and Whiten, who compare chimpanzees to children at the secondary representational level (sensu Perner 1991, term not to be confused with the second-order intentionality of Dennett 1983, see Box 1; Whiten 1996; Suddendorf 1998; Suddendorf and Whiten 2001). On the secondary representation level children pass tasks of mirror self-recognition, and show rudimentary helping and sympathetic behaviour, but do not have a full developed ToM and do not pass false belief tests. Current evidence on chimpanzee cognitive skills suggests that chimpanzees may be placed approximately at this level, albeit not all the tasks that children manage at this stage have been tested in chimpanzees (Suddendorf and Whiten 2001; Tomasello et al. 2003a; Call and Tomasello 2005; Hare et al. 2006).

### **The aims and outline of this study**

The aim of this study was to investigate chimpanzee social cognition in the framework of conflict resolution. Especially, I investigated the occurrence, function and mechanisms of post-conflict interactions. The assessment of their occurrence was done by determining the most important factors that influence post-conflict behaviour, and assessing how occurrence of these behaviours influences one another. Addressing the function of post-conflict behaviours obviously cannot be operated at the level of ultimate fitness consequences of behavioural strategies in such a short-term, observational study; instead I approached the functions at the level of reasons to perform the behaviour and the effects, costs and benefits involved in these behaviours. The mechanisms

were addressed at the levels of possible emotional and cognitive processes underpinning post-conflict behaviour.

**In the first study (Chapter 2)** I investigate the function of reconciliation. Reconciliation denotes selective, friendly contacts between the opponents soon after aggression of a conflict has ceased. Since the first description of reconciliation in the Arnhem chimpanzees more than 25 years ago (de Waal and van Roosmalen 1979), it has been a topic of extensive research. Reconciliation is now described in over 30 primate and some non-primate species (Aureli et al. 2002). The function of reconciliation is tested on various species and is generally agreed upon. The most widely accepted view is that the function of reconciliation is relationship repair with the opponent (Aureli et al. 2002). As reconciliation also carries risks, reconciliation should be attempted when maintaining the benefits associated with the relationship are more important than the risks of reconciling. Thus, reconciliation is more prevalent among partners with a high quality relationship. In addition, reconciliation provides immediate benefits to conflict opponents by decreasing the post-conflict stress and the chance of further aggression. These two levels of explanations were combined in the integrated hypothesis (Aureli 1997; Aureli and Smucny 2000), which proposes that opponents' post-conflict anxiety depends on their relationship's quality. Opponents of a high quality relationship become more distressed by the conflict than dyads of a weaker quality relationship. As reconciliation decreases this anxiety, opponents are more likely to seek stress alleviation when its levels are higher. Thus, distress provides a mediating mechanism for the conciliatory behaviour. However, despite its obvious theoretical appeal, the integrated hypothesis has only been tested on macaque species (Aureli 1997; Kutsukake and Castles 2001), which comply with the framework of the hypothesis. In chimpanzees, as in other apes, the hypothesis had not been tested.

The first study tests the integrated hypothesis. Especially, I was interested in investigating the role of anxiety as the mediating mechanism on reconciliation. The second aim of the study was more general. Even though in recent years chimpanzee conflict resolution has attracted a renewed research interest

prompting several studies in the wild and captivity (Arnold and Whiten 2001; Preuschoft et al. 2002; Fuentes et al. 2002; Wittig and Boesch 2003a,b; Kutsukake ad Castles 2004), the studies reported differing results. Furthermore, the conclusions from some of these studies were weakened by a limited sample size. Therefore, the second aim of the study was simply to provide comparable, well controlled results on chimpanzee reconciliation with a fairly decent sample size.

In the light of the general aim of the thesis, investigating the function of a post-conflict interaction and its emotional mediator was particularly interesting. By testing the integrated hypothesis I combined the functional side of reconciliation (i.e., relationship quality in relation to the frequency of reconciliation) to the mediating mechanism of post-conflict anxiety.

**The second study (Chapter 3)** takes a more general view on chimpanzee post-conflict interactions (PCI). The conflict opponents and the other group members have a variety of behaviours to choose from, and it is currently unclear how the choices between these options are made (cf. Wittig and Boesch 2003b). Opponents may affiliate with each other and/or with other group members, or direct further aggression to each other or to other group members. Other group members, in turn, have the option of getting involved with an opponent affiliatively or aggressively, or to refrain from interactions. This study aimed at determining the predictors for occurrence and the inter-relatedness between these PCI. I investigated the occurrence of four PCI, plus a counterpart option 'no interactions'. The four PCI were reconciliation, third-party affiliation (the term we introduced to replace 'consolation', see Ch 4), further (or redirected) aggression and third-party aggression. The conventional method is to assess, which factors of the conflict or of the opponent dyad determine the occurrence of one particular PCI in isolation from other PCI. Studying PCI separately from one another ignores their potential interrelatedness (cf. Wittig and Boesch 2003a;). Furthermore, the factors influencing the occurrence of PCI are rarely examined simultaneously, which does not allow assessment of their relative importance as determinants (see exceptions Call et al. 1999; Wittig and Boesch 2003a, 2005; Schino et al. 2004). Thus, the aim was to first investigate

whether and how the PCI influence one another. Thereafter, I investigated for each PCI the relative importance of several possibly determining factors. This study was designed to give a more complete picture on the 'decision-making' process after conflicts, providing information both on the determinants of each PCI and on the factors an individual needs to take into account upon 'deciding' which, if any, PCI to employ. This study weighs more on the functional level but provides some insights to the mechanistic level as well.

**The third study (Chapter 4)** focuses on consolation. Consolation was described together with reconciliation in the seminal paper of chimpanzee post-conflict interactions by de Waal and van Roosmalen (1979). Consolation describes friendly contacts by a former bystander towards a conflict participant. Traditionally, the definition of consolation included only contacts towards conflict victims (de Waal and van Roosmalen 1979), whereas the contacts towards aggressors were labelled as 'appeasement' (de Waal and van Hooff 1981; Das 2000; Kutsukake and Castles 2004). However, since little was known about consolation and appeasement and both terms denote a similar behaviour, I included both under the term 'consolation'. Like reconciliation, consolation has received extensive attention in primate studies. However, it is understood considerably less well than reconciliation, in terms of both its function(s) and mechanism(s). This is largely due to its confirmed existence only in some ape species but not in monkeys, in spite of extensive research effort (apes: de Waal and van Roosmalen 1979; de Waal and Aureli 1996; Kutsukake and Castles 2004; Palagi et al. 2004, 2006; Mallavarapu et al. 2006; monkeys: reviewed by Das 2000; Watts et al. 2000; but see Call et al. 2002. Ch 3-5). As the label suggests, consolation is assumed to calm down the recipient's stress. It has also been suggested to provide comparable benefits to reconciliation, and therefore to be a substitutive interaction when reconciliation is not provided or possible (Watts et al. 2000; Wittig and Boesch 2003a). A few studies have supported the 'substitution' hypothesis, in that consolation occurred more often when reconciliation did not (Wittig and Boesch 2003a; Palagi et al. 2004). These studies, however, did not address the stress reduction function, which underlies the functional significance of the substitution hypothesis.

In this study I tested the fundamental assumption of consolation, namely alleviation of stress of the recipient of affiliation. Secondly, I tested the substitution function of consolation, both regarding the absence/presence in relation to reconciliation, and the identity of the consoler. This study provided fundamental information on the interaction labelled 'consolation', which prompted us to rename it as third-party affiliation, and served as the basis on which to build the following studies.

**The fourth study (Chapter 5)** continues with what had started in Chapter 4, namely, finding a possible function for third-party affiliation. We investigated whether third-party affiliation would benefit the actors instead of the receivers, the traditionally assumed beneficiaries of third-party affiliation. Specifically, we addressed the possibility that affiliation protects the third parties from further aggression from the opponents. This hypothesis has been suggested by a few authors (Call et al. 2002; Palagi et al. 2004), but was never tested (with the exception of an unpublished study on long-tailed macaques; Das 1998). This study is thus the first one to test and find evidence for a new function of third-party affiliation. In addition, the new information provided in this study in combination with the studies of Chapters 3 and 4, allowed me to make some inferences about the possible cognitive processes underlying third-party affiliation.

**The fifth study (Chapter 6)** focuses on the cognitive processes in third-party affiliation. In particular, I addressed empathy as a possible underlying process of third-party affiliation. First, I reviewed the empathic process and introduced different levels of empathy, stemming from human developmental psychology. Thereafter, I sought for the most parsimonious explanation for cognitive capacities required for chimpanzee third-party affiliation. Although the principle of parsimony in cognitive research is debated both conceptually (whether parsimony provides the best explanatory model) and practically (whether the 'mentalistic' or 'behaviourist' explanation is more parsimonious) (e.g., Heyes 1998; Flack and de Waal 2000; Povinelli and Vonk 2004), I aimed at explaining third-party affiliation with the simplest mechanism possible. I distinguished between affiliation by kin and by unrelated individuals, since kin

may have a different predisposition for empathic affiliation than non-kin. Further, I underlined the importance of specifying the level of empathy that is sufficient for affiliative behaviour. This chapter emphasises the proximate level of post-conflict behaviour, but bases its views strongly on the functions. Further, by putting into the spotlight the most famous example of chimpanzee empathic behaviour, the study has a more general goal of discussing chimpanzee empathic skills.

Altogether, this study scrutinises chimpanzee social behaviour with the aim of combining functional and mechanistic approaches. This is achieved by studying the occurrence, function and mechanism of post-conflict interactions.

## *CHAPTER 2*

---

### RECONCILIATION, RELATIONSHIP QUALITY

### AND POST-CONFLICT ANXIETY:

Testing the integrated hypothesis in captive chimpanzees.

---

Sonja E. Koski\*, Kathelijne Koops, and Elisabeth H.M. Sterck

*Published in American Journal of Primatology 2007: 69, 158-172.*

## **ABSTRACT**

Reconciliation is a conflict-resolution mechanism common to many gregarious species with individualized societies. Reconciliation repairs the damaged relationship between the opponents and decreases post-conflict (PC) anxiety. The “integrated hypothesis” links the quality of the opponents’ relationship and PC anxiety, since it proposes that conflicts among partners with high relationship quality will yield high levels of PC anxiety, which in turn will lead to an increased likelihood of reconciliation. We tested the integrated hypothesis in captive chimpanzees (*Pan troglodytes*) in the Arnhem Zoo, the Netherlands. We applied the standard PC – matched control (MC) method. Our study mostly supported the Integrated hypothesis, in that more valuable and compatible partners (i.e. males and frequent groomers) reconciled more often than less valuable and weakly compatible partners (i.e. females and infrequent groomers). In addition, PC anxiety was higher after conflicts among males than among females. Emotional arousal thus appeared to be a mediator facilitating reconciliation. However, in contrast to the predictions derived from the integrated hypothesis, PC anxiety appeared only in aggressees, and not in aggressors, of conflicts. This suggests that while relationship quality determines PC anxiety, it is dependent on the role of the participants in the conflict.

## **INTRODUCTION**

In group living animals, the inevitable competition over limited resources leads to conflicts of interest between group members. In order to maintain group coherence and the social relationships therein, disruptions caused by possibly aggressive conflicts should be minimized. Escalation of conflicts can be prevented by various management strategies, such as signaling formal dominance, performing rituals, and respecting possession [e.g., de Waal, 1992a; Cords and Killen, 1998; Koyama, 2000; Preuschoft and van Schaik, 2000]. When aggressive conflicts do occur, the deleterious effects on the group and on the relationships can be mitigated after the conflict [Kappeler and van Schaik, 1992; Aureli and de Waal, 2000]. Several post-conflict (PC) resolution mechanisms exist, such as friendly social interactions with the former opponent and with other group members [e.g., Aureli and de Waal, 2000; reviewed by Aureli *et al.*, 2002].

Reconciliation, or friendly interaction between the previous opponents soon after a conflict, was first described by de Waal and van Roosmalen [1979] in chimpanzees (*Pan troglodytes*) in the Arnhem Zoo, the Netherlands. Since then, reconciliation has been found in some 30 primate species [Aureli and de Waal, 2000; reviewed by Aureli *et al.*, 2002] and in a few non-primate species [reviewed by Schino, 2000]. Combined evidence from these studies indicates that reconciliation reduces the occurrence of further aggression [e.g., Aureli and van Schaik, 1991a; de Waal, 1993; Watts, 1995; Silk, 1996; Kutsukake and Castles, 2001], reduces anxiety caused by the conflict [Aureli and van Schaik, 1991b; Castles and Whiten, 1998b; Das *et al.*, 1998], and restores the damaged relationship to pre-conflict levels [Cords, 1992; Koyama, 2001; Wittig and Boesch, 2005].

The quality of the opponents' relationship has been shown to be an important determinant of reconciliation. Reconciliation carries risks. Approaching the former opponent can lead to renewed aggression [Aureli and van Schaik, 1991a; Aureli *et al.*, 2002], and therefore reconciliation should only be attempted when the benefits overcome the risks for both opponents. Thus, after a conflict

with a valuable partner, the gained benefit of repairing the relationship is greater than the risk associated with reconciliation [the valuable relationship hypothesis: de Waal and Yoshihara, 1983; Kappeler and van Schaik, 1992; de Waal and Aureli, 1997]. Value is understood on the ultimate level as increasing the fitness of both partners [cf. Kummer, 1978]. Indeed, many studies have confirmed that reconciliation is more likely after conflicts between valuable partners; among kin in kin-bonded species [e.g., *Macaca* spp.: reviewed by Aureli *et al.*, 1997 and by Thierry, 2000], among affiliating individuals [rhesus macaques: de Waal and Yoshihara, 1983; chimpanzees: Preuschoft *et al.*, 2002; bonobos: Palagi *et al.*, 2004], and among frequently co-operating individuals [chimpanzees: de Waal and van Roosmalen, 1979; de Waal, 1986; Wittig and Boesch, 2003; gorillas: Watts, 1995; Assamese macaques: Cooper *et al.*, 2005].

The risk of receiving further aggression is greater for the aggressee of the conflict [Aureli and van Schaik, 1991b]. However, as not only aggressees but also aggressors of conflicts experience elevated levels of anxiety [reviewed by Aureli *et al.*, 2002], Aureli [1997; Aureli and Smucny, 2000] proposed in the integrated hypothesis that the PC anxiety relates to uncertainty regarding the future of the relationship with the former opponent. Experienced emotional disturbance after a conflict is greater when the damaged relationship has a high value to the opponents. Hence, anxiety acts as an emotional mediator in the act of reconciliation [Aureli and Schaffner, 2002]. The integrated hypothesis was the first to connect the relationship quality between the opponents and the emotional disturbance after conflicts. It thus provides a link between the function and the possible proximate mechanism of reconciliation.

It was recently pointed out that relationship quality consists of three dimensions: value, security and compatibility [Cords and Aureli, 2000]. Value refers to the direct fitness benefit gained from the relationship for example via support in conflicts or mating accessibility. Security refers to the predictability of a partner's future actions, relating to the consistency of interactions in time. Compatibility is the general tenor of the relationship, the 'friendliness' of the interaction partners. All three dimensions are likely to affect the occurrence of reconciliation [Cords and Aureli, 2000; Aureli *et al.*, 2002; Cooper *et al.*, 2005].

A high value will lead to more reconciliation, and supposedly has the most profound effect on reconciliation. Since security influences the predictability of the relationship, low security may lead to a higher need to reconcile conflicts. Compatibility influences the accessibility of the partner. Compatible partners can access each other with ease making reconciliation less risky [Cords and Aureli, 2000].

Thus far, the integrated hypothesis has been directly tested only with the genus *Macaca* [*M. fascicularis*: Aureli, 1997; *M. fuscata fuscata*: Kutsukake and Castles, 2001]. These studies provided support for the hypothesis, in that PC stress depended on the relationship quality of the opponents, and reconciliation was more likely after conflicts between 'friends' or valuable partners. In this study we tested the integrated hypothesis in captive chimpanzees. Although many recent studies have shown a remarkably increased interest in chimpanzee conflict resolution [captivity: Casperd, 1997; Preuschoft *et al.*, 2002; Fuentes *et al.*, 2002; Palagi *et al.*, 2006; wild: Arnold and Whiten, 2001; Wittig and Boesch, 2003a, b, 2005; Kutsukake and Castles, 2004], only one of these studies included measures of PC anxiety, which was not shown to increase after conflicts [Arnold and Whiten, 2001]. One of the cornerstones of the function of reconciliation -- stress alleviation -- has yet to be tested in chimpanzees. Therefore, we tested the dependence of PC stress on the relationship quality of the opponents and incorporated value and compatibility in the measure of relationship quality. 1) We expect that relationship quality determines the tendency to reconcile. Based on chimpanzee social structure and demography, we expect male chimpanzees to have the highest relationship value with each other compared to female-female and inter-sex relationships (e.g., Nishida, 1979; Goodall, 1986; Wrangham, 1986; Watts, 2002). Hence, we predicted that male-male conflicts would be more often reconciled than female-female and inter-sex conflicts. 2) We predicted that conciliatory tendency would reflect the dyadic relationship compatibility, and hence that strongly compatible dyads would reconcile more often than dyads of weak compatibility. 3) We expected that relationship quality determines PC anxiety; therefore, we predicted that male-male conflicts yield higher levels of PC anxiety than female-female

conflicts. 4) We predicted that reconciliation would alleviate PC anxiety. Based on the integrated hypothesis, we further expected that both conflict participants experience anxiety after conflicts, since the anxiety is presumed dependent of the relationship quality of the opponents [Aureli, 1997].

## **METHODS**

### Study group

We studied a group of chimpanzees in the Burgers' Zoo in Arnhem, the Netherlands. The group was established in 1971. During the summer months, the group lives in an outside enclosure of about 0.7 ha, whereas during the winter months they stay indoors in a hall of 21x18 m. For further details of the colony and husbandry, see van Hooff [1973a], Adang *et al.* [1987] and Takeshita and van Hooff [2001].

The groups consisted of 30-34 individuals during the study period: 3-5 adult males, 15-18 adult females, 0-2 adolescent males, 1-3 adolescent females, 7-9 juveniles and infants [age classes as in Preuschoft *et al.*, 2002]. All but five individuals were born in the group and none were introduced to the group during the study. Four chimpanzees were born, three infants and one adult female died, one adult male and three adult females were sent to other zoos.

### Data collection

The first author together with several students observed the chimpanzees during June 2002- February 2004. Inter-observer reliability was ensured by >95% similarity in focal observations of each student and SEK. We collected data using continuous focal animal sampling of 15 minute duration [Altmann, 1974] on adults and adolescents. Observations were evenly spread throughout the day. We recorded social interactions within the focal individual's social space (defined as two arm lengths). Data on grooming we recorded as the duration of a grooming bout to the nearest second. A new bout was assigned when direction of grooming changed, or when there was a  $\geq 30$  sec break between bouts. Altogether we collected 872.9 hrs of focal data. Each individual was observed on

average 39.7 hrs (range 36.9-41.5 hrs). The ethogram was based on van Hooff [1973b].

Data on conflicts we collected *ad libitum*. We recorded conflicts of adults and adolescents. An aggressive interaction was defined as a conflict if it included at least one of the following: chase, push, grab, hit, jump-on, trample, bite, and if the recipient of aggression showed at least open-bared-teeth and screams. The roles of aggressor and aggressee were assigned based on the initial direction of aggression. We categorized conflicts in terms of directionality (unidirectional= aggression only from aggressor to aggressee; bidirectional= both combatants direct aggression to each other), intensity (low=only chase and/or one hit by aggressor, scream by the aggressee; high= all other physical aggression), and context of the conflict (food or non-food).

We conducted PC observations following de Waal and Yoshihara [1983] and Aureli *et al.* [1989]. Duration of PC observations was 10 minutes, during which we recorded all interactions of the focal animal with other group members, timing them to the second. We conducted PC observations on both aggressors and aggressees simultaneously, whenever possible. As a measure of PC anxiety we recorded scratching, as scratching is the most prevalent self-directed behaviour of chimpanzees in stressful situations [Baker and Aureli, 1997; Aureli and de Waal, 1997; Leavens *et al.*, 2001]. A new scratching bout was assigned when the scratched body part changed, or when scratching was resumed after >5 sec. If the conflict was resumed within 2 min, we cancelled the PC and started anew when aggression ceased.

PC observations were matched with control observations (MC) on the next possible day, within 7 days from the conflict. We conducted MCs at the same time of the day as the conflict, controlling for context (i.e., presence or absence of food) and availability of the former conflict partner (i.e., the former partner was present in the enclosure). Since we conducted the study in captivity and all group members had in principle an equal chance to interact with each other, we did not control for the inter-opponent distance at the beginning of the MCs [Call, 1999]. We applied similar methods during both indoor and outdoor observations.

### Data Analysis

We recorded a total of 456 conflicts, of which in 406 we obtained simultaneous data on both aggressors and aggressees ( $N_{\text{aggressees}} = 449$ ,  $N_{\text{aggressors}} = 413$ ). 97 conflicts (21.3%) included at least one supporting party. However, we included only the original opponent dyads in the analyses and thus excluded the supporting parties as independent opponent pairs.

We demonstrated the occurrence of reconciliation using two methods. First, we used the PC-MC method [de Waal and Yoshihara, 1983], in which the timing of the first affiliative contact between the former opponents is compared between PC and MC. Following contacts were defined as affiliative: contact sit, gentle touch, fingers/wrist to mouth, embrace (ventro-ventral or sideways), mount, genital touch or inspection, mate, kiss, kiss bite, groom, and contact play. If the affiliative contact occurred earlier, or only, in PC the pair was labeled 'attracted'. If the contact occurred earlier, or only, in MC the pair was labeled 'dispersed'. If the affiliation occurred exactly at the same time in PC and MC, or if there was no affiliation in either PC or MC, the pair was labeled 'neutral'. The proportions of attracted and dispersed pairs were compared with Wilcoxon signed-ranks tests. We obtained the corrected conciliatory tendency (CCT) of each individual with a measure that corrects for the baseline affiliation [Veenema *et al.*, 1994]:

$$\text{CCT} = 100 * ((\text{attracted} - \text{dispersed}) / \text{total number of pairs}).$$

We calculated CCT of each individual, from which we obtained the mean CCT of the group. Thereafter, individual CCTs were calculated according to sex class representing relationship value (i.e., male-male, female-female and inter-sex conflicts), context (food and non-food) and characteristics (uni- and bidirectional, low and high intensity) of a conflict, and the relationship compatibility of conflict participants (strongly, moderately and weakly compatible). Thus, each individual contributed two (in the case of context, conflict intensity and directionality, and sex class) or three (in the case of relationship quality) CCT values for comparisons. To calculate individual CCTs we used the minimum criterion of three qualifying PC-MC pairs for each individual in each conflict category.

Second, we used the time-rule method [Aureli *et al.*, 1989], which compares the temporal distribution of the first affiliative contact between the former opponents during PC to that during MC.

We considered the occurrence of renewed aggression as a factor possibly influencing the occurrence of reconciliation. However, the occurrence of renewed aggression was very low (N= 4) and we therefore discarded these conflicts from the analyses.

We assessed PC anxiety following Aureli and van Schaik [1991b] and Castles and Whiten [1998b]. First, we calculated the temporal distribution of scratching during unreconciled PCs. We calculated individual means for each minute of PC, and from individual means calculated the group average scratching rate for each minute of PC. This was compared to the baseline rate (with 95% confidence intervals) derived from each individual's mean MC rate over ten minutes. We checked the generality of the results by comparing PC and MC rates of each individual with Wilcoxon signed-ranks tests. To investigate the effect of reconciliation on scratching rates, we derived a time window during which the group average scratching rate deviated from the 95% confidence intervals of the group average MC rate. Within that time window we calculated the individuals' mean scratching rates after reconciliation and compared that to individual scratching rates in PCs without reconciliation, to pre-reconciliation rates and to MCs. The rates after reconciliation were calculated from the moment of actual reconciliation, and rates without reconciliation after the average latency to reconciliation. The PC scratching rates were calculated separately for aggressors and aggressees. Although all individuals participated in both roles, some individuals did not provide sufficient scratching data in every category. We obtained scratching rates of unreconciled conflicts for 19 and 22 individuals as aggressors and aggressees, respectively, and on reconciled conflicts for 10 and 20 individuals as aggressors and aggressees, respectively. We followed the operational definition of reconciliation by including only attracted pairs as reconciled conflicts [Cords, 1993]. The scratching rates of conflict sex classes were inferred from PCs before and PCs without reconciliation and averaged over aggressor and aggressee data to ensure a sufficient sample size per individual.

To investigate the effect of relationship compatibility on conciliatory tendency, we classified dyadic relationships into strongly, weakly and moderately compatible. We assessed the compatibility category by summing grooming durations and contact sitting rates, respectively, of each dyad corrected to the observation hours [Preuschoft *et al.*, 2002]. The dyadic scores were ranked individually and the scores falling into the top quartile were labeled as strongly compatible, the lowest quartile was labeled as weakly compatible and the mid 50% as moderately compatible [Cords and Aureli, 2000; Arnold and Whiten, 2001]. Thus, each dyadic value was evaluated within each individual's own range of grooming and contact sitting activity. The conflicts were classified according to these relationship quality categories.

All analyses of CCTs, relationship qualities, and anxiety levels were conducted at the individual level. Individual values were tested with Wilcoxon-signed ranks (Wilcoxon), Friedman two-way analysis of variance (ANOVA Friedman), and Mann-Whitney U (MWU) tests. All analyses were two-tailed unless stated otherwise and the level of significance was set at  $\leq 5\%$ .

## **RESULTS**

### Demonstration of reconciliation

We confirmed the occurrence of reconciliation in the Arnhem chimpanzee colony. The proportion of attracted pairs was significantly greater than the proportion of dispersed pairs (mean proportion of attracted pairs= 26.4%, dispersed pairs= 4.7%; Wilcoxon:  $z=-4.29$ ,  $p<0.001$ ,  $N=24$ ). This indicates that the majority of affiliative contacts between the opponents occurred earlier in PC than in MC. The time rule method confirmed the result, former opponents affiliated significantly earlier in PCs than in MCs (Wilcoxon:  $T+=1$ ,  $p=0.011$ ,  $N=10$ ; figure 1). The mean latency to the first affiliative contact between the opponents was 3.31 min (median 1.97 min), and the majority (57.8%) of contacts occurred within the first three minutes.

The average corrected conciliatory tendency (CCT) of the group was 21.6% ( $\pm 9.4$  SD) calculated by taking the mean of individual CCTs. Affiliation in PC was more likely between the opponents than with any other group member,

as is expected if reconciliation is not due to a general elevation of affiliation levels after aggression ('selective attraction'; Wilcoxon: aggresses: N=23,  $z=-3.86$ ,  $p<0.001$ ; aggressors: N=23,  $z=-2.50$ ,  $p=0.012$ ).

There was no difference in CCT due to context, directionality or intensity of the conflicts (mean CCTs: food conflicts=18.6% ( $\pm 13.1$  SD), non-food conflicts=20.9% ( $\pm 10.6$  SD), unidirectional= 23.9% ( $\pm 14.2$  SD), bidirectional=16.6% ( $\pm 11.4$  SD), high intensity= 21.4% ( $\pm 13.5$  SD), low intensity=21.1% ( $\pm 14.4$  SD); all comparisons n.s.), nor between outdoor and indoor observation periods (pooled data: indoor vs. outdoor:  $\chi^2= 1.05$ ,  $p=0.33$  Fisher's exact) which allowed us pool the conflicts in the analyses.

#### Reconciliation and relationship quality

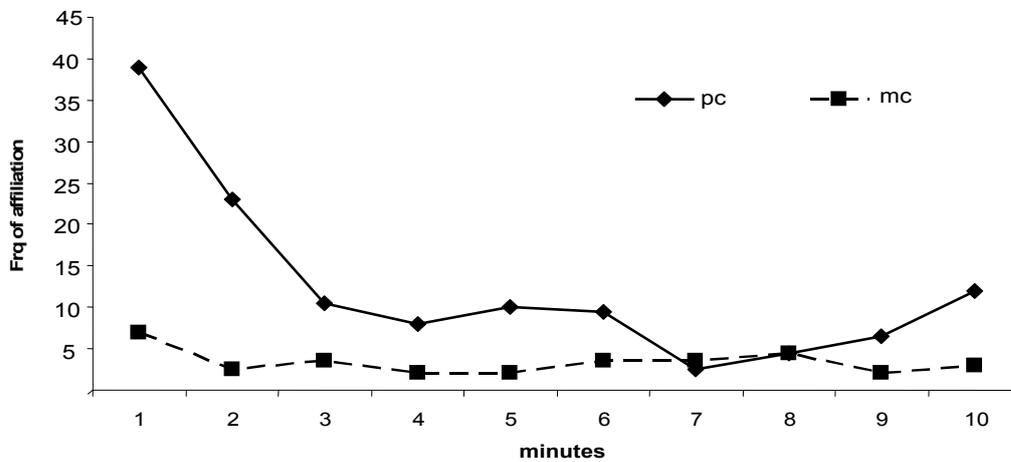
To test the prediction (1), we assessed the tendency to reconcile in relation to the sex class of the conflict. Male-male conflicts were reconciled significantly more often than female-female conflicts (m-m vs. f-f: MWU:  $U=22.0$ ,  $p=0.032$ ,  $N_1=6$ ,  $N_2=18$ ; f-f vs. inter-sex: Wilcoxon:  $z=-1.54$ ,  $p=0.12$ ,  $N=17$ ; m-m vs. inter-sex: Wilcoxon:  $T+=5$ ,  $p=0.31$ ,  $N=6$ ; Table 1).

To test the prediction (2), we assessed CCT with regards to relationship compatibility, which was done separately for grooming and for contact sitting (see methods). Conciliatory tendencies between compatibility categories measured by grooming differed significantly from each other (Friedman:  $N=20$ ,  $k=3$ ,  $F=6.14$ ,  $p=0.006$ ; Table 1). Post-hoc test (Siegel and Castellan, 1988, p.180) revealed that dyads having a strongly compatible relationship reconciled significantly more often than dyads having a weakly compatible relationship. To confirm the result, we tested females and males separately, and in both the difference remained significant (females: strongly compatible= 27.8%, weakly compatible =10.1%, Wilcoxon:  $z=1.76$ ,  $p=0.04$  one-tailed,  $N=16$ ; males: 29.0% vs. 13.7%, Wilcoxon:  $T+=0$ ,  $p=0.031$  one-tailed,  $N=5$ ). When relationship compatibility was measured by contact sitting, it did not significantly affect the conciliatory tendency (Friedman:  $N=22$ ,  $k=3$ ,  $F=2.1$ ,  $p=0.14$ ; Table 1).

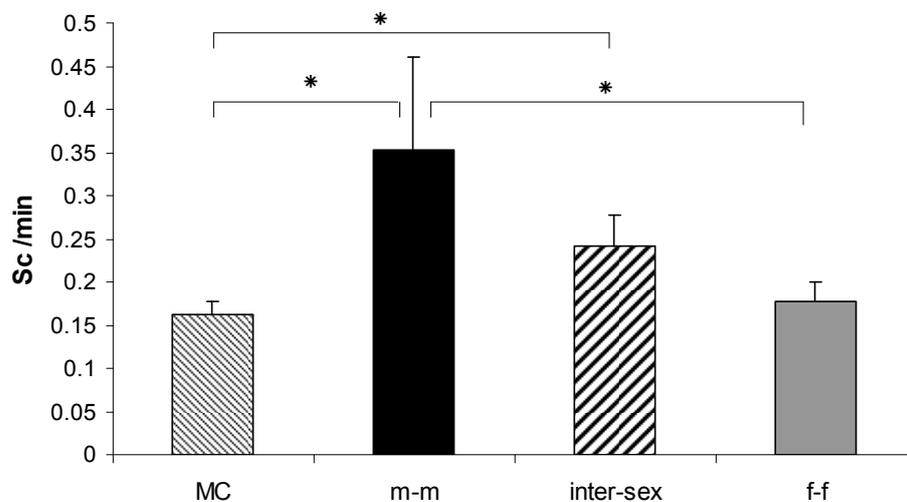
**Table 1.** Corrected conciliatory tendencies (CCT) per sex class (relationship value) and per relationship compatibility category.

Value	CCT % (SD) N		
	High Male-male	Intermediate Inter-sex	Low Female-female
	23.5 (4.3) N=6	24.4 (16.9) N=23	12.0 (11.1) N=18
Compatibility	Strong	Moderate	Weak
grooming	28.1 (18.6) N=22	19.2 (14.9) N=21	10.9 (14.8) N=21
contact sit	22.5 (17.3) N=22	19.2 (16.3) N=22	16.4 (14.6) N=22

CCTs are given as mean % (SD) of individual values, N indicates the number of individuals contributing to the mean. Compatibility categories are distinguished on the basis of grooming durations and of contact sitting rates.



**Figure 1.** Distribution of the first affiliative contacts between the opponents in time. PC =post-conflict; MC =matched control.



**Figure 2.** Post-conflict scratching rates of conflicts of different sex classes (MC=baseline scratching rate; m-m = male-male; m-f = male-female and female-male; f-f = female-female; mean  $\pm$  SEM). \*  $P < 0.05$ .

#### Relationship quality and post-conflict anxiety

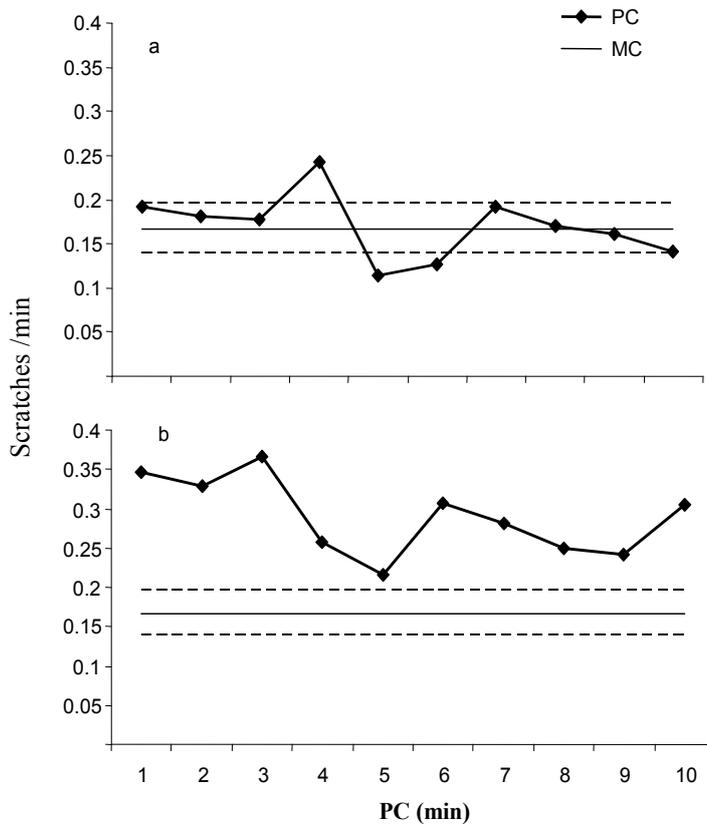
To test the prediction (3), we compared scratching rates after conflicts of different sex classes. Scratching rates after male-male and inter-sex conflicts were significantly higher than MC rates, while scratching rates after female-female conflicts did not differ significantly from baseline rates during MC (m-m vs. MC: Wilcoxon:  $T^+ = 0$ ,  $p = 0.04$  one-tailed,  $N = 5$ ; m-f vs. MC: Wilcoxon:  $z = -2.48$ ,  $p = 0.01$ ,  $N = 22$ ; f-f vs. MC: Wilcoxon:  $z = -0.28$ ,  $p = 0.78$ ,  $N = 18$ ; figure 2). To make sure the difference was not due to higher MC rates of either sex, we tested the MC rates of females against those of males and found no difference (mean MC: males =  $0.17(\pm 0.82)$  sc/min; females =  $0.17(\pm 0.06)$  sc/min; MWU:  $U = 42.5$ ,  $p = 0.85$ ,  $N_1 = 5$ ,  $N_2 = 18$ ).

Male-male conflicts yielded significantly higher scratching rates than female-female conflicts, while there was no difference between scratching rates after inter-sex and male-male or female-female conflicts (m-m =  $0.35(\pm 0.27)$  sc/min; f-f conflicts =  $0.18(\pm 0.10)$  sc/min; m-f =  $0.24(\pm 0.17)$  sc/min; f-f vs. m-m: MWU:  $U = 18.5$ ,  $p = 0.046$  exact,  $N_1 = 5$ ,  $N_2 = 18$ ; f-f vs. m-f: Wilcoxon:  $z = -1.54$ ,  $p = 0.13$ ,  $N = 17$ ; m-f vs. m-m: Wilcoxon:  $T^+ = 3.5$ ,  $p = 0.38$  exact,  $N = 5$ ; figure 2).

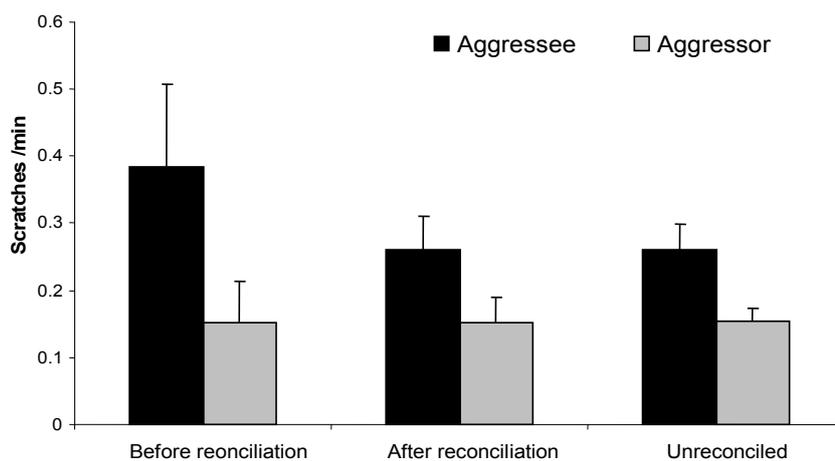
### Reconciliation and post-conflict anxiety

To test the prediction (4), we assessed the scratching rates of aggressors and aggressees, respectively, after unreconciled and reconciled conflicts. Aggressors did not present elevated post-conflict anxiety; the scratching rates of aggressors per each minute of unreconciled PCs did not rise above the 95% confidence interval of MC-baseline, except on the fourth minute of PC (figure 3a). Furthermore, the aggressors' scratching rates before, after and without reconciliation were consistently similar to the baseline rates (before =0.15 ( $\pm 0.20$ ), after=0.15( $\pm 0.12$ ), unreconciled=0.15( $\pm 0.10$ ), MC=0.16( $\pm 0.07$ ) sc/min; N=10; Wilcoxon: all comparisons n.s.; figure 4).

Scratching rates of aggressees were above the 95% confidence interval of MC-baseline throughout the ten minute PC (figure 3b). We confirmed that the result was not due to a few individuals by testing individual rates of unreconciled PCs against individual MC rates (unreconciled mean=0.26( $\pm 0.15$ ) sc/min, MC=0.16 ( $\pm 0.07$ ) sc/min; Wilcoxon:  $z=-2.87$ ;  $p=0.004$ , N=22). Therefore, the time window for calculating scratching rates after reconciliation was the full ten minutes. The scratching rates after reconciliation did not significantly differ from the rates before reconciliation (before affiliation=0.39( $\pm 0.54$ ), after affiliation=0.26( $\pm 0.22$ ) sc/min, Wilcoxon:  $z=-0.056$ ,  $p=0.96$ , N=20). Furthermore, scratching rates after reconciliation did not differ from those of unreconciled conflicts (Wilcoxon:  $z=-0.224$   $p=0.82$ , N=20, figure 4). The analysis yielded similar results when scratching rates of females and males were tested separately.



**Figures 3a and 3b.** Post-conflict scratching rates of (a) aggressors and (b) aggressees in the absence of reconciliation during the 10 min PC observations (MC = baseline  $\pm$  95% confidence intervals).



**Figure 4.** Post-conflict scratching rates of aggressors and aggressees before, after, and in absence of reconciliation (mean  $\pm$  SEM).

## **DISCUSSION**

The occurrence of reconciliation in the Arnhem Zoo chimpanzees was confirmed. The CCT of the group (mean 21.6%) is lower than previously reported for this colony [35% with a method that did not correct for the baseline of affiliation: de Waal and van Roosmalen, 1979; de Waal 1986] and for the captive group in Yerkes [41.2%: Preuschoft *et al.*, 2002], while it falls close to the range of other reports on chimpanzee reconciliation [Fuentes *et al.*, 2002; Kutsukake and Castles, 2004; Arnold *et al.*, 2001; Wittig and Boesch, 2005].

We set out to test the integrated hypothesis [Aureli, 1997], according to which conflicts among partners with high relationship quality yield high levels of post-conflict anxiety, which in turn leads to an increased likelihood of reconciliation. Thus, increased anxiety levels after a conflict mediate the occurrence of reconciliation. We formulated four predictions in order to test the Integrated Hypothesis. We were able to confirm most of our predictions (predictions 1-3) but not the last one (prediction 4).

Our first prediction concerned the influence of the relationship value of the opponents on the tendency to reconcile. In accordance with the prediction, conflicts among males were reconciled significantly more often than conflicts among females. This likely reflects the high value of male-male relationships. The relatively low conciliatory tendency of female-female conflicts is also in accordance with the prediction, as females are presumed to have a low relationship value. However, in captivity females have been observed to form strong bonds [de Waal, 1982, 1992b], which enhances the value of female relationships. This is likely the case at Arnhem as well, since the group includes females that have been together for years, even decades. In addition to these strong bonds, female relationships at Arnhem may also be relatively secure compared to male relationships [de Waal, 1982, 1992b], given their long history, the high association rate inherent to captive conditions and the stability of the female dominance relationships. Indeed, the association level between individuals appears to be related to the security experienced [Kutsukake, 2003], and a long communal history between individuals makes relationships less

susceptible to damage [Brosnan *et al.* 2005]. Secure relationships suffer less damage after conflicts and need thus less repair [Schaffner and Caine 2000; Schaffner *et al.*, 2005], leading to a low probability of reconciliation [Cords and Aureli, 2000]. Females may thus reconcile less often due to the high security of their relationships. Support for this suggestion is provided by the fact that females did not have elevated scratching rates after conflicts with other females, which implies that females were not distressed by conflicts with each other. Unfortunately, since we did not employ direct measures of relationship value [inferred from e.g. support frequency: Cords and Aureli, 2000; Preuschoft *et al.*, 2002], the question whether Arnhem female chimpanzees reconciled relatively rarely due to relationships being of low value, high security, or both, remains open.

Inter-sex relationships were expected to be of intermediate value. Accordingly, the inter-sex conflict CCTs did not differ significantly from male-male or female-female CCTs, although we obtained the highest mean CCT for inter-sex conflicts. Furthermore, the PC anxiety levels were equal after conflicts among males and between sexes. Apparently male-female relationships in chimpanzees hold a value equal, or close, to male-male relationships. This has been suggested to reflect male mating investment in females as potential mating partners [Wittig and Boesch, 2003a], or females' interest in maintaining good relationships with males in order to get the males to buffer female intra-sexual competition and to reduce male harassment [Arnold and Whiten, 2001].

In accordance with our second prediction, strongly compatible dyads reconciled more often than dyads with a weakly compatible relationship. However, only grooming seemed to reflect relationship compatibility in this population of chimpanzees, as only compatibility measured by grooming, but not by contact sitting, was found to predict the CCTs. This suggests that these two measures of compatibility are not equal. We tested *a posteriori* the presumed correlation between dyadic contact sitting and grooming frequencies by row-wise matrix correlation [de Vries, 1993] with 2000 permutations using Matman 1.1.4 [Noldus Information Technology, 2003]. Contact sitting and grooming were significantly positively correlated, although the correlation coefficient was low

( $K_r=1862$ ,  $\tau_{rw}=0.42$ ,  $p_{right}=0.005$ ). The weak positive correlation may indicate that while contact sitting and grooming reflect similar aspects of a relationship, contact sit may not be as strong of an indicator of compatibility as grooming. Grooming can be considered as an active investment in time and energy [e.g. Dunbar, 1993; Cords, 1997; Arnold and Whiten, 2003], whereas contact sitting is perhaps more of a passive form of friendly behaviour that merely reflects tolerance to proximity. This may be the case especially in egalitarian species, such as chimpanzees, where contact sitting with other group members can be expected to be less risky than in strictly despotic species.

In sum, we found support for the predictions (1) and (2) of the integrated hypothesis: more valuable and compatible partners (i.e., males and frequent groomers) reconciled more often than less valuable and weakly compatible partners (i.e., females and infrequent groomers). However, the low level of reconciliation among females may also result from their very secure relationships. Inter-sex conflicts were reconciled in high proportions, which may reflect a high value of relationships between females and males.

Our third prediction concerning relationship quality and PC anxiety was supported; male-male and inter-sex conflicts caused a significant increase in scratching rates compared to baseline, while female-female conflicts did not. Moreover, male-male resulted in significantly higher scratching rates than female-female conflicts. A high level of PC anxiety after male-male conflicts was probably not caused by uncertainty of receiving further aggression [Aureli and van Schaik, 1991b], since the prevalence of renewed aggression between the opponents was exceedingly low ( $N=4$ ). Therefore, anxiety was probably due to damage of the relationship, indicating that the chimpanzees of Arnhem showed a connection between relationship quality and post-conflict anxiety.

Our fourth prediction stated that conflicts cause elevated scratching rates, which reconciliation decreases to the baseline levels. Additionally, we expected equally elevated scratching rates in both conflict opponents. Our results partly fulfilled the predictions. Aggressees showed an elevated stress response after conflicts; scratching rates of unreconciled conflicts stayed above the baseline throughout the observed ten minutes. However, scratching rates of aggressors

were not elevated after conflicts. This is in contrast to the findings of several studies on monkeys, which showed that both conflict participants have increased post-conflict anxiety [e.g., long-tailed macaques: Aureli, 1997; Aureli and van Schaik, 1991b; Das *et al.*, 1998; baboons: Castles and Whiten, 1998b]. This implies that chimpanzee aggressors are not as disturbed by conflicts as aggressees are. One possible explanation for this is asymmetry in the experienced damage to the relationship with the former opponent. Aggressees may thus be more prone to suffer from the relationship damage due to the conflict than aggressors. This would indicate that, while relationship quality determines experienced anxiety, it is dependent on the role of the participants in the conflict. Furthermore, aggressees were stressed only after male-male and inter-sex conflicts but not after conflicts between females. Although we have no evidence of the actual damage to the relationships after conflicts, we can hypothesize about losses of the benefits for the aggressee. Female targets of male aggression may be interested in reconciling in order to keep up the good relationships for male protection and buffering purposes [Arnold and Whiten, 2001]. Males, in turn, may want to reconcile after being aggressed by females, since they are possible mating partners [Wittig and Boesch, 2003], and by males, in order to maintain cooperative relationships.

Finally, reconciliation did not effectively decrease the scratching rates of aggressees. This finding is surprising, since nearly all earlier studies on PC anxiety have shown that reconciliation is an effective mechanism to alleviate anxiety [e.g., Aureli and van Schaik, 1991b; Castles and Whiten, 1998b; Das *et al.*, 1998]. The only published study thus far examining post-conflict anxiety in chimpanzees did not find elevated PC scratching rates [Arnold and Whiten, 2001], while the current study did find an overall increase in PC scratching rates of aggressees. However, it is possible that pooling PCs with reconciliation and PCs with triadic affiliation blurred the effect of reconciliation on anxiety reduction [Koski and Sterck, *in press*]. Another limitation in our study is that rough and gentle scratching were scored together. As rough scratching has proved to be the most reliable anxiety indicator in chimpanzees [Baker and Aureli, 1997; Aureli

and de Waal, 1997], scoring rough and gentle scratching together may have concealed the effect of reconciliation on the stress alleviation.

In conclusion, our study on captive chimpanzees mostly supports the integrated hypothesis. We showed that more valuable and compatible partners (males and frequent groomers) reconciled in higher frequency than less valuable and weakly compatible partners (females and infrequent groomers). Conflicts among males resulted in higher PC anxiety than conflicts among females. Therefore, we were able to connect the main factors of the integrated hypothesis: relationship quality determined both reconciliation and PC stress. Reconciliation as a conflict resolution strategy thus seems to depend predominantly on relationship attributes, and emotional arousal appears to be an important emotional mediator facilitating conflict resolution. However, anxiety after conflicts seems to depend on the participant's role in the conflict, which may reflect differing interests of conflict participants in repairing the relationship with the opponent.

#### **ACKNOWLEDGMENTS**

We gratefully acknowledge Dr. Jan van Hooff for inspiring discussions and constructive advice, Dr. Han de Vries and Dr. Maria Schipper for statistical advice, and the Burger's Zoo staff for excellent logistic support. M. Bauwens, E. Kenbeek, M. Heesen, C. van Maanen, O. van Velthuisen, L. Visser, M. Beterams and R. van den Toorn are thanked for their invaluable help in data collection. Dr. Simon Reader and two anonymous reviewers are thanked for helpful comments on the manuscript. Lucie Burgers Foundation for Comparative Behaviour Research is thanked for financial support (for SEK).

## *CHAPTER 3*

---

### WHAT TO DO AFTER A FIGHT?

The determinants and inter-dependency of  
post-conflict interactions in chimpanzees

---

Sonja E. Koski\*, Han de Vries,  
Saskia W. van den Tweel & Elisabeth H.M. Sterck

*Submitted manuscript*

## **ABSTRACT**

Primates resolve conflicts through post-conflict interactions (PCI). However, the occurrence of different PCI in relation to one another is not well understood. Furthermore, the factors influencing the occurrence of PCI are rarely addressed together, and thereby their relative impact is usually ignored. We investigated the occurrence and interrelatedness of five PCI, namely reconciliation, further (or redirected) aggression, third-party affiliation, third-party aggression, and 'no PCI' in captive chimpanzees. Most PCI were found to occur independently from each other. Reconciliation was determined by relationship attributes between the opponents. Further aggression was mainly determined by directionality and intensity of conflicts. Opponents received third-party affiliation most often when they were likely to redirect aggression to third parties. The predictors for third-party aggression and 'no PCI' remained unclear or insignificant. Overall, the results indicate that (1) most PCI do not directly depend on one another, and that (2) the conflict opponents and the bystanders each make their own 'decisions' about which PCI to employ depending on specific conflict characteristics, the conflict outcome and the relationship attributes among the opponents. This study emphasises the multidimensionality of primate conflict resolution.

## **INTRODUCTION**

A variety of behavioural mechanisms to manage aggressive conflicts have been described in group living mammals, ranging from preventive strategies such as a dominance hierarchy and respect of possession, to conflict resolution occurring after conflicts (e.g., de Waal, 1996; Kappeler & van Schaik, 1992; Aureli & de Waal, 2000; Preuschoft & van Schaik, 2000). Conflict resolution via post-conflict interactions (PCI) can take place between the opponents as well as between opponents and bystanders (Das, 2000; Watts et al., 2000; Wittig & Boesch, 2003a). Some of the PCI repair the damaged relationships between the opponents, while others decrease the risk of further aggression and alleviate post-conflict anxiety (Aureli & de Waal, 2000; Aureli et al., 2002). Although several kinds of PCI are recognised, little is known about their interrelatedness. The common practice is to assess each PCI separately, yet the opponents and bystanders have the choice to employ one, none or several PCI after a particular conflict. Furthermore, conflict resolution is affected by several aspects, such as features of the conflict itself, the relationship attributes of the combatants, the role of participants in the conflict, and the conflict outcome (e.g., Call et al., 1999; Aureli et al., 2002; Wittig & Boesch 2003a). Yet, the factors that determine the occurrence of different post-conflict interactions are rarely assessed simultaneously (see exceptions Call et al., 1999; Wittig & Boesch 2003a; Schino et al., 2004). Therefore, in order to gain a complete picture on conflict resolution, many PCI and their possible determinants should be assessed together.

In Table 1 we summarise the known or suggested benefits and determinants of four PCI occurring in primates: reconciliation, further (a.k.a. redirected) aggression, third-party affiliation and third-party aggression. Reconciliation is defined as selective affiliation between the opponents soon after the conflict (de Waal & van Roosmalen, 1979). Nearly all studied primate species and some non-primate mammals exhibit reconciliation after conflicts (Aureli & de Waal, 2000; Schino, 2000), and evidence has mounted that it serves as an effective means of conflict resolution (reviewed by Aureli et al., 2002). While reconciliation offers many benefits, not all conflicts are reconciled.

The most important determinant of reconciliation appears to be the relationship quality between the opponents; the higher their relationship quality the more likely reconciliation is to take place (de Waal & Yoshihara, 1983; Kappeler & van Schaik, 1992; Cords & Aureli, 2000; Aureli et al., 2002; Watts, 2006; Koski et al., in press).

Further aggression by opponents to third parties (i.e., formerly uninvolved bystanders) is common in many primate species (e.g., Cheney & Seyfarth, 1989; Aureli & van Schaik, 1991a; Aureli et al., 1992; Aureli et al., 1994), and is mostly described to be specifically a victim's (or loser's) behavioural strategy (Scucchi et al., 1988; Kazem & Aureli, 2005; see for further aggression by aggressors Das, 1998). Further aggression decreases the aggresses' risk of receiving aggression from third parties and may serve as an 'emergency exit' to reduce conflict-induced frustration and stress (Aureli & van Schaik, 1991b; Watts et al., 2000; Wittig & Boesch, 2003a; Kazem & Aureli, 2005). Further aggression is thought to take place when the risk of receiving further aggression from the former opponent or bystanders is the highest, and reconciliation or retaliation of aggression is not possible (Aureli & van Schaik, 1991b; Wittig & Boesch, 2003a).

Third-party affiliation can occur by a former opponent towards a third party, or a third party may spontaneously contact the opponent (labelled 'solicited consolation' and 'true consolation', respectively; de Waal & van Roosmalen, 1979; de Waal & Aureli, 1996; Verbeek & de Waal, 1997). In this study we focus on third party initiated affiliation (see below rationale), which has been described only in chimpanzees, bonobos, western lowland gorillas and stump-tailed macaques (de Waal & Aureli, 1996; Call et al., 2002; Palagi et al., 2004, 2006; Mallavarapu et al., 2006; Koski & Sterck, 2007). What determines the occurrence of third-party affiliation is largely unclear. Some studies suggest that it substitutes reconciliation and provides an alternative way to alleviate anxiety (e.g., Aureli & van Schaik, 1991a; Watts et al., 2000; Wittig & Boesch, 2003a; Palagi et al., 2004, but see Koski & Sterck, 2007, for contradicting evidence).

Lastly, conflict participants can receive further aggression from third parties (Aureli & van Schaik, 1991a; Aureli, 1992; Castles & Whiten, 1998). In macaques, third-party aggression is described to occur mostly in the absence of reconciliation and further aggression by aggresses (Aureli & van Schaik, 1991a; Aureli, 1992), whereas in chimpanzees most third-party aggression was found after long and intensive social conflicts possibly relating to the increased general tension in the group (Wittig & Boesch, 2003a).

In this study we investigated the occurrence of the four aforementioned PCI plus a counterpart option 'no PCI' (see Table 1 for definitions) in captive chimpanzees (*Pan troglodytes*). The category 'no PCI' is a combined category of avoidance and 'business as usual'; it includes post-conflict observations where no interactions with or among conflict participants took place and observations where only opponent-initiated third-party affiliation (a.k.a. 'solicited consolation') took place. The latter was added to 'no PCI' since its occurrence is not affected by the preceding conflict in this group (Koski & Sterck, 2007). To understand how the PCI influence one another and what determines their occurrence, we assessed the relative influence of several conflict and relationship characteristics (see Table 2), which were chosen for their known effect on at least one of the PCI assessed. Moreover, we investigated whether the occurrence of the PCI depends on each other. We conducted all the analyses separately for the aggressors and the aggresses, since the functions of the triadic contacts are likely to differ for aggressors and aggresses (e.g., Das, 2000, Watts et al., 2000).

The aim of this study was to investigate in captive chimpanzees (i) whether and how the PCI depend on each other, (ii) which features of the conflicts determine the occurrence of each PCI, and (iii) the relative influence of the determining factors.

**Table 1.** Post-conflict interactions (PCI) considered in this study and their possible benefits and determinants.

<b>PCI</b>	<b>Description</b>	<b>Suggested /shown benefits</b>	<b>Determinants</b>
<b>Reconciliation</b>	Affiliative contact between the former opponents after a conflict	Repairs opponents' relationship <sup>(1,2)</sup> Reduces further aggression <sup>(3-6)</sup> Reduces PC-stress <sup>(7-9)</sup>	Opponents' high relationship quality <sup>(10-13)</sup> High <sup>(14)</sup> or low <sup>(15)</sup> conflict intensity
<b>Further aggression</b>	Physical aggression by a former opponent towards a previously uninvolved bystander. By aggressors or aggressees.	Reduces further aggression from opponent and/or bystanders <sup>(3,7,26)</sup> Reduces PC- stress <sup>(7,8)</sup>	By victim the absence of reconciliation and retaliation <sup>(25,27)</sup> High risk of further aggression <sup>(7,17)</sup>
<b>Third-party affiliation</b>	Affiliative contact between a former opponent and a previously uninvolved bystander, initiated by the bystander (behaviour previously known as consolation). Towards aggressors or aggressees	Reduces stress <sup>(3,16-19)</sup> Indirect or substitute reconciliation <sup>(17,18,20)</sup> Reduces further aggression <sup>(18, 21-23)</sup>	Absence of reconciliation <sup>(16-18,23)</sup> High conflict intensity <sup>(24)</sup>
<b>Third-party aggression</b>	Physical aggression by a previously uninvolved bystander towards a former opponent, initiated by the bystander. Can occur towards aggressors or aggressees.	Defeat a weakened opponent <sup>(7,25)</sup> Psychological victory <sup>(16)</sup>	Absence of reconciliation and further aggression <sup>(3,26)</sup> Long and high intensity conflict <sup>(17)</sup>
<b>No PCI, or 'business as usual'</b>	No interactions with a former opponent, or only opponent initiated affiliation towards third parties (behaviour previously known as solicited consolation)	Avoid risk of aggression	

(1) Cords, 1992; (2) Wittig and Boesch, 2005; (3) Aureli and van Schaik, 1991a; (4) Watts, 1995; (5) Silk, 1996; (6) Kutsukake and Castles, 2001 (7) Aureli and van Schaik, 1991b; (8) Castles and Whiten, 1998; (9) Das *et al.*, 1998; (10) de Waal and Yoshihara, 1983; (11) Kappeler and van Schaik, 1992; (12) Cords and Aureli, 2000; (13) Aureli *et al.*, 2002; (14) Kutsukake and Castles, 2004; (15) Arnold and Whiten, 2001; (16) Watts *et al.*, 2000; (17) Wittig and Boesch 2003a; (18) Palagi *et al.*, 2004; (19) evidence contra: Koski and Sterck, in press; (20) Judge, 1991; (21) Das, 1998; (22) Call *et al.*, 2002; (23) Palagi *et al.*, 2006; (24) de Waal and Aureli, 1996; (25) Kazem and Aureli, 2005; (26) Aureli, 1992; (27) Scucchi *et al.*, 1988.

## **MATERIALS AND METHODS**

### **Subjects and Housing**

We studied a group of chimpanzees in the Burgers' Zoo in Arnhem, the Netherlands, established in 1971. During the study period, the group consisted of 23-34 individuals: three to five adult males, 14-18 adult females, zero to two adolescent males, one to three adolescent females, and four to nine juveniles and infants (age classes as in Preuschoft et al., 2002); changes were due to natural demography and zoo management. All but five individuals were born in the group and none were introduced to the group during the study. When the temperature is at least 10°C, the group lives on an outdoor island of about 0.7 ha, surrounded by a moat and enriched with natural trees as well as wooden climbing structures, nets and ropes. During winter months the chimpanzees stay indoors in a hall of 21x18 m, containing wooden platforms, plastic barrels, nets and ropes, and play objects such as balls and sticks. Water is available *ad libitum* and fresh straw is provided daily as nesting material. For further details of the colony and husbandry see Koski & Sterck (2007) and Takeshita & van Hooff (2001).

### **Data Collection**

Data were collected by S.E.K. together with several students during November 2002- August 2005. Inter-observer reliability was ensured by >95% similarity in focal observations of each student and S.E.K. We collected data using continuous focal animal sampling of 15 minute duration (Altmann, 1974) of adults and adolescents, including all social interactions within two arm lengths. Data on grooming were recorded as the duration of a grooming bout to the nearest second. A grooming bout ended when the direction of grooming in a dyad changed or grooming halted for  $\geq 30$  sec. Altogether we collected 1540.74 hrs of focal data; an individual was observed on average 70.0 hrs (median 74.1 hrs, range 45.7-76.9 hrs).

Conflicts were observed *ad libitum* throughout the observational time frame. We recorded conflicts amongst adults and adolescents. Details of the conflict recordings including the operational rules are available in Koski et al.

(in press) and Koski & Sterck (2007). We applied the standard post-conflict (PC) -- matched control (MC) method of de Waal & Yoshihara (1983) and Aureli et al. (1989). The PC was of 10 min duration, during which we recorded all interactions of the focal animal with the opponent and other group members. We conducted simultaneous observations on both aggressors and aggresses whenever possible. The MC was conducted on the next possible day, within seven days from the conflict, with a criterion of no agonistic interactions with the focal animals for one hour prior to, or during, the MC, and time and context matching with the conflict. We applied similar methods during both indoor and outdoor observations.

### **Operational Definitions**

From each conflict we noted the following characteristics (see categories and definitions in Table 2): (1) conflict context, (2) conflict intensity, (3) directionality of aggression, (4) opponent sex class; and (5) opponent compatibility. We did not record conflict duration. Opponent's compatibility was assessed for both conflict participants separately from summed dyadic grooming durations obtained from focal observations (Preuschoft et al., 2002; Koski et al., in press). For each chimpanzee the dyadic grooming durations with other individuals were divided into quartiles; the top quartile individuals were labelled as strongly compatible, the lowest quartile as weakly compatible and the mid 50% as moderately compatible with this chimpanzee (Cords & Aureli, 2000; Arnold & Whiten, 2001).

Reconciliation between the opponents was assessed with the PC-MC method (de Waal & Yoshihara, 1983), in which the PC-MC pair is labelled as 'attracted', 'dispersed' or 'neutral' according to the timing of the first affiliative contact between the opponents. In attracted pairs the contact occurs earlier, or only, in PC; in dispersed pairs the contact occurs earlier, or only, in MC; in the absence of a contact in both PC and MC, or if the affiliation occurs at the same time in PC and MC, the pair was labelled neutral. Only attracted pairs were deemed as reconciled (Cords, 1993).

We applied the PC-MC method also to third-party affiliation (Call et al., 2002; Palagi et al., 2004, 2006; Koski & Sterck, 2007). We only considered it third-party affiliation when the third party initiated the affiliative contact (a.k.a. 'true consolation': Verbeek & de Waal, 1997). When the focal animal initiated the contact we discarded it as third-party affiliation, since we have shown previously that in this chimpanzee group opponent-initiated third-party affiliation does not differ from the baseline level of affiliation (Koski & Sterck, 2007). We labelled the PC-MC pairs as attracted, dispersed or neutral in a similar manner as with reconciliation. Only attracted pairs were considered as presenting third-party affiliation. The procedure was done separately for aggressors and aggressees.

In the case of post-conflict aggression we could not assign the attracted/dispersed pair -label, due to the criterion employed in the MC observations (i.e., no aggression with the focal animal). To operationally define further aggression, we calculated for each individual the rate of further aggression (i.e., opponent-initiated aggression towards third parties) corrected to the PC hours of the individual as: ( $\#PC$  with redirection/  $\Sigma PC$  hours). The rate of further aggression was calculated for individuals separately as an aggressor and as an aggressee. The obtained rates were compared to the baseline rate of aggression of the same individual calculated as: ( $\#$ conflicts as an aggressor +  $\#$ conflicts as an aggressee +  $\#$ conflicts as a supporting party)/  $\Sigma$ observed hours. The individual rates of further and baseline aggression were tested pair-wise, and when the redirection rate was significantly greater than the rate of baseline aggression, redirection was assumed to be due to the preceding conflict.

We followed the same method for third-party aggression towards an opponent in PC. For each individual as an aggressor and as an aggressee, respectively, we calculated the rate of aggression in PCs received from third parties ( $\#PC$  with received third-party aggression/ $\Sigma PC$  hours). These rates we compared to the individual baseline rate of aggression, and tested pair-wise.

We did not include renewed aggression between the opponents in the analyses, as there was a very small number of such cases in the data (N= 8 in

the total of 696 conflicts), and we excluded these conflicts from the analyses. We combined the data from indoors and outdoors, as there was no difference in conflict rate (Koski, unpublished data) or in conciliatory tendency (Koski et al., in press) between indoor and outdoor observations.

### **Data Analysis**

We recorded 696 conflicts, of which we obtained full data of aggressors on 632 conflicts and of aggressees on 659 conflicts. Conflicts of the same opponent dyad, having the same conflict characteristics (i.e. independent factors) and followed by the same type of PCI were reduced to one data point, thereby eliminating repeated observations of the same conflict type per dyad (cf., Wittig & Boesch, 2003a). This was done separately for the aggressor and the aggressee data sets, resulting in a data set of  $N_{\text{aggressor}} = 559$  and  $N_{\text{aggressees}} = 565$ .

The comparison of baseline aggression rates to rates of further aggression and third-party aggression were done at the individual level with Wilcoxon signed ranks (WSR) test. The inter-dependency of PCI was tested by comparing the occurrence of each interaction alone and in combination with the other PCIs against the expected occurrence (Chi-Square test; separately for aggressors and aggressees). We conducted the analysis on both reduced (see above) and non-reduced data sets.

We employed a logistic regression analysis to investigate which variable(s) predicted the occurrence of each PCI. We modelled each PCI separately. The independent variables used as possible predictors in the model are listed in Table 2. To select the best model we used a backward stepwise logistic regression with the inclusion criterion based on the maximum likelihood-ratio statistics. The significance of predictors and their coefficients of the selected model were assessed with Wald statistics (two-tailed). Even though we balanced the data set by reducing the chance of a biasing contribution of certain dyads (see above), the data nevertheless contained repeated measures of each individual. To control for a possible inflation of the risk to make a type I

**Table 2.** Independent variables considered as predictors of PCI.

<b>Predictor</b>	<b>Categories</b>	<b>Type</b>	<b>Definition</b>
Conflict context	Food/ social	Binomial	food = food present in the enclosure; social= food absent
Conflict intensity	Low/ high	Binomial	low= only chase and/or one hit by aggressor and scream from the recipient of aggression; high= all other physical aggression
Conflict directionality	Unidirectional/ bidirectional	Binomial	unidirectional= only one party directs aggression to the other; bidirectional = both opponents direct aggression to each other
Opponent sex class	Male-male/ mixed-sex/female-female	Multinomial	m-m = both opponents male; mixed-sex = male and female opponents; f-f = both opponents female
Opponent compatibility for aggressee/ for aggressor	Strong/ medium/ weak	Ordinal multinomial	Grooming time with opponent is evaluated with regard to individual's total grooming time. Strong = opponent grooming time in the top quartile; medium = opponent grooming time in the mid 50%; weak = opponent grooming time in the bottom quartile of total grooming time
Interactions of predictors	Context * directionality Context * sex class Directionality * sex class Intensity * sex class Compatibility (aggressee) * sex class		

error, we entered the identity of the conflict aggressor (analysing aggressor data) and aggressee (analysing aggressee data) as an independent variable to the best model, after which predictors and their coefficients of this best model were tested again (similar procedure was used by Côté & Festa-Biachet 2001 and Wittig & Boesch, 2003a). When the significant predictors remained significant, we could assume that these results were not due to over-representation of certain individuals (Bland & Altman, 1995).

Note that in the analysis of reconciliation the aggressor data set and the aggressee data set are nearly the same. The slight differences are due to a smaller total number of observations of aggressors, and the differences in which particular conflicts remained in the data sets after removing the identical conflicts, as the occurrence of triadic PCI differed between aggressors and aggressees. Note also that, although the aggressor and aggressee data sets

are virtually the same regarding reconciliation, the analysis results can differ when the identity of the aggressor or the aggressee is entered in the model (see below). Therefore, just as for the triadic PCI, reconciliation was analysed for aggressors and aggressees separately.

All the analyses were performed in SPSS 12.0.1. We report the parameter ( $\beta$ ) values and test results for those parameters that remained significant ( $p \leq 0.05$ ) or as trends ( $0.05 < p \leq 0.10$ ) when the conflict participant identity was included in the model.

## **RESULTS**

### **Inter-dependency of PCI**

The occurrence of the PCI alone (including 'no PCI') and in combinations with the other PCI were tested against their expected occurrence (Table 3). In aggressees the occurrence of all PCI was independent, thus, none of them occurred either alone or in particular combination more often than expected ( $\chi^2 = 15.9$ ,  $df = 11$ ,  $p = 0.14$ ). In aggressors, the occurrence of PCI was not independent from each other ( $\chi^2 = 32.1$ ,  $df = 11$ ,  $p = 0.001$ ). The significant result was due mostly to the more frequent than chance co-occurrence of further aggression and third-party aggression. The affiliative interactions by and towards aggressors occurred independently of each other, as did the affiliative interactions and the aggressive interactions, whereas the aggressive interactions to and by aggressors co-occurred significantly more often than occurred alone. Similar results for both aggressors and aggressees we obtained when conducting the analyses on the non-reduced, full data set.

### **The predictors for PCI**

The results of the significant predictors for the different PCI are presented in Tables 4 and 5. We present the results for aggressees and aggressors separately, except in the case of reconciliation, of which we present the results on the analysis on aggressee data set due to the strong similarity in the results of the analyses.

*Reconciliation (Table 4)*

The occurrence of reconciliation was predicted by sex class and relationship compatibility of the conflict participants. Male-male conflicts and conflicts in which the aggressee considered the relationship with the opponent as strongly compatible were reconciled most often. In addition, an interaction effect between sex class and conflict intensity showed that low intensity in mixed-sex conflicts increased the likelihood of reconciliation in comparison to high intensity mixed-sex conflicts. The results of the aggressor and aggressee models were highly similar, which was to be expected considering that reconciliation is a dyadic event between the two conflict partners and the data sets consisted of virtually the same events.

*Further aggression (Table 5 a,b)*

The rate of further aggression was significantly higher than the baseline rate of aggression in both conflict participants (mean (SD): baseline 0.037 (0.02) conflicts/h; further aggression by aggressees 0.59/h (0.39); baseline vs. redirection: WSR test  $z = 3.92$ ,  $N = 20$ ,  $p < 0.001$ ; redirection by aggressors 1.06/h (0.92); baseline vs. redirection:  $z = 3.61$ ,  $N = 17$ ,  $p < 0.001$ ). Therefore, we assumed further aggression to be due to the preceding conflict.

Individuals in the aggressor role directed further aggression after conflicts significantly more often than in the aggressee role (aggressors vs. aggressees; WSR test  $z = 2.26$ ,  $N = 22$ ,  $p = 0.009$ ). The occurrence of further aggression was predicted by the directionality of conflicts. Aggressors were more likely to redirect aggression after unidirectional conflicts, whereas aggressees further aggression more often after bidirectional conflicts. The occurrence of further aggression by aggressors was additionally predicted by sex class: further aggression occurred more often after male-male and mixed-sex conflicts than after female-female conflicts. Finally, in aggressors also conflict intensity influenced the occurrence of further aggression; highly intensive male-male conflicts and low intensity mixed-sex conflicts increased the prevalence of further aggression by aggressors.

**Table 3.** The inter-dependency of PCI.

<b>PCI</b>	<b>Aggressors</b>		<b>Aggressees</b>	
	<b>Frequency</b>	<b>Exp. frq.</b>	<b>Frequency</b>	<b>Exp. frq</b>
# Reconciliation	143		146	
# Third party affiliation	226		246	
# Further aggression	159		61	
# Third party aggression	68		83	
Reconciliation alone	47	53.54	48	62.61
Third party affiliation alone	104	105.71	128	138.67
Further aggression alone	55	61.91	20	21.74
Third party aggression alone	15	21.57	25	30.93
No PCI	172	155.76	196	179.26
Rec. + t.p. affil.	42	36.34	58	48.44
Rec. + further aggr.	18	21.28	7	7.59
Rec. + t.p. aggr.	3	7.42	13	10.80
T.p. affil. + further aggr.	33	42.02	17	16.82
T.p. affil. + t.p. aggr.	10	14.64	24	23.93
Further aggr + t.p.aggr.	17	*8.57	7	3.75
Rec. + t.p. affil. + further aggr.	20	14.44	7	5.87
Rec. + t.p. affil. + t.p. aggr.	7	5.03	11	8.36
T.p. affil. + further aggr. + t.p. aggr.	10	*5.82	1	2.90
Rec. + further aggr. + t.p. aggr.	6	*2.95	2	1.31
All together	0	2.00	0	1.01
<b># conflicts</b>	<b>559</b>		<b>564</b>	
	<b>CHI-SQ</b>	<b>32.069</b>		<b>15.943</b>
	<b>P</b>	<b>0.001</b>		<b>0.143</b>

The actual and expected frequencies of PCI in all combinations are given. Rec. = reconciliation; T.p.affil. = third-party affiliation, T.p.aggr. = third-party aggression, Further aggr. = further aggression by opponents; \* indicates a fairly large st.residual.

*Third-party affiliation (Table 5 c,d)*

The general occurrence of third-party affiliation was high: 40.3 % for aggressors and 43.5 % for aggressees. However, there were no significant predictors for third-party affiliation given to aggressees, indicating that they received third-party affiliation irrespective of conflict conditions or – characteristics. The only predictor bordering a statistical trend for third-party affiliation to aggressees was an interaction effect between context and directionality: most third-party affiliation occurred after bidirectional social conflicts. Aggressors, on the other hand, were more likely to receive third-

party affiliation after high intensity conflicts, especially after highly intensive male-male conflicts. After mixed-sex conflicts, however, low conflict intensity elicited more third-party affiliation.

*Third-party aggression (Table 5 e,f)*

The rate of third-party aggression was significantly higher than the baseline rate of aggression in both conflict participants (mean (SD): baseline 0.037 (0.02) conflicts/h; third-party aggression to aggresses 0.62/h (0.46), third-party aggression vs. baseline WSR test  $z = 3.72$ ,  $N = 18$ ,  $p < 0.001$ ; third-party aggression to aggressors 0.94/h (0.70); third-party aggression vs. baseline:  $z = 3.82$ ,  $N = 19$ ,  $p < 0.001$ ). The rate of third-party aggression towards both opponents was thus consistently higher than the baseline rate of aggression, and therefore we assumed third-party aggression to be due to the preceding conflict. Individuals in the aggressor role received third-party aggression slightly more often than in the aggresses role, the difference reaching a statistical trend (aggressors vs. aggresses: WSR test  $z = 1.90$ ,  $N = 22$ ,  $p = 0.057$ ). The overall prevalence of third-party aggression was low (12.2 % to aggressors and 14.7% to aggresses). Only one interaction effect between the variables predicted the occurrence of third-party aggression towards aggressors: the interaction between directionality and sex class. Aggressors received third-party aggression more often after bidirectional male-male, and unidirectional female-female conflicts. The only nearly significant predictor for third-party aggression to aggresses was the interaction between opponent compatibility (from the aggresses' perspective) and sex class. Aggresses of female-female conflicts of weak relationship compatibility appeared to receive third-party aggression least often (5.4%). However, the overall effect of this variable reached only a trend ( $p = 0.08$ ), and as the prevalence of third-party aggression to aggresses was low, the conclusions concerning third-party aggression directed to aggresses remain tentative.

**Table 4.** Factors determining the occurrence of reconciliation

<b>PC-Interaction</b>	<b>Wald</b>	<b>df</b>	<b>p</b>	<b>category</b>	<b>N</b>	<b>f(%)</b>	<b>β</b>	<b>Wald</b>	<b>p</b>
<b>Reconciliation</b>						<b>26.0</b>			
Sex class	<b>7.8</b>	<b>2</b>	<b>0.020</b>	mm	71	33.8	0.44	4.87	0.018
				mix	338	29.0	0.41	0.08	0.923
				ff	156	16.0	-0.49	7.39	0.007
Compatibility (assessed by aggresses)	<b>11</b>	<b>2</b>	<b>0.004</b>	strong	177	33.9	0.43	9.31	0.002
				medium	243	25.9	0.08	0.33	0.556
				weak	145	16.6	-0.51	8.62	0.003
Intensity * Sex Class	<b>7.4</b>	<b>2</b>	<b>0.025</b>	low* mm	45	28.9	-0.03	0.03	0.87
				high* mm	26	42.3	0.03		
				low* mix	205	31.2	0.25	4.18	0.041
				high* mix	133	25.6	-0.25		
				low* ff	108	12.0	-0.22	1.41	0.234
				high* ff	48	25.0	0.22		

The significant variables of the best models are presented, with the number of conflicts (N) in each category, frequency of occurrence of reconciliation in percentages (f (%)) in general and within each category, estimated coefficients (β), Wald statistics (Wald) and corresponding p-values. Note that the analysis was performed for aggressor data set and aggressee data set separately, but since the results were very similar in these analyses, we present only the results of the analysis on the aggressee data set.

*No PCI*

This category included PCs with absence of all interactions by/with the former opponent, and PCs with only opponent-initiated third-party affiliation. The frequency of 'no PCI' was 29.5% for aggressors and 33.1% for aggressees. However, for neither aggressors nor aggressees was 'no PCI' predicted by any particular conflict characteristic. Aggressors chose the 'no PCI' more often after female-female conflicts, and aggressees more often after food conflicts and after conflicts between weak compatibility opponents, but all of these predictors failed to remain significant after entering the aggressor/aggressee identity in the model.

**Table 5.** Factors determining the occurrence of triadic post-conflict interactions

PC- Interaction	Wald	df	p	category	N	f (%)	$\beta$	Wald	p
<b>a. Further aggression by aggressors</b>						<b>28.6</b>			
Directionality	<b>12.7</b>	<b>1</b>	<b>&lt;0.001</b>	uni	360	35.3	0.46	12.7	0.001
				bi	199	16.6	-0.46		
Sex class	<b>10.0</b>	<b>2</b>	<b>0.007</b>	mm	69	30.4	0.37	3.17	0.075
				mix	336	35.1	0.27	2.71	0.100
Intensity*	<b>11.1</b>	<b>2</b>	<b>0.004</b>	ff	154	13.6	-0.64	9.69	0.002
Sex class				low*mm	41	26.8	-0.45	4.92	0.027
				high* mm	28	35.7	0.45		
				low* mix	201	42.8	0.36	9.12	0.003
				high* mix	135	23.7	-0.36		
				low* ff	106	16.0	0.09	0.19	0.664
				high* ff	48	8.3	-0.09		
<b>b. Further aggression by aggressees</b>						<b>10.8</b>			
Directionality	<b>6.2</b>	<b>1</b>	<b>0.013</b>	uni	359	8.9	-0.37	6.20	0.013
				bi	206	14.1	0.37		
Context* Directionality	<b>3.77</b>	<b>1</b>	<b>0.056</b>	food* uni	110	2.7	-0.29	3.77	0.052
				social* uni	249	11.7	0.29		
				food*bi	65	13.8	-0.29		
				social*bi	141	14.2	0.29		
<b>c. Third-party affiliation to aggressors</b>						<b>40.3</b>			
Intensity	<b>4.12</b>	<b>1</b>	<b>0.042</b>	low	348	38.8	-0.22	4.12	0.042
				high	210	42.9	0.22		
Intensity*	<b>4.8</b>	<b>2</b>	<b>0.088</b>	low*mm	41	26.8	-0.36	3.78	0.052
Sex Class				high* mm	28	53.6	0.36		
				low* mix	201	41.3	0.26	4.16	0.042
				high* mix	134	39.6	-0.26		
				low* ff	106	38.7	0.10	0.46	0.449
				high* ff	48	45.8	-0.10		
<b>d. Third-party affiliation to aggressees</b>						<b>43.5</b>			
Context*	<b>2.75</b>	<b>2</b>	<b>0.097</b>	food*uni	110	42.7	0.14	2.75	0.097
Directionality				social*uni	249	41.0	-0.14		
				food*bi	65	38.5	-0.14		
				social*bi	141	51.1	0.14		
<b>e. Third-party aggression to aggressors</b>						<b>12.2</b>			
Directionality	<b>7.26</b>	<b>2</b>	<b>0.027</b>	uni* mm	42	2.4	-0.63	6.18	0.013
*Sex class				bi* mm	27	22.2	0.63		
				uni* mix	261	11.9	0.08	0.18	0.672
				bi* mix	75	9.3	-0.08		
				uni* ff	57	21.1	0.55	6.29	0.012
				bi* ff	97	11.3	-0.06		
<b>f. Third-party aggression to aggressees</b>						<b>14.7</b>			
Compatibility	<b>8.5</b>	<b>4</b>	<b>0.076</b>	strong*mm	28	7.1	0.00	0.00	0.990
(assessed by				med*mm	13	15.4	-0.28	0.78	0.378
aggressees)				weak*mm	30	16.7	0.29	0.82	0.365
*Sex class				strong*mix	109	11.0	-0.43	3.70	0.054
				med*mix	170	17.1	-0.01	0.00	0.967
				weak*mix	59	23.7	0.44	3.71	0.053
				strong*ff	40	15.0	0.43	2.39	0.120
				mid*ff	60	16.7	0.23	1.06	0.053
				weak*ff	56	5.4	-0.72	5.78	0.016

The significant variables of the best models are presented, with the number of conflicts (N) in each category, frequency of occurrence of PCI in percentages (f (%)) in general and in each category, estimated coefficients ( $\beta$ ), Wald statistics (Wald) and corresponding p-values.

## **DISCUSSION**

We set out to investigate what determines the events after conflicts and how the different PCI occur in relation to one another. We found that the occurrence of PCI was largely independent from each other, but influenced by conflict features, the conflict outcome and the relationship attributes among opponents. Below, we discuss the results concerning each PCI, after which we reflect on the findings in a broader perspective.

### **Reconciliation**

Chimpanzees of the Arnhem Zoo reconciled their disputes when the benefit of the relationship repair was the largest. The occurrence of reconciliation increased with the relationship quality; conflicts among males and between sexes were reconciled more often than conflicts among females. Moreover, high compatibility of a relationship increased the probability of reconciliation. This agrees with the earlier results in chimpanzees and other primates, and supports the notions of relationship quality being the most important determinant of reconciliation (de Waal & Yoshihara, 1983; de Waal, 1986; Kappeler & van Schaik, 1992; Cords & Aureli, 2000; Arnold & Whiten, 2001; Aureli et al., 2002; Wittig & Boesch, 2003a, 2005; Watts, 2006; Koski et al., in press). The high value of male-male relationships due to a high degree of cooperation (e.g., Watts, 2002, 2006), and of inter-sex relationships due to mating benefits (Arnold & Whiten, 2001; Wittig & Boesch, 2003a) reflected on a high prevalence of reconciliation in these sex-classes. In addition, relationship quality in terms of compatibility (see Cords & Aureli, 2000; Cords, 1997; Silk, 2002) increased the likelihood of reconciliation. Interestingly, relationship compatibility appeared to influence reconciliation asymmetrically: strong compatibility from aggresses' perspective increased the tendency to reconcile, while compatibility from aggressors' perspective did not influence reconciliation. We have shown earlier that in the Arnhem chimpanzee group only aggresses show elevated levels of post-conflict stress, in contrast to aggressors (Koski et al., in press; Koski & Sterck, 2007). The unequal stress

response together with the unequal influence of compatibility on reconciliation suggests that aggresses are more susceptible to the relationship damage caused by conflicts than aggressors are.

### **Further aggression**

Both conflict participants directed further aggression to other group members after conflicts. The main determinant of further aggression by both opponents was directionality of conflicts; the prevalence of further aggression increased after the opponent likely had won the conflict (i.e., by aggressors after unidirectional conflicts, by aggresses after bidirectional conflicts). In addition, in aggressors further aggression occurred more often after male-male conflicts, especially when they were of high intensity, and after low intensity mixed-sex conflicts. Overall, aggressors gave further aggression more often than aggresses, which contrasts with the common pattern of further aggression as a strategy of victims (Scucchi et al., 1988; Watts et al., 2000). In monkeys, further aggression has been suggested to be the victim's way to decrease post-conflict anxiety and possibly to escape a "loser-effect", which otherwise would increase the likelihood of being a target of further aggression (Thierry, 1985; Aureli & van Schaik, 1991b; Watts et al., 2000; Kazem & Aureli, 2005). The loser-effect, i.e. a defeat causing an increased probability of further defeats irrespective of the opponent is known from many species (reviewed by Chase et al., 1994; Hsu et al., 2006). However, escaping from the loser-effect is likely not underpinning chimpanzee further aggression. Firstly, it was more prevalent by aggressors. Second, it occurred after a probable winning of the conflict. Therefore, further aggression might be a consequence of the counterpart of the loser-effect, namely the 'winner-effect', i.e. an increased tendency of winning consecutive conflicts after winning a prior conflict. The winner-effect is associated with an increased willingness to initiate further contests (Chase et al., 1994; Hsu et al., 2006), and could explain the opponents' willingness to engage in further conflicts. Supporting this notion, previous studies on chimpanzees have reported more redirection by aggressors (Arnold & Whiten, 2001) and by winners (Wittig & Boesch, 2003a) of conflicts.

Further research is required to test this hypothesis, as to our knowledge no studies to date have assessed the winner or loser effects in primates, or whether they would account for further aggression (see Kazem & Aureli, 2005).

### **Third-party affiliation**

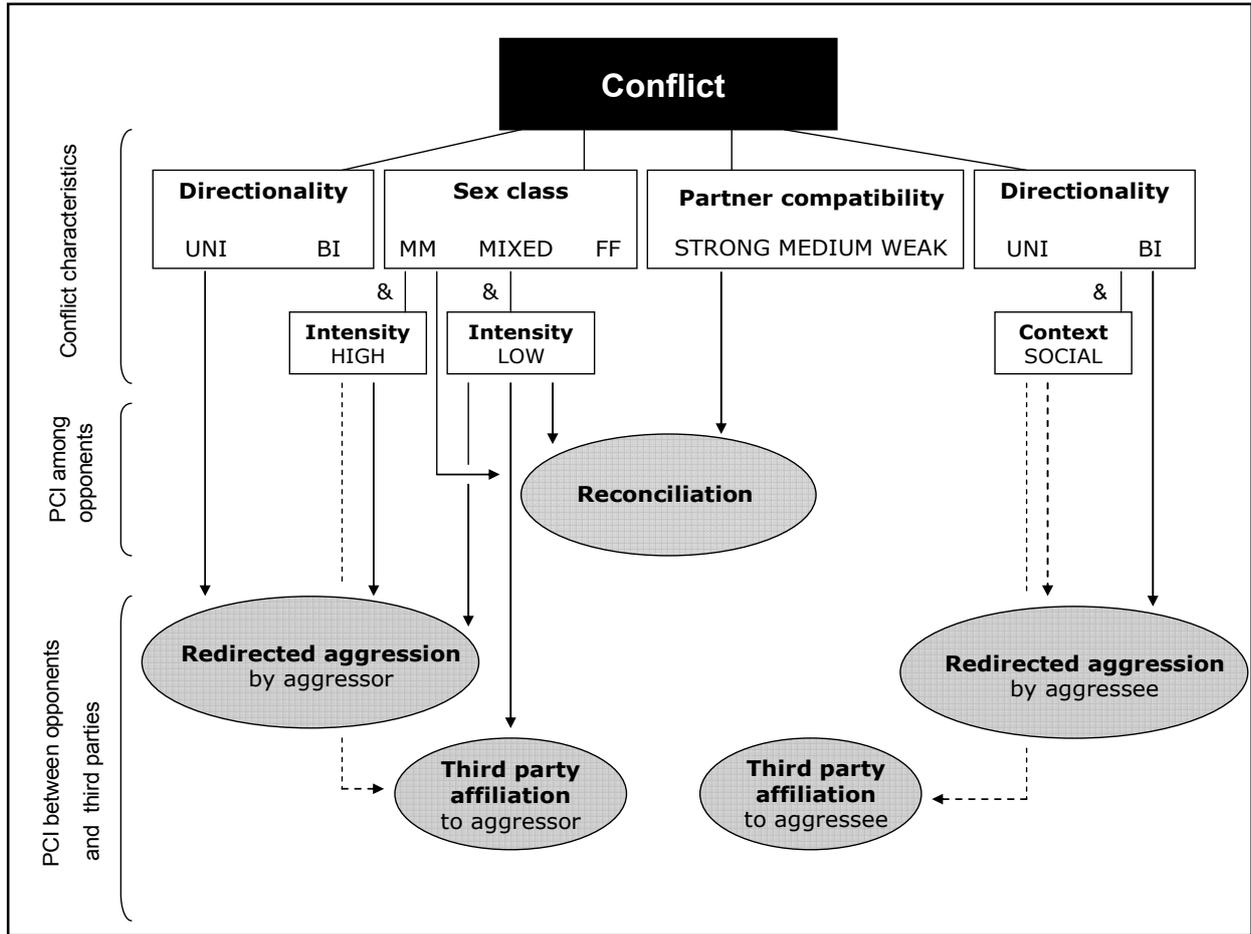
The prevalence of third-party affiliation to both opponents was rather high: 40.3% and 43.5% to aggressors and aggressees, respectively. The main predictor of third-party affiliation given to aggressors was high conflict intensity, especially of male-male conflicts, and additionally low intensity mixed-sex conflicts. In contrast, aggressees received third-party affiliation nearly irrespective of conflict characteristics or conditions, as third-party affiliation was not significantly predicted by any conflict characteristics. Only after bidirectional conflicts of social context aggressees received slightly more often third-party affiliation, the significance reaching a statistical trend.

Since third-party affiliation and reconciliation were shown to occur independently from each other, the results do not support the hypothesis that third-party affiliation would occur in the absence of reconciliation (Wittig & Boesch, 2003a; Palagi et al., 2004, 2006). Since we also have shown that third-party affiliation does not effectively alleviate conflict opponents' stress, and does not seem to function as a form of triadic reconciliation (*sensu* Judge 1991; Koski & Sterck, 2007), it is unlikely that third-party affiliation would function as a substitute for reconciliation, at least in this group of chimpanzees. An alternative hypothesis is that third-party affiliation decreases the chance of bystanders to receive further aggression from the opponents or from other group members (Das, 1998; Call et al., 2002; Palagi et al., 2004, 2006). We found that third-party affiliation was more often given to aggressors when they were likely to direct further aggression (see Figure 1). Furthermore, the similar, albeit weaker, connection was found in the aggressee data; the prevalence of third-party affiliation to aggressees was slightly higher when aggressees were likely to direct further aggression, i.e. after bidirectional social conflicts. This gives tentative support for the hypothesis that third parties affiliate with opponents in order to protect themselves from further aggression,

either directly or via a general decrease of social tension. Whether third-party affiliation truly functions to decrease the risk of receiving further aggression remains to be investigated.

### **Third-party aggression**

The fact that aggresses received slightly less often third-party aggression than aggressors further supports the suggestion that chimpanzee aggresses are not prone to undergo a loser-effect leading to further received aggression. However, the overall occurrence of third-party aggression was low and the results are rather ambiguous. Third-party aggression towards aggresses was not clearly explicable by the conflict characteristics; it was only found that third-party aggression occurred the least often after conflicts among females that had a weakly compatible relationship. However, due to the infrequent occurrence in general and the lack of positive predictors, the result's importance remains questionable. Third-party aggression towards aggressors was determined by a combination of sex class and directionality: aggressors of bidirectional male-male conflicts and of unidirectional female-female conflicts received more often third-party aggression. Although apparently not a common strategy, third-party aggression given to the aggressors of bidirectional male-male conflicts might reflect bystanders' interest in defeating a frequent opponent who loses a conflict it started and thus scoring 'psychological victories' (Watts et al., 2000). In the case of unidirectional female-female conflicts, third-party aggression towards aggressors may reflect male- or group controlling of female aggression (Watts et al., 2000). However, we stress that as the prevalence of third-party aggression was low and none of the variables alone explained its occurrence, the conclusions should be treated with caution.



**Figure 1.** A schematic representation of the choice of post-conflict interactions (PCI). Elliptic shapes represent the PCI, rectangles represent the conflict characteristics. Arrows indicate the significant predictors or combinations of predictors for the occurrence of the PCI. Dashed arrows indicate a statistical trend. Triadic interactions are depicted for both conflict participants separately.

### No PCI

The fifth considered option was the absence of particular PCI, which also could be taken as a category of 'business as usual'. Although in one third of the PCs (29.5% by aggressors, 33.1% by aggressees) the chimpanzees continued 'business as usual', for neither of the opponents any significant predictors of 'no PCI' were found. Rather, the variables that showed a significant effect prior to entering identities of aggressors or aggressees to the model fell out of significance with controlling the individual identity effect. This indicates that 'no

PCI' is an option chosen more often by particular individuals, but there is no group level determinant of when the chimpanzees continue their 'business as usual' after a conflict. A possible determinant for 'no PCI' might have been conflict duration, since Wittig & Boesch (2003a) reported the wild chimpanzees in Taï National Park to choose 'no PCI' after very short conflicts. Unfortunately, we did not record conflict duration and therefore the influence of conflict duration on 'no PCI' and on other PCI remains open.

### **General discussion**

This study revealed that the both conflict participants and the bystanders assess whether, and if so, how and with whom to interact after conflicts. The independent occurrence of reconciliation and further aggression, both post-conflict interactions performed by the opponents, indicates that these behaviours depend on different aspects of the conflict, namely relationship attributes in the case of reconciliation, and the conflict outcome in the case of further aggression. Further aggression by and third-party aggression toward aggressors co-occurred more often in the same PC than expected by chance, which may reflect counter-aggression from either third parties towards an aggressor who gives further aggression, or vice versa by opponents to third parties. However, we did not address the order of the PCI or the identities of the interaction partners, and therefore the possibility of counter-aggression remains open. Third parties directed affiliative contacts to the conflict opponents partly when the risk of receiving further aggression was high. In addition, aggresses received third-party affiliation at a consistently high rate, indicating that bystanders were little influenced by conflict characteristics in their affiliation to aggresses. Finally, third-party affiliation and third-party aggression occurred independently from each other towards both aggressors and aggresses indicating that these two triadic interactions depend on different aspects of the conflict and its outcome.

This research sheds light on the process of 'decision-making' in the complex social network of chimpanzees. The 'decisions' on which PCI to employ and when were based on a number of factors, namely the relationship attributes between conflict opponents, the specific characteristics of a conflict,

and the prospect of opponents' further interactions. The two conflict opponents were shown to have different patterns of post-conflict interactions with third parties, as did the third parties with respect to both opponents. Therefore, in future studies, we recommend treating the roles of both conflict participants separately. Finally, the PCI were shown to be largely independent from each other and to be determined by different aspects of the conflicts, which emphasises the importance of assessing several PCI in conflict resolution research.

### **Acknowledgements**

Financial support was generously given to S.E.K by Lucie Burgers Foundation for Comparative Behaviour Research, Arnhem, The Netherlands. We thank the Burger's Zoo for strong logistical support throughout the study; Prof. Dr. Jan van Hooff and Kathelijne Koops for inspiring discussions; and K. Koops, E. Kenbeek, M. Heesen, C. van Maanen, O. van Velthuisen, M. Beterams, R. van den Toorn, L. Visser, A. Dupouy, M. van Dongen, M. Heitman, E. van Rooij, H. Wiggers, and M. Schoe for their invaluable help in data collection. Commentary by Eva Kallio greatly improved the manuscript.

## *CHAPTER 4*

---

TRIADIC POST-CONFLICT AFFILIATION IN CAPTIVE  
CHIMPANZEES:  
Does Consolation Console?

---

Sonja E. Koski\* & Elisabeth H.M. Sterck

*Published in Animal Behaviour 2007: 73, 133-142.*

## **ABSTRACT**

Consolation is a triadic post-conflict interaction between a conflict participant and an uninvolved third party. The term consolation implies stress alleviation. Consequently, consolation has been suggested to be an effective mechanism to alleviate post-conflict stress. However, to date this assumption has not been tested. We tested whether consolation alleviates post-conflict stress in captive chimpanzees (*Pan troglodytes*). In addition, we examined whether consolation is a substitute post-conflict interaction for reconciliation. We collected 643 post-conflict-matched control pairs on aggressees and 576 on aggressors. Consolation occurred equally frequently with aggressees and aggressors. However, we found no evidence that consolation alleviated stress, regardless of the identity of the consoler. In addition, consolation was also directed to conflict participants with no evident post-conflict stress. Furthermore, we found no evidence for consolation being a substitute for reconciliation. The occurrence of consolation did not depend on the occurrence of reconciliation and consolation was not more prevalent with the sex class that reconciled less often or had the highest post-conflict stress levels. We conclude that consolation is a post-conflict interaction in its own right, the function of which is likely not connected to stress alleviation of the consoled individual. We propose that the function of triadic post-conflict affiliation, previously labelled as consolation, should be reassessed with regards to the third parties' reasons to affiliate with conflict opponents.

## **INTRODUCTION**

Gregariousness inevitably leads to competition over limited resources and thereby to conflicts of interest between group members. Conflicts may jeopardise the cohesion of the group and the relationships therein. Therefore, to maintain the benefits of group living, the negative repercussions of possibly aggressive conflicts should be minimized. Several conflict management mechanisms have been described in social animals, among which friendly post-conflict interactions between the former opponents and with other group members (e.g., de Waal 1989, 1996; Cords & Aureli 1996; Cords & Killen 1998; Das 2000; reviewed in Aureli & de Waal 2000; Aureli et al. 2002). Reconciliation, or selective affiliation between the former opponents soon after the conflict, was first described by de Waal and van Roosmalen (1979) in chimpanzees (*Pan troglodytes*), and reconciliation has since been found in some 30 primate species (reviewed in Aureli & de Waal 2000; Aureli et al. 2002) and a few non-primate species (Schino 2000).

In addition to dyadic conflict resolution, triadic post-conflict affiliation has been described in several primate species (reviewed by Das 2000; Watts et al. 2000). Triadic post-conflict affiliation refers to affiliation between conflict members and uninvolved bystanders, i.e. 'third parties'. Such contacts may involve either conflict aggressors or victims, and the third parties may be kin to either one of the opponents, or unrelated to both conflict participants (de Waal & Yoshihara 1983; Judge 1991; Das et al. 1997; Castles & Whiten 1998a). The function of such contacts presumably varies according to the identity of the third party and whether the affiliation is directed to the former aggressor or the victim (Das 2000).

Consolation is a triadic post-conflict resolution mechanism that involves the former conflict victim and a third party (de Waal & van Roosmalen 1979). The term consolation has been specified to signify friendly contacts that are initiated by the third party, as opposed to contacts solicited or initiated by the victim (de Waal & Aureli 1996; Verbeek & de Waal 1997). Consolation has been thought to occur in apes but not in monkeys (de Waal & Aureli 1996; Castles 2000; Palagi et al. 2004). However, recently consolation was described in stump-tailed

macaques (*Macaca arctoides*) when specific behaviours were analysed separately (Call et al. 2002).

Although consolation is a functional label, the presumed function has not been rigorously tested. Consolation as a label carries the implicit assumption of stress alleviation. Consequently, several authors suggest consolation to be a mechanism for post-conflict stress reduction (de Waal & Aureli 1996; Aureli 1997; Matheson 1999; Wittig & Boesch 2003; Palagi et al. 2004; Kutsukake & Castles 2004). The assumption of stress alleviation is also implied in the substitute for reconciliation hypothesis, which proposes that consolation is the 'next best option' available for a former conflict opponent when reconciliation is not possible (Watts et al. 2000; Wittig & Boesch 2003). Reconciliation has been shown to repair the relationship between the former opponents and to reduce post-conflict stress (e.g., Aureli & van Schaik 1991b; Cords 1992; Aureli 1997; Das et al. 1998; Castles & Whiten 1998b; Koyama 2001; Aureli et al. 2002; Wittig & Boesch 2005). As a substitute conflict resolution mechanism consolation is assumed to result in stress alleviation equal to reconciliation (Watts et al. 2000; Wittig & Boesch 2003; Palagi et al. 2004) and possibly also to relationship repair with the former opponent via triadic reconciliation i.e., affiliation with former opponent's kin (Aureli & van Schaik 1991a; Judge 1991, Das 2000). Indeed, recent findings on chimpanzees and bonobos, *Pan paniscus*, give indirect support for the substitution for reconciliation hypothesis; consolation was found to occur more often in the absence of reconciliation (chimpanzees: Palagi *et al.* 2006; bonobos: Palagi et al. 2004), and when reconciliation was presumably not beneficial or too risky for conflict participants (chimpanzees: Wittig & Boesch 2003).

However, no studies have assessed whether consolation indeed alleviates post-conflict stress in former conflict victims. Since stress alleviation is the essence of the term consolation and the underlying assumption in the Substitution for Reconciliation Hypothesis, we consider research on the effect of consolation to be long overdue. We investigated whether consolation results in alleviation of post-conflict stress in chimpanzees. In addition, we tested the substitute for reconciliation hypothesis. We investigate whether consolation truly

is a substitute, i.e. occurring only or most likely in the absence of reconciliation, and resulting in effective alleviation of post-conflict stress and/or in relationship repair with the former opponent via affiliation with the former opponent's kin.

We generated four predictions. First, if consolation is an alternative post-conflict resolution mechanism to reconciliation, we predicted that (1) consolation should be more frequent in the absence of reconciliation and less frequent when reconciliation does occur. Second, dyad-specific trends for consolation may be found. As an equivalent stress alleviating mechanism to reconciliation, consolation should occur more often with conflict participants that show the highest levels of post-conflict stress. We have shown in a previous study on the same population that conflicts among males result in the highest levels of post-conflict stress, compared to conflicts among females and between females and males (Koski et al. in press). Hence we predicted (2a) that consolation should occur more often after conflict among males. Alternatively, consolation may also be more frequent among partners that are less likely to reconcile (Wittig and Boesch 2003). As has been shown in several studies, the highest reconciliation tendency in chimpanzees occurs among males and between females and males, whereas the lowest reconciliation tendency is found among females (de Waal 1986, Arnold & Whiten 2001; Wittig & Boesch 2005). Hence, as an alternative possibility we predicted that (2b) consolation should occur more often after conflicts among females than after conflicts among males and between females and males. Third, concerning possible relationship repair via triadic reconciliation, we predicted that (3) consolation should occur more often with opponent's kin than with own kin or with unrelated individuals. Finally, we predicted that (4) consolation should alleviate post-conflict stress comparably to reconciliation.

As opposed to previous studies that have functionally differentiated triadic affiliative contacts with aggressors from those with targets of aggression (de Waal & Aureli 1996; Das 2000; Watts et al. 2000; Palagi et al. 2004), we are interested in affiliative contacts directed to both conflict opponents (c.f. Call et al. 2002; Kutsukake & Castles 2004). Therefore, we use the term 'consolation' to describe third party affiliation not only with the victims, or aggressees, but also

with the aggressors of conflicts (termed as 'appeasement' by Das 2000; Kutsukake & Castles 2004).

## **METHODS**

### **Subjects and Housing**

We studied a group of chimpanzees, established in 1971, in the Burgers' Zoo in Arnhem, the Netherlands. During the summer months, the group lives in an outside enclosure of about 0.7 ha, which is an island surrounded by a moat. The island contains natural trees as well as wooden climbing structures, nets and ropes. During the winter months, when temperature is below 10°C, the chimpanzees stay indoors in a hall of 21x18 m, enriched with wooden platforms, plastic barrels, nets and ropes, as well as loose objects such as balls and sticks. Fresh straw is provided daily. The chimpanzees are fed in the mornings and evenings with vegetables, fruit, milk and monkey chow. Additionally twice during the afternoons they receive fruit, vegetables, seeds or peanuts. Water is available ad libitum throughout the day. For further details of the colony and husbandry, see van Hooff (1973a), Adang et al. (1987) and Takeshita & van Hooff (2001).

During the study period, the group consisted of 30-34 individuals: 3-5 adult males, 15-18 adult females, 0-2 adolescent males, 1-3 adolescent females, 7-9 juveniles and infants (age classes as in Preuschoft et al. 2002). All but five individuals were born in the group and none were introduced to the group during the study. During the study four chimpanzees were born, three infants and one adult female died, one adult male and three adult females were sent to other zoos.

### **Data Collection**

The first author together with several students observed the chimpanzees during June 2002- January 2005. Inter-observer reliability was ensured by >95% similarity in focal observations of each student and SEK. The ethogram was based on van Hooff (1973b). We observed the chimpanzees all day, during the time they were present in their indoor enclosure or outdoor compound. During

the observational time frame, we aimed at recording all the occurring conflicts. If visibility limited observation of at least one conflict partner, we halted data collection. We recorded conflicts amongst adults and adolescents. An aggressive interaction was defined as a conflict if it included at least one of the following: chase, push, grab, hit, jump-on, trample, bite, and if the recipient of aggression showed at least open-bared-teeth and screams. The roles of aggressor and aggressee were assigned based on the initial direction of aggression. We use the term aggressee for the targets of aggression since in chimpanzees the 'victim' is not necessarily the loser of the conflict and there is a high prevalence of bi-directional aggression (Wittig & Boesch 2003; Koski unpublished data). During the conflict we noted descriptively the events, identities of all conflict participants, and all interactions among and with conflict participants.

We conducted post-conflict (PC) observations following de Waal & Yoshihara (1983) and Aureli et al. (1989). PC observations were of 10 minutes duration, during which we recorded all interactions of the focal animal with other group members timed to the second. We conducted simultaneous observations on both aggressors and aggressees. If the conflict was resumed within 2 min, we cancelled the PC and started anew when aggression ceased. PC observations were matched with control observations (MC) on the next possible day, within 7 days from the conflict, with a criterion of no agonistic interactions with the focal animals for 1h prior to MC. We conducted MC at the same time of the day as the conflict, controlling for context (i.e. presence or absence of food) and availability of the former partner for interactions (i.e. partner was present in the enclosure). Since we conducted the study in captivity and all group members had in principle an equal chance to interact with each other, we did not control for the inter-opponent distance at the beginning of MC (Call 1999). We applied similar methods during both indoor and outdoor observations.

As a measure of post-conflict anxiety we recorded scratching rates (Schino et al. 1996; Aureli & de Waal 1997; Baker & Aureli 1997; Kutsukake 2003). A new scratching bout was assigned when the scratched body part changed, or when scratching was resumed after more than 5 sec.

With respect to the consoler's identity, we distinguished three categories regarding the relationship with the focal animal: own kin, opponent's kin, and unrelated to both conflict opponents. Kinship was based on maternal relatedness, including (grand-)mother-offspring pairs and siblings and excluding aunts, uncles and cousins (Aureli et al. 1989; Das et al. 1997; Chapais et al. 2001).

### **Data Analysis**

We recorded in total 669 conflicts, of which we obtained full data on 578 PC-MC pairs on aggressors and 642 PC-MC pairs on aggresses. We combined the data from indoors and outdoors, as there was no difference in conflict rate (Koski unpublished data) or in conciliatory tendency (Koski et al. in press) between indoor and outdoor observations.

To examine reconciliation, we applied the PC-MC method (de Waal & Yoshihara 1983), in which the timing of the first affiliative contact between the former opponents is compared between PC and MC. If the contact occurred earlier, or only, in PC the pair was labelled attracted. If the contact occurred earlier, or only, in MC the pair was labelled dispersed. If the affiliation occurred exactly at the same time in PC and MC, or if there was no affiliation in either PC or MC, the pair was labelled neutral. The proportion of attracted pairs to proportion of dispersed pairs was compared with Wilcoxon signed-ranks tests. We obtained the corrected conciliatory tendency (CCT) of each individual with the measure that corrects for the baseline affiliation (Veenema et al. 1994):

$$\text{CCT} = 100 \times ((\text{attracted} - \text{dispersed}) / \text{total number of pairs}).$$

We calculated CCTs for only the original opponent dyad, thus excluding other opponent pairs in polyadic conflicts. CCTs were calculated for each individual with the minimum criterion of three qualifying PC-MC pairs. Subsequently, we calculated the mean CCT for each sex class of conflicts from individual CCT values.

To study consolation we followed Call et al. (2002) and Palagi et al. (2004), applying a similar method as for CCT but labelling the affiliation tendency between former opponents and other group members as triadic contact tendency (TCT). PCs were first divided according to who initiated the third-party contact;

when the focal animal initiated the contact it was labelled solicited consolation, whereas when the third party initiated the contact it was labelled true consolation (Verbeek & de Waal 1997). Based on this assignment, the PC-MC pair was further labelled as attracted, dispersed or neutral in a similar manner as with reconciliation. We calculated TCTs for each individual as aggressor and aggressee, respectively, for both solicited and true consolation. In case of true consolation, we further calculated TCTs for males and females separately, and for participants of different sex classes of conflicts. Lastly, we calculated TCTs of true consolation for each individual according to kin class of the consoler, i.e. consoler being own kin, opponent's kin or unrelated individual. For each kin class of each individual we obtained thus one data point (TCT value), which was used in pairwise comparisons (c.f. Call et al. 2002).

To test whether reconciliation and consolation are substitute interactions, we divided PCs according to the presence or absence of reconciliation, and subsequently according to whether or not true consolation occurred. We compared the conditions with a Fisher's exact test. We followed the operational definition of reconciliation by including only attracted pairs as reconciled conflicts (Cords 1993), and applied the rule also to consolation throughout the analyses.

To assess post-conflict anxiety levels we used scratching as an indicator self-directed behaviour. We followed the methodology of Aureli & van Schaik (1991a) and Castles & Whiten (1998b). First, we divided PCs into four categories: PCs with (1) no affiliation, (2) only reconciliation, (3) only consolation, and (4) both reconciliation and consolation. Thereafter, we calculated the temporal distribution of scratching in PCs with no affiliation by calculating individual means for each minute of PC. From individual means we calculated the group average scratching rate for each minute of PC. This was compared to the baseline scratching rate derived from each individual's mean MC rate over ten minutes with 95% confidence intervals. We checked the generality of the results by comparing PC and MC rates of each individual with Wilcoxon signed-ranks test.

To investigate the effect of post-conflict affiliations on scratching rates, we calculated the mean scratching rates of each individual after PC-affiliation and

compared that to pre-affiliation rates. Scratching rates before and after affiliation were calculated from the actual time point of affiliation. In the category (4), where reconciliation and consolation occurred in the same PC, we calculated the 'before affiliation'-rates before consolation, as it occurred on average earlier than reconciliation, and consequently the 'after affiliation'- rates after reconciliation. Lastly, we combined the 'before affiliation' scratching rates from categories (2), (3), and (4) to get a better representative sample of mean scratching rates for each individual prior to affiliation.

All analyses on TCTs and scratching rates were conducted separately for aggressors and aggresses. We tested CCTs, TCTs, and scratching rates at the individual level with Wilcoxon-signed ranks (Wilcoxon) and Mann-Whitney *U* tests. All analyses were two-tailed unless stated otherwise and the level of significance was set at  $\leq 5\%$ , probabilities up to 10% are reported as trends. Means are given  $\pm$ SD.

## RESULTS

We confirmed the existence of true consolation as a post-conflict interaction in this colony of chimpanzees. The proportion of attracted pairs was significantly greater than the proportion of dispersed pairs for aggresses (mean proportion of attracted vs. dispersed pairs: 43.3% vs. 30.0%; Wilcoxon:  $Z=-2.78$ ;  $N=24$ ,  $P=0.005$ ) while for aggressors the difference reached only a statistical trend (attracted vs. dispersed pairs = 42.6% vs. 32.6%, Wilcoxon:  $Z=-1.72$ ;  $N=21$ ,  $P=0.085$ ). The mean triadic contact tendency (TCT) of the group averaged from individual means was 12.7% ( $\pm 17.2$  SD). TCTs of aggressors and aggresses did not differ from each other (mean TCT aggressors vs. aggresses: Wilcoxon  $Z=-0.34$ ,  $N=21$ ,  $P=0.74$ , Table 1). We also compared the TCTs between aggressors and aggresses within females and males, respectively, and found no difference (female aggressors vs. aggresses: Wilcoxon  $Z=-0.40$ ,  $N=16$ ,  $P=0.69$ ; male aggressors vs. aggresses:  $T=7$ ;  $N=5$ ,  $P=0.50$ , Table 1).

Solicited consolation was not found in this group of chimpanzees; the proportion of attracted pairs was not different from the proportion of dispersed

pairs for either aggresses or aggressors (aggresses: attracted vs. dispersed: 43.7% vs. 35.4%, Wilcoxon  $Z=-1.43$ ,  $N=23$ ,  $P=0.15$ ; aggressors attracted vs. dispersed pairs: 41.5% vs. 34.7%; Wilcoxon  $Z=-1.24$ ,  $N=17$ ,  $P=0.21$ ). Therefore, all consecutive analyses concern only true consolation.

The average latency to true consolation was for aggresses 108.7 sec (median 53 sec) and for aggressors 142.7 sec (median 96 sec) and thus shorter than the average latency to reconciliation of 191.35 sec (median 142 sec).

### **Consolation as a Substitute for Reconciliation**

To test the prediction 1, we assessed the relative occurrence of reconciliation and consolation (Fig. 1). The occurrence of reconciliation did not influence the occurrence of consolation given to aggresses. In the presence of reconciliation ( $N=153$ ) consolation occurred in 49.1% of the cases, while in the absence of reconciliation ( $N=489$ ) consolation occurred in 42.1% of the cases (Fisher's exact:  $\chi^2= 2.25$ ,  $df=1$ ,  $P=0.14$ ). For aggressors, consolation was more likely in the presence than in the absence of reconciliation; with reconciliation ( $N=135$ ) consolation occurred in 46.6% of the cases, while in the absence ( $N= 443$ ) of reconciliation consolation occurred in 37.0% of the cases ( $\chi^2= 4.04$ ,  $df=1$ ,  $P=0.05$ ).

With regards to the predictions 2a and 2b, we compared the corrected conciliatory tendencies (CCT) and triadic contact tendencies (TCT) of conflict sex classes. Male-male conflicts were reconciled significantly more often than female-female conflicts (m-m vs. f-f:  $U= 26.5$ ,  $N_1=6$ ,  $N_2=19$ ,  $P=0.05$ ; m-m vs. inter-sex:  $T=7$ ,  $N=6$ ,  $P=0.46$ ; f-f vs. inter-sex:  $Z= 0.28$ ,  $N=19$ ,  $P=0.78$ , Table 1). Thereafter, we calculated the mean TCT of females and males, and of conflict sex classes. The mean TCT of females did not differ from the mean TCT of males for either aggresses or aggressors (females vs. males aggresses  $U=43$ ,  $N_1=19$ ,  $N_2=5$ ,  $P=0.75$ ; aggressors  $U=39$ ,  $N_1=16$ ,  $N_2=5$ ,  $P=0.93$ , Table 1). The mean TCTs of conflict sex classes did not differ from each other either for aggresses or for aggressors (aggressive f-f vs. m-m:  $U=32.5$ ,  $N_1=15$ ,  $N_2=5$ ,  $P=0.66$ ; aggressor: f-f vs. m-m:  $U=29.5$ ,  $N_1=15$ ,  $N_2=4$ ,  $P=0.96$ , Table 1). We confirmed the absence of a difference with an analyses on pooled data (tested as proportion

of attracted pairs against proportion of dispersed and neutral pairs with Fisher's exact; aggressor: f-f vs. m-m:  $X^2=0.73$ ,  $df=1$ ,  $P=0.79$ ; f-f vs. inter-sex:  $X^2=1.56$ ,  $df=1$ ,  $P=0.23$ ; m-m vs. inter-sex:  $X^2=0.43$ ,  $df=1$ ,  $P=0.55$ . Aggressor: f-f vs. m-m:  $X^2=0.09$ ,  $df=1$ ,  $P=0.78$ ; f-f vs. inter-sex:  $X^2=1.63$ ,  $df=1$ ,  $P=0.21$ ; m-m vs. inter-sex:  $X^2=0.34$ ,  $df=1$ ,  $P=0.59$ ).

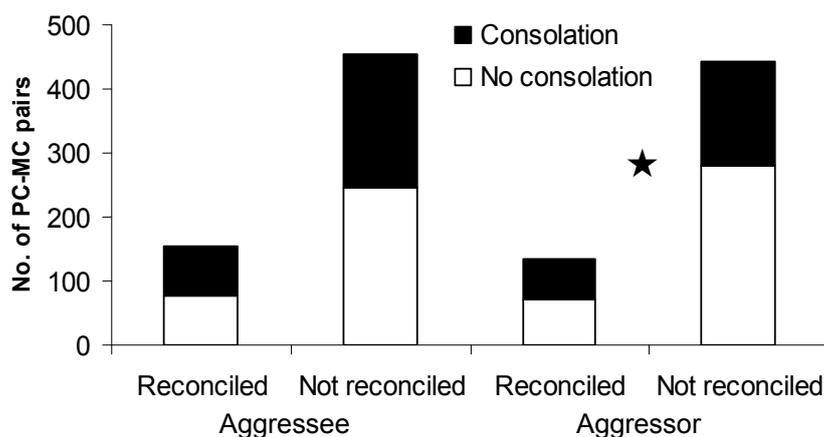
**Table 1.** Triadic contact tendencies (TCT) and corrected conciliatory tendencies (CCT) former conflict opponents .

	males	fema- les	m-m	inter- sex	f-f	own kin	opp. kin	unrela- ted
TCT %	11.45	9.54	10.47	11.17	7.18	0.44	3.35	13.25
aggressor	(16.6)	(29.9)	(18.9)	(28.8)	(36.5)	(26.1)	(20.7)	(30.2)
	$N = 5$	$N = 16$	$N = 4$	$N = 9$	$N = 15$	$N = 15$	$N = 15$	$N = 20$
TCT %	10.80	13.99	17.35	13.70	10.75	10.13	0.38	10.25
aggressee	(25.5)	(18.0)	(33.3)	(27.1)	(34.9)	(20.3)	(8.0)	(21.9)
	$N = 5$	$N = 19$	$N = 5$	$N = 21$	$N = 15$	$N = 21$	$N = 20$	$N = 24$
CCT %	26.22	17.14	20.80	19.02	14.30	(--)	(--)	(--)
	(9.9)	(8.1)	(6.4)	(15.1)	(8.1)			
	$N = 6$	$N = 19$	$N = 6$	$N = 25$	$N = 19$			

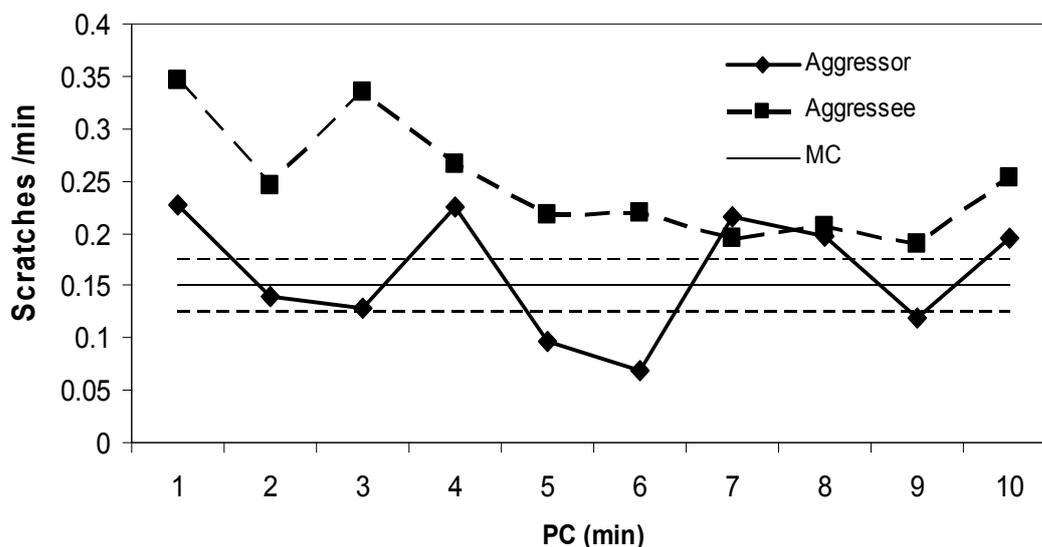
Mean  $\pm$ SD of individual values are given. TCT refers to true consolation, i.e. contacts initiated by the third party. M-m = male-male conflicts, inter-sex= male-female and female-male conflicts, f-f = female-female conflicts. Own kin= consoler is kin to receiver of consolation, opponent kin= consoler is kin to the conflict opponent of the receiver of consolation, unrelated= consoler is unrelated to both conflict opponents. Kinship classes are based on maternal kinship.

### Identity of Consolers

To test the prediction 3, we calculated TCT according to consolers' kinship class, i.e., consoler being kin to the receiver of consolation ('own kin'), kin to the receiver's former opponent ('opponent's kin'), or unrelated to both conflict opponents ('unrelated') (Table 1). Unrelated individuals directed significantly more often consolation to both aggressees and aggressors than opponents' kin



**Figure 1.** The occurrence of consolation in the presence and absence of reconciliation, for aggressees and aggressors, respectively. (\*)  $p = 0.05$



**Figure 2.** The mean post-conflict (PC) scratching rates of aggressors and aggressees in PCs with no affiliation. MC= the mean baseline scratching rate with 95% confidence intervals.

did (aggressees, unrelated vs. opponents' kin:  $Z = -1.93$ ,  $N = 20$ ,  $P = 0.05$ ; aggressors unrelated vs. opponent's kin:  $Z = -2.17$ ,  $N = 15$ ,  $P = 0.03$ ). Aggressors received consolation from unrelated individuals more often than they did from own kin, the difference reaching a statistical trend (own kin vs. unrelated:  $T = 18$ ,  $N = 14$ ,  $P = 0.055$ ). Aggressees received consolation from unrelated individuals equally often as from own kin (own kin vs. unrelated:  $Z = -0.19$ ,  $N = 21$ ,  $P = 0.85$ ).

### **The Effect of Consolation on Stress Alleviation**

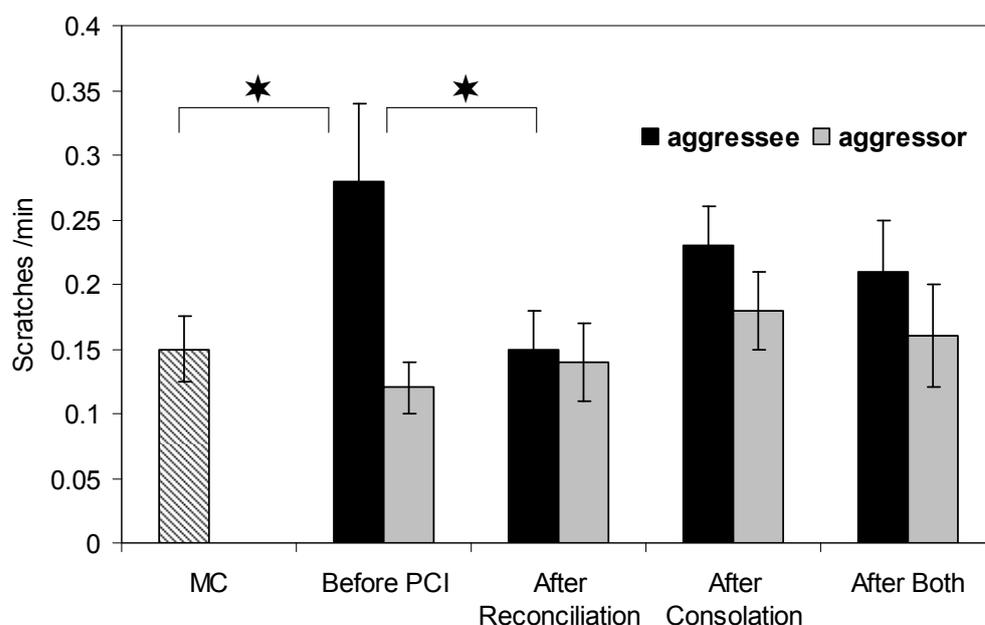
The prediction 4 concerned the stress alleviation effect of consolation. First we assessed whether aggressors and aggressees had an elevated stress response after conflicts (Fig. 2). Aggressees showed an elevated stress response after conflicts whereas aggressors did not. In PCs without affiliation the scratching rates of aggressees stayed above the baseline throughout the ten minute PC. In contrast, aggressors showed no increase in scratching rates after conflicts except on the first minute of PC, after which their scratching rates remained on the baseline.

To assess the effect of consolation on post-conflict stress, we compared the scratching rates after reconciliation, after consolation, and after both reconciliation and consolation occurring in the same PC to the scratching rates before any affiliation took place. In aggressors, there were no differences in scratching rates before affiliation compared to rates after any PC affiliation (mean  $\pm$ SD: before affiliation = 0.12 sc/min  $\pm$  0.1; after reconciliation = 0.14 sc/min  $\pm$  0.1; after consolation = 0.18 sc/min  $\pm$  0.16; after both = 0.16 sc/min  $\pm$  0.13 sc/min; all comparisons NS; Fig 3).

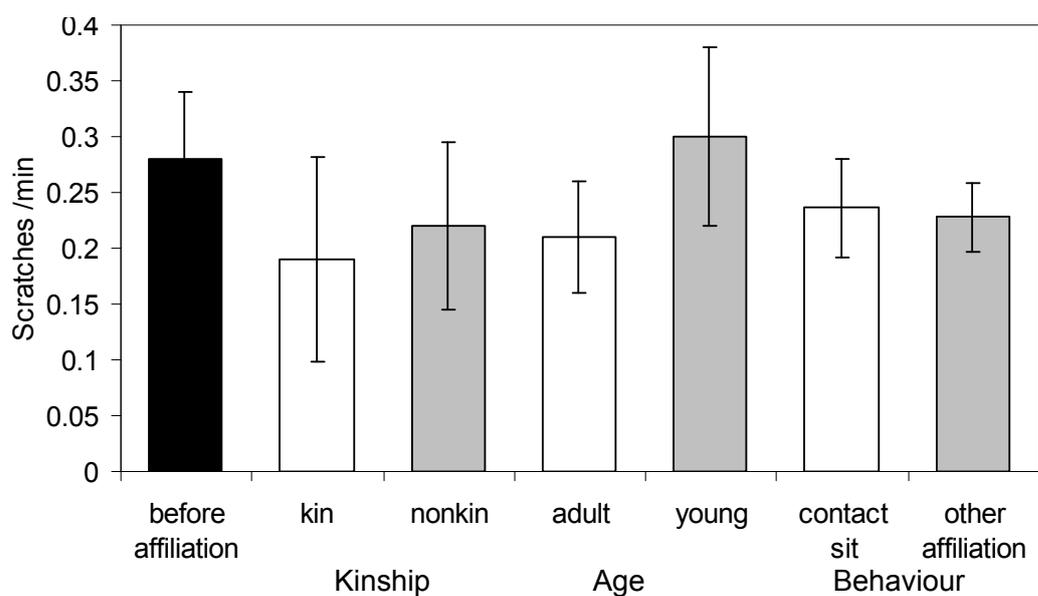
Aggressees showed significantly decreased scratching rates after reconciliation compared to rates before affiliation (mean  $\pm$ SD: before affiliation = 0.28 sc/min  $\pm$  0.28; after reconciliation = 0.15 sc/min  $\pm$  0.13; Wilcoxon  $T=19.5$ ,  $N=15$ ,  $P=0.021$ ; Fig. 3). In contrast, mean scratching rates did not decrease after consolation compared to rates before affiliation (after consolation = 0.23 sc/min  $\pm$  0.17; Wilcoxon  $Z=-0.5$ ,  $N=23$ ,  $P=0.61$ ; Fig 3), nor did they decrease after reconciliation and consolation together (after both affiliations = 0.21 sc/min  $\pm$  0.19; Wilcoxon  $Z=-0.32$ ,  $N=19$ ,  $P=0.75$ ; Fig. 3).

We also calculated scratching rates of aggressees after consolation according to the consoler's identity (Fig. 4). Mean scratching rates of aggressees after consolation by own kin did not differ from the scratching rates after consolation by unrelated individuals (own kin = 0.19 sc/min  $\pm$  0.15; unrelated = 0.22 sc/min  $\pm$  0.15; Wilcoxon  $T=29$ ,  $N=12$ ,  $P=0.72$ ). Second, we assessed whether scratching rates after consolation were dependent on age of a consoler. Scratching rates of aggressees after consolation by young (i.e., infant and

juvenile) consolers did not differ from the scratching rates after consolation by adults (consoler young=0.30 sc/min  $\pm$ 0.4; adult= 0.22 sc/min  $\pm$ 0.2; young vs. adult: Wilcoxon  $Z=-1.18$ ,  $N=21$ ,  $P=0.24$ ). Lastly, we assessed whether certain behaviours used in consolation would affect scratching rates of aggresses. We separated consolation by contact sitting, and consolation by other affiliative behaviours. However, scratching rates were not affected by the behaviour used in consolation (after consolation by contact sit: 0.24 sc/min  $\pm$ 0.22; after consolation by other affiliatives: 0.23 sc/min  $\pm$ 0.14; Wilcoxon  $Z= -0.04$ ,  $N= 21$ ,  $P=0.97$ ).



**Figure 3.** Post-conflict scratching rates of aggressors and aggresses before affiliation, after reconciliation, after consolation and after both reconciliation and consolation occurring in the same PC (mean  $\pm$  SEM). MC= baseline scratching rates. (\*)  $p < 0.05$ .



**Figure 4.** Post-conflict scratching rates of aggresses before affiliation, and after consolation according to consoler's identity (kin to consoled individual or unrelated to both conflict opponents), age (adults or infants and juveniles), and consolatory behaviour (contact sit or other affiliative behaviours).

### Facilitation of Reconciliation

As an *a posteriori* hypothesis we assessed whether consolation, when occurring together with reconciliation, would facilitate reconciliation. We measured the average latency to reconcile when consolation preceded reconciliation as compared to when consolation occurred after reconciliation or not at all. The latency to reconcile was not shorter when consolation preceded it. In fact, reconciliation appeared significantly delayed when it occurred after consolation compared to when reconciliation occurred without or before consolation (average latencies to reconcile: when consolation preceded reconciliation = 256.7 s [median 237.2 s]; when reconciliation alone or before consolation = 153.2 s [median 158.6 s]; Wilcoxon  $Z = -322$ ,  $N = 19$ ,  $P < 0.001$ ). Hence, reconciliation did not appear to be facilitated by consolation, rather the opposite.

### DISCUSSION

The presumed effect of consolation on stress alleviation has to date not been tested, even though it is implied by the term consolation, first coined by de Waal

& van Roosmalen (1979). We tested the assumption that consolation reduces post-conflict stress in the targets of consolation and considered the substitute for reconciliation hypothesis, according to which consolation occurs in the absence of reconciliation and is an effective conflict resolution mechanism when reconciliation is not possible (Watts et al. 2000; Wittig & Boesch 2003). The presumed alleviating effect of consolation on stress is an inherent part of this hypothesis. Moreover, consolation as a substitute for reconciliation could possibly provide a relationship repair mechanism via affiliation with a former opponent's kin (Judge 1991, Das 2000).

We found no support for the substitute for reconciliation hypothesis. Consolation did not occur more often in the absence of reconciliation; in aggressees the occurrence of reconciliation did not influence the occurrence of consolation, while in aggressors consolation was, in fact, less likely in the absence of reconciliation than vice versa. Furthermore, most consolation events took place earlier than reconciliation; the average latency of consolation was shorter than that of reconciliation. Finally, we found no support for either of the alternative predictions concerning differences in consolation tendency between sex classes. We predicted that either consolation would be more likely after conflicts of the sex class that reconciles less often, i.e. females (Wittig and Boesch 2003), or alternatively, that consolation would be more likely after conflicts among males due to their high levels of post-conflict anxiety (Koski et al. in press). We confirmed that male-male conflicts were reconciled more often than female-female conflicts, while there were no differences between conflict sex classes in the tendency to receive consolation. These findings do not give support for the hypothesis that consolation would be an alternative post-conflict interaction to take place when reconciliation is not possible or worthwhile.

We found no evidence that consolation, as an alternative conflict resolution mechanism, provides benefits comparable to reconciliation for the target of consolation. To function as a relationship repair mechanism we predicted consolation to be performed predominantly by conflict opponent's kin. However, we found few events of consolation by opponent's kin. The most frequent consolers were unrelated to both conflict opponents, and aggressees, in addition,

were consoled by their own kin. Therefore, it is unlikely that consolation would serve as a relationship repair mechanism via triadic affiliation with opponent's kin in chimpanzees, as shown for macaques (Aureli & van Schaik 1991a; Judge 1991, Das et al. 1997). In macaques, triadic reconciliation via opponents' kin is explicable by strong bonds in kin relationships and the linear dominance hierarchy formed around matriline (Das 2000). In contrast, the chimpanzee social structure is not built upon extensive kin bonding (e.g. Pusey 1979; Vigilant et al. 2001; Mitani et al. 2002; Lukas et al. 2005), and therefore applying the assumption of triadic reconciliation to chimpanzees may not be plausible. Although kinship relationships become important in captive chimpanzee groups since family members often stay in the group, providing a source of support and affiliation (de Waal 1982, 1984), triadic reconciliation as a conflict resolution mechanism may be absent in chimpanzees.

Finally, we found no evidence for stress reduction due to consolation. Scratching rates of aggresses were elevated after conflicts, and reconciliation with the former opponent effectively brought stress levels back to baseline. However, scratching rates after consolation did not decrease compared to rates before affiliation but stayed significantly higher than the baseline rates. Furthermore, when reconciliation and consolation both occurred in the same PC, the scratching rates stayed higher than baseline rates. Thus, consolation did not alleviate post-conflict stress in aggresses, and when occurring together with reconciliation, consolation seemed even to counteract the effect of reconciliation on stress reduction.

To assure the generality of the result, we proceeded to investigate whether the identity or age of the consoler would influence the scratching rates following consolation. However, the scratching rates after consolation were not influenced by the identity or age of the consoler. We found no indication of stress alleviation due to consolation regardless of the kinship relationship between the consoler and the target, or the age of the consoler. Lastly, we assessed whether the type of affiliation during consolation would influence the scratching rates. However, the effect of contact sit as a consolatory contact did not differ from that of other affiliative behaviours. In sum, consolation did not alleviate post-conflict stress in

former conflict aggresses, and this depended neither on the identity or age of the consolers nor on the type of affiliative behaviour in consolation. Hence, consolation did not seem to 'console'.

We therefore conclude that we found no support for any of our four predictions concerning the occurrence and effects of consolation as a substitute post-conflict interaction for reconciliation. Below, we discuss the implications of our results.

### **What is Consolation if it Does Not Console?**

Concerning the occurrence of consolation, our results contrast the findings in a wild chimpanzee population in Tai National Park, in which consolation was found to occur more often when reconciliation was not possible or likely; thus, consolation was most frequent after conflicts between same sex partners (Wittig & Boesch 2003). Wittig & Boesch (2003), however, employed a different operational definition on post-conflict interactions to ours, so that consolation and reconciliation could not by definition occur in the same PC. This may mask the possibility that consolation and reconciliation are independent post-conflict interactions that may occur in the same PC, as we found in the current study. Alternatively, it is possible that different study populations present differences in the frequency and employment of post-conflict interactions (cf. Arnold & Whiten 2001; Kutsukake & Castles 2004).

With regard to the effect of consolation, we found no evidence of stress alleviation due to consolation. This result is in sharp contrast with what was thus far assumed. If consolation fails to 'console', as it seems at least in this study group, and yet it appears to be a frequent post-conflict interaction in chimpanzees, what is its function? Both the presumed stress alleviation effect of consolation and the substitute for reconciliation hypothesis concern benefits to the receiver of consolation without assessing the reasons to console for the actor. To understand the function of consolation as a post-conflict interaction, one should assess the function for both the receiver and for the actor.

From the receiver's point of view, it remains possible that even though consolation did not effectively alleviate post-conflict stress in aggresses, the

friendly contacts may have still been perceived as benevolent, socio-positive behaviour. The principal cause of post-conflict stress is probably the damage to the relationship with the former opponent (Aureli 1997; Aureli et al. 2002). Perhaps we should not, therefore, expect effective stress alleviation from affiliation with another group member as it has little benefit for relationship repair with the conflict opponent. However, how the targets of consolation actually perceive 'consolatory' contacts remains open, as we have no other measure of their psychological state than scratching rates.

To assess the reasons to console for the actor, we should assess both the ultimate function of the behaviour, as well as the proximate cues evoking the affiliative response. The consolatory response may be evoked by an empathic understanding of the victim's distressed state (social cognition hypothesis: de Waal & Aureli 1996). The chimpanzees may have a capacity for cognitive empathy (O'Connell 1995, but see e.g. Heyes 1998 and Povinelli and Vonk 2004 for criticism), and hence probably for lower level empathic processes, such as emotional contagion, i.e., copying the other's emotion without a cognitive differentiation of the mental state of self and of the other (Preston and de Waal 2002). In contrast, evidence of monkeys suggests lack of capacities required for cognitive empathy (e.g. Tomasello and Call 1997) as well as absence of true consolation (reviewed by Watts et al. 2000, but see Call et al. 2002). Furthermore, Schino et al. (2004) reported the absence of both true consolation and emotional contagion in Japanese macaque (*Macaca fuscata*) mothers after aggression directed to their offspring. These evidence support the hypothesis that the consolation behaviour of apes, as opposed to monkeys, might rely on their capacity to feel (a degree of) empathy. However, if consolation does not 'console', the reasons to affiliate might have little to do with alleviating the target's distress, while that is implied when cognitive empathy prompts this behaviour. This premise is supported by the finding that aggressors of conflicts also received consolation, at rates not different from aggresses, even though they did not have elevated scratching rates after conflicts. In addition, we showed in our earlier study on the Arnhem colony that conflicts among females do not cause an elevated stress response (Koski et al. in press) and yet,

participants of female-female conflicts received consolation as often as participants of other conflict sex classes. Thus, consolation was also directed to conflict participants that were not distressed to begin with. Therefore, it seems possible that the distressed state of a former conflict participant is not a necessary prerequisite to evoke an affiliative behavioural response in a third party. However, this does not exclude the possibility that affiliation may be based on emotional contagion, in which case the third parties are merely seeking contact in order to alleviate their own stress after witnessing a conflict. Unfortunately, we have no data on the emotional state of the third parties prior to affiliation to assess this possibility. Therefore, what triggers triadic affiliative contacts in chimpanzees remains to be established.

To understand why third parties affiliate with conflict participants it is crucial to assess the benefits it provides for the consoler, as well as the risks associated with such affiliative contacts. A possible risk for the third party might be receiving redirected aggression (Goodall 1986; Aureli et al. 1994; Kutsukake & Castles 2004). However, in chimpanzees the associated risk of further aggression may be rather small due to the relatively tolerant dominance structure (de Waal & Aureli 1996; Watts et al. 2000). Alternatively, affiliating with former opponent might provide protection for the third parties from further aggression by reducing the likelihood of redirected aggression by a former conflict opponent (c.f. Das 2000, Call et al. 2002) or by reducing the general social tension in the group (Kutsukake & Castles 2004; Palagi et al. 2006). As to date we do not know whether the suggested, or some other, factors underlie the occurrence of post-conflict third party affiliation in chimpanzees, the assessment of costs and benefits for the third parties is the necessary next step in order to understand the essence of 'consolation'.

In conclusion, we found no support for the hypothesis that consolation is an alternative conflict resolution mechanism occurring in the absence of reconciliation. This suggests that consolation is a post-conflict interaction in its own right and not dependent on the occurrence of reconciliation. The function of consolation remains open. We found no evidence for the assumed stress alleviation effect of consolation; consolation failed to decrease the scratching

rates of aggresses. Therefore, it seems that consolation does not 'console'. Furthermore, consolation was also directed to conflict participants without increased levels of post-conflict stress. This further implies that the purpose of such third-party contacts is something else than 'consoling'. For this reason, we suggest that triadic post-conflict affiliation should be retained as a functionally neutral term for triadic interactions hitherto called consolation. We stress the importance of assessing the third parties' incentives to direct affiliative contacts to conflict participants. Only by studying the reasons to affiliate both on the proximate and on the ultimate level, can we assess the function of this post-conflict behaviour in chimpanzees.

#### **ACKNOWLEDGMENTS**

Lucie Burgers Foundation for Comparative Behaviour Research is thanked for financial support (for SEK). We gratefully acknowledge the Burger's Zoo for allowing this research to take place, and the staff for logistic support. We thank Dr. Jan van Hooff for spirited discussions, Dr. Han de Vries and Dr. Maria Schipper for statistical advice, and K. Koops, E. Kenbeek, M. Heesen, C. van Maanen, O. van Velthuisen, M. Beterams, R. van den Toorn, L. Visser, A. Dupouy, M. van Dongen, M. Heitman, E. van Rooij, S. van den Tweel, H. Wiggers, and M. Schoe for their invaluable help in data collection. Two anonymous referees are thanked for helpful comments.

## CHAPTER 5

---

SELFISH 'CONSOLERS':  
Bystander Chimpanzees Protect  
Themselves from Further Aggression

---

Sonja E. Koski \* & Elisabeth H.M. Sterck

*Submitted manuscript*

## **ABSTRACT**

Chimpanzees (*Pan troglodytes*) regularly initiate affiliation with former participants of an aggressive conflict. This consolation is generally assumed to reflect bystanders' empathy to conflict participants' discomfort. Since empathy requires advanced cognitive capacities, the presence of consolation in apes and absence in monkeys has served as an argument for a cognitive divide between these taxa. Yet, the function and cognitive mechanism of consolation are unknown. Recent evidence suggests that consolation does actually not 'console' the recipients of affiliation. We tested an alternative hypothesis, concerning a benefit for the bystander, in captive chimpanzees. Specifically, we assessed whether third-party affiliation (or 'consolation') protects the affiliating third parties from further aggression by opponents. We found support for this 'self-protection hypothesis', in that affiliation was selectively given to those opponents, who more often gave further aggression to third parties, and it effectively decreased the chance of receiving aggression from opponents. This function of third-party affiliation in chimpanzees for the bystander opposes the common assumption that it functions to benefit the recipient and casts doubts on empathy prompting third-party affiliation. Thus, not empathic concern for the opponent, but self-regard seems to guide the bystanders' behaviour. Whether third-party affiliation reflects a difference in cognitive capacities or different benefits of and options for affiliation with former opponents in apes and monkeys requires further scrutiny.

## INTRODUCTION

Many primate and some social non-primate species exhibit affiliative behaviour after aggressive conflicts (Aureli & de Waal 2000; Aureli *et al.* 2002). Post-conflict affiliation between a conflict opponent and a bystander is known as consolation. Specifically, consolation denotes post-conflict affiliative contacts by an uninvolved bystander ('third party') to a participant of an aggressive conflict (de Waal & van Roosmalen 1979; de Waal & Aureli 1996) and is considered an example of other-regarding behaviour. Consolation is described in chimpanzees (de Waal & van Roosmalen 1979; de Waal & Aureli 1996; Wittig & Boesch 2003; Kutsukake & Castles 2004; Koski & Sterck 2007), as well as in other apes (bonobos *Pan paniscus* Palagi *et al.* 2004; western low-land gorillas *Gorilla gorilla gorilla* Mallavarapu *et al.* 2006). In contrast, despite extensive research effort (Watts *et al.* 2000; Das 2000), consolation is found only in one monkey species (stump-tailed macaques *Macaca arctoides*: Call *et al.* 2002 and possibly also in long-tailed macaques *M. fascicularis* aggressors: Das 1998). This discrepancy between apes and monkeys has been attributed to presumed empathic skills of apes, which may be lacking in monkeys (de Waal & Aureli 1996).

The assumption of empathy prompting consolation derives from the assumed effect of consolatory contacts, that is, a soothing effect of affiliation by the bystander on a conflict opponent that experiences post-conflict stress. However, no evidence so far exists for this effect. In fact, we recently found that in captive chimpanzees (*Pan troglodytes*) consolation given to conflict aggresses did not decrease their post-conflict stress, and it was even given to aggressors despite an absence of increased post-conflict stress (Koski & Sterck 2007). This implies that consolation may not benefit the conflict opponents in a way that has thus far been assumed. Instead, consolation may benefit the third parties who provide affiliation. No studies to date have tested the function of consolation regarding the third parties, in terms of their incentives for affiliation and the possible risks and benefits involved.

Since consolation does not function to console its recipient, we maintain a functionally neutral term 'third-party affiliation' to describe third-party initiated affiliation towards both opponents (Koski & Sterck 2007). Third-party affiliation

has been suggested to potentially protect the third parties from further aggression from opponents (Call *et al.* 2002; Das 1998) or from the other group members (Palagi *et al.* 2004, 2006). We call this the 'protection hypothesis'. By 'further aggression' we mean aggression by either of the former conflict opponents towards a bystander (a.k.a. redirected aggression in aggresses: de Waal & van Hooff 1981; Watts *et al.* 2000) within ten minutes of the cessation of the original conflict.

In this study we tested the protection hypothesis in captive chimpanzees at the Arnhem Zoo, the Netherlands. We addressed the possible connection of third-party affiliation and further aggression from both the conflict opponents' and the third parties' perspective.

## **METHODS**

### **Study Group**

Observations were conducted in the Burgers Zoo, the Netherlands, between November 2002 and August 2006. When the temperature exceeds 10°C, the group lives on an outdoor island of ca. 7ha, and during the winter months the chimpanzees stay in an indoor enclosure of 21x18 m. The group consisted of 23-34 individuals during the study (3-5 adult and 0-2 adolescent males, 14-18 adult and 1-3 adolescent females, and 4-9 juveniles and infants).

### **Data collection**

Data were collected by S.E.K. and several students under her supervision. The inter-observer reliability was assured by >95% similarity in focal observations between S.E.K. and students. A detailed description of the observational methods as well as on the decision rules has been given in our earlier publications (Koski & Sterck 2007; Koski *et al.* 2007). The data were obtained by focal animal sampling and by ad libitum observations of the conflicts. Both conflict participants were observed simultaneously whenever possible. We employed the standard post-conflict (PC)- matched control (MC) -method (de Waal & Yoshihara 1983; Aureli *et al.* 1989). The duration of PC observation was 10min. Inter-individual distances

after conflicts were recorded in distance categories every minute (0=contact; 1= one arm length; 2= 2 arm lengths; 3=up to 5m; 4= >5m).

### **Data Analyses**

We recorded 696 conflicts, of which we obtained full data on 632 PC-MC pairs of aggressors and 659 PC-MC pairs of aggressees. To operationally define third-party affiliation we employed the attracted/dispersed pair method, in which the timing of the first interaction between an opponent and a third party (initiated by the third party) is compared between PC and MC (de Waal & Yoshihara 1983; Call *et al.* 2002). The method essentially corrects for the baseline level of affiliation of each individual; attracted pairs representing the contacts that surplus the baseline. We deemed only the attracted pairs to represent third-party affiliation. We could not employ the same operational definition for further aggression, as the MC recordings were not permitted to contain aggression involving the focal animal. Previously, we have compared the rate of further aggression to the baseline rate of aggression per individual, and showed that the rate of further aggression is significantly greater than the baseline aggression rate across all individuals (Koski *et al.* in prep.).

All calculations and analyses were performed at the individual level and separately for aggressors and aggressees, except in the case of row-wise correlations (in which the data of aggressors and aggressees were lumped) due to sample size limitations. The individual rates of further aggression given in the presence and absence of third-party affiliation (opponents' point of view), and the rates of further aggression received from kin or non-kin opponent (third parties' point of view) were tested pair-wise with Wilcoxon signed ranks test. Individual frequencies of further aggression given and third-party affiliation received (as opponents), and third-party affiliation given and further aggression received (as third parties) were compared with row-wise matrix correlations (de Vries 1993) of directional, square matrices with MatMan 1.1.4 (Noldus Information Technology 2003). In a row-wise matrix correlation complete rows are permuted (instead of cells), which allows controlling for inter-individual variation. In this way, we could assess whether individuals gave aggression to those third parties relatively more

often from whom they received more often affiliation, and vice versa for the third parties. Note that in these matrices zeroes were true data points. Note also that always one of the matrices in the correlation was transposed so that the 'givers' of affiliation or aggression were in the rows in one matrix and in columns in the other matrix. Transposing the matrices allowed us to assess the connection of further aggression and third-party affiliation from both the opponents' and third parties' point of view. We conducted a Spearman correlation test separately for aggressors and aggressees of their frequency of receiving third-party affiliation and giving further aggression (again, at the individual level). Inter-individual distances were calculated as means over the time prior to third-party affiliation and prior to further aggression per individual and tested pair wise.

## RESULTS

First, we addressed the connection between third-party affiliation and further aggression from the conflict opponents' point of view. Affiliation received by opponents from third parties did not influence the overall rate of further aggression by opponents (Table 1). Thereafter, we tested whether the opponents who directed further aggression more often would receive more often affiliation from the targets of further aggression. This was the case, as the opponents' propensity to direct further aggression to particular individuals correlated significantly, albeit weakly, positively with their propensity to receive third-party affiliation from those individuals (row-wise matrix correlation:  $K_r = 246$ ;  $Tau_{rw} = 0.074$ ;  $P_{right} = 0.012$ ). Since the correlation was weak, we tested the correlation of further aggression given and third-party affiliation received separately in aggressors and aggressees. The correlation remained significant in aggressors, whereas in aggressees the positive correlation only reached a statistical trend (Spearman correlation: aggressors  $r_s = 0.76$ ;  $P = 0.001$ ; aggressees:  $r_s = 0.37$ ;  $P = 0.09$ ; Figure 1.).

Second, we addressed the possible connection of third-party affiliation and further aggression from the third parties' point of view. Individuals who as third parties received more often further aggression from particular opponents, gave more often affiliation to those opponents (row-wise matrix correlation  $K_r = 640$ ,

$\tau_{rw} = 0.15$ ;  $P_{right} = 0.001$ ). Yet, third parties never, bar one occasion, received further aggression after a conflict if they gave affiliation to an opponent (1 out of 171  $PC_{aggressors}$  + 58  $PC_{aggressees}$  in which both further aggression and third-party affiliation occurred in the same post-conflict observation). The rate of receiving further aggression was significantly lower for individuals when they had given third party affiliation than when they had not (corrected to individuals' tendency to give third-party affiliation; mean (median)  $\pm$ SD: 0.04 (0.04) $\pm$ 0.04 bouts/h no affiliation; 0.03(0.0) $\pm$ 0.14 bouts/h with affiliation; Wilcoxon test two tailed:  $z=3.39$ ;  $n=22$ ;  $P=0.001$ ).

**Table 1.** The rates of further aggression given by aggressors and aggressees.

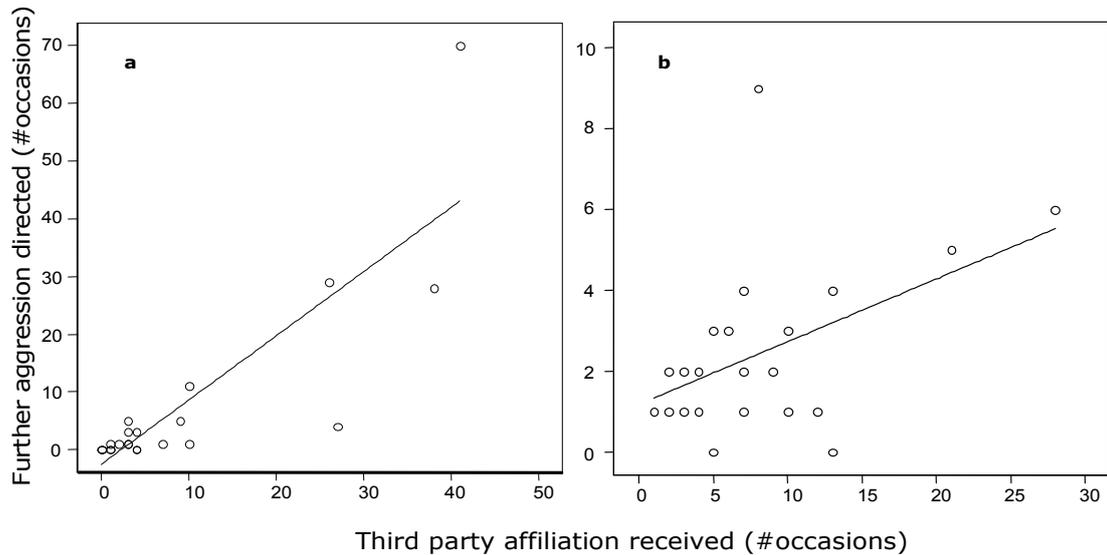
Conflict opponent	Rate of further aggression (bouts/h)			WSR test: Z (P); N
	General	No affiliation	With affiliation	
<b>Aggressors</b>	1.06 ( $\pm$ 0.91)	0.52 ( $\pm$ 0.58)	0.54 ( $\pm$ 0.70)	0.40 (0.69); 17
<b>Aggressees</b>	0.59 ( $\pm$ 0.39)	0.35 ( $\pm$ 0.38)	0.24 ( $\pm$ 0.20)	1.0 (0.32); 20

(Values are given as means  $\pm$  SD; WSR=Wilcoxon Signed Ranks test.)

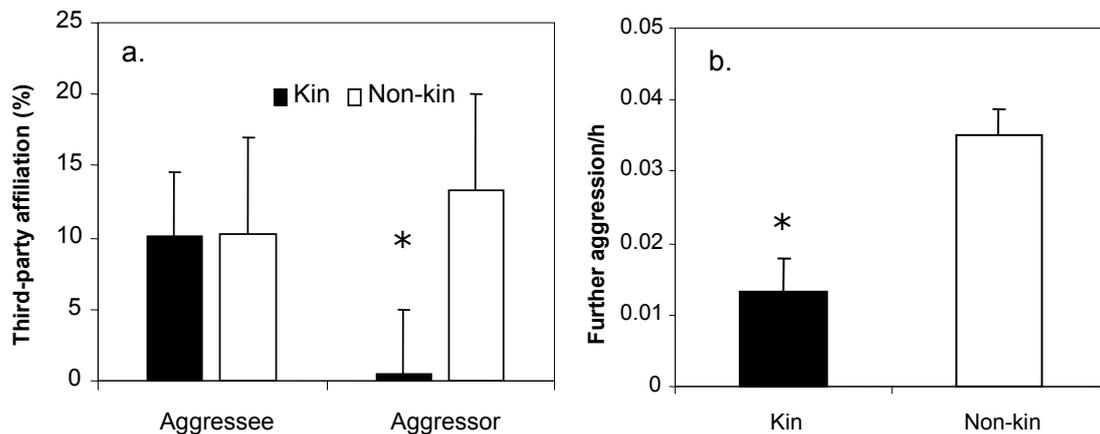
A possible confounding factor was third parties' proximity to opponents prior to third-party affiliation and further aggression. However, this was not supported by the data, since the inter-individual distance (assessed in distance classes; see Methods) between conflict opponents and third parties was significantly greater before further aggression than before third-party affiliation (mean  $\pm$ SD: before aggression: 3.6  $\pm$ 0.37; before affiliation: 2.80  $\pm$ 0.64; Wilcoxon test two tailed:  $z = 4.05$ ,  $n = 29$ ,  $P < 0.001$ ). Therefore, recipients of further aggression received aggression when they were further apart from the opponents than the ones who gave the opponents third-party affiliation.

We also assessed whether there was a kinship effect. Kin received further aggression from opponents significantly less often than non-kin (mean  $\pm$  SD: kin 0.011  $\pm$  0.02 bouts/hour; non-kin 0.035  $\pm$  0.02 bouts/hour; Wilcoxon test two

tailed:  $z=3.29$ ,  $n =18$ ,  $P =0.001$ ; Fig 2b). Thus, the protection hypothesis may thus apply only to non-kin of the conflict opponents.



**Figure 1.** The occasions per individual of further aggression given and third-party affiliation received by (a) aggressors and (b) aggressees



**Figure 2.** (a) Third party affiliation corrected to baseline affiliation (cf. Call et al. 2002) given by kin and non-kin third parties, to aggressees and aggressors, respectively (Koski and Sterck, 2007); (b) further aggression received by third parties from kin and non-kin opponents. \* indicates  $p < 0.05$

## **DISCUSSION**

This study provides the first evidence for a possible function of third-party affiliation in chimpanzees. Our results support the protection hypothesis, which proposes that third parties give affiliation to conflict opponents to protect themselves from further aggression. We found that after conflicts bystanders assessed their relative risk of receiving further aggression and gave more often affiliation to the opponents who directed aggression at them more often. This appeared to be an effective protection mechanism, since chimpanzees received aggression from opponents significantly less often (in fact, nearly never) when they had given affiliation to an opponent than when they had not. Such a direct benefit for third parties casts doubts on the previously assumed empathic response directing third-party affiliation. The cognitive mechanism involved may instead be based on behaviour assessment and cue reading during and after conflicts.

The correlation between further aggression given and third-party affiliation received by aggressees was weak. This may be due to third-party affiliation by kin to aggressees. Kin-affiliation was provided to aggressees (but not to aggressors; Koski & Sterck 2007), while kin received significantly less often further aggression than non-kin individuals (Fig. 2). This suggests that kin of aggressees engaged in third-party affiliation to aggressees for reasons other than warding off aggression. To explore the possibility of kin-affiliation reflecting an empathic response (de Waal & Aureli 1996; Preston & de Waal 2002; Schino *et al.* 2004), we assessed whether it was given to aggressees when the aggressee was likely to have lost the conflict (i.e. after unidirectional aggression). We supposed that especially losing a conflict might evoke an empathic response in kin (de Waal & Aureli 1996). Indeed, aggressees received relatively more often affiliation from their kin after unidirectional than bidirectional conflicts (Chi-square:  $\chi^2 = 4.74$ ,  $df = 1$ ,  $P = 0.030$ ). Therefore, it seems possible that kin affiliated with aggressees for 'empathic' reasons. However, we do not know on which level of the empathic response, emotional contagion or truly cognitive empathy (Preston & de Waal 2002), kin-affiliation might operate. Unfortunately, we have no data on the stress levels of kin prior to providing third-party affiliation, which would be necessary for

differentiating between emotional contagion and cognitive empathy (Schino *et al.* 2004). In addition, third-party affiliation among kin is less common than among non-kin (Koski & Sterck 2007; Fig. 2), rendering kin-affiliation a less prevalent phenomenon. Although we suggest kin-affiliation as a candidate for empathy-based third-party affiliation, we refrain from conclusions about the level of empathy possibly involved.

## **CONCLUSIONS**

Our study is the first to show evidence for a possible function of third-party affiliation in chimpanzees. Third-party affiliation appears as a multifaceted behaviour that is likely to have at least two functions in chimpanzees. We provide evidence for self-protection from further aggression among unrelated individuals and suggest that empathy-based affiliation may be found among relatives. Other possible functions, such as bond strengthening (Das 2000; Call *et al.* 2002) and emotional encouragement (de Waal & van Hooff 1981) are not excluded by the protection from aggression –function and the kin-directed (empathic) affiliation. The protection function may not apply only to chimpanzees, but also to other species in which further aggression occurs and in which affiliation with opponents carries relatively small risks (de Waal & Aureli 1996).

This research opposes the common assumption that the function of third-party affiliation initiated by the bystander is to benefit the recipient. Our study underscores the general importance of assessing why third parties (as the acting individuals) conduct behaviour instead of focusing on the effect on the recipients. Shifting the attention to third parties' incentives to affiliate, to the opponents' role in the conflict and their further behaviour, and possibly to different types of affiliative behaviour (cf. Call *et al.* 2002) may reveal novel aspects of post-conflict behaviour in various species. Only by attending to these aspects with the effect of the third-party affiliation can we understand the function and cognitive mechanism of third-party affiliation.

### **Acknowledgements**

We thank the Burger's Zoo for support throughout the research; Prof. Jan van Hooff and Kathelijne Koops for commentary on the manuscript; and K. Koops, E. Kenbeek, M. Heesen, C. van Maanen, O. van Velthuisen, M. Beterams, R. van den Toorn, L. Visser, A. Dupouy, M. van Dongen, M. Heitman, E. van Rooij, H. Wiggers, S. van den Tweel, and M. Schoe for help in data collection. The study was financially supported by Lucie Burgers Foundation for Comparative Behaviour Research, Arnhem, NL (to S.E.K.).



# CHAPTER 6

---

## CHIMPANZEE CONSOLATION — Spinning the Empathy Wheel

---

Sonja E. Koski \* & Elisabeth H.M. Sterck

*Unpublished manuscript*

## **ABSTRACT**

Empathy at the adult human level requires cognitive perspective taking of another's emotional state. The gradual development of cognitive empathy enables distinctions between different cognitive levels of empathy. In the first developmental stages of empathy three levels can be distinguished: emotional contagion, secondary representational empathy and cognitive empathy. This view of empathy, as a process of gradually increasing levels of cognitive representation, can serve as a basis to address empathic processes in animals. Chimpanzees, the closest living relatives of humans, are assumed to be empathic in their behavior towards group mates. Especially the post-conflict affiliation termed 'consolation' has been suggested to demonstrate the chimpanzee's cognitively empathic tendencies. Yet, evidence on chimpanzees' emotion attribution skills in general, and in consolation in particular, is scarce. In this paper we discuss chimpanzee's empathic skills, focusing on consolation. We review consolation regarding both its function and its possible empathic mechanism. We raise the possibility that the majority of 'consolation' is not empathic, other-regarding behavior, since it appears to be self-regarding and directly benefits the givers of affiliation. However, a minority of these contacts, given by relatives to conflict aggresses, may be other-regarding behavior with a potentially empathic basis. Although experimental evidence suggests that chimpanzees may be capable of secondary representational empathy, we cannot conclude whether affiliation by relatives is based on secondary representational empathy or on emotional contagion. We do, however, conclude that it is unlikely to be based on cognitive empathy.

## **INTRODUCTION**

Can chimpanzees feel empathy? Do chimpanzees show empathic behavior? Chimpanzees appear very empathic to their human observers and have often been claimed to show empathic concern for each other (de Waal 1982, 1996, 2005; Goodall 1986; O'Connell 1995; Flack and de Waal 2000; Boesch and Boesch-Achermann 2000; Preston and de Waal 2002a, b). However, evidence beneath these assumptions is fairly thin.

Empathy at the cognitive level requires understanding of other's mental states and an ability to take other's perspective (Povinelli et al. 1992; rev. Preston and de Waal 2002a,b). Thus, emotion attribution closely relates to general mental state attribution skills. Yet, little research is done to address chimpanzees' emotion attribution skills (see exceptions in Parr 2001; Anderson et al. 2004), in contrast to ample research on other cognitive realms (e.g., Povinelli and Eddy 1996; Tomasello and Call 1997; Tomasello et al. 2003a,b; Hare et al. 2006; Matsuzawa et al. 2006). Consequently, the connection between chimpanzees' empathic and other mental state attribution skills is rather unexplored.

In this article we discuss the possibility of chimpanzee empathy. We define levels of cognitive involvement in empathy and parallel chimpanzees' cognitive skills with those levels. Thereafter, we discuss the role of empathy in a particular behavior that is frequently cited as evidence for chimpanzees' empathic tendencies, namely post-conflict consolation (e.g., O'Connell 1995; de Waal 1996, 2005; Flack and de Waal 2000; Preston and de Waal 2002 a,b; de Waal et al. 2005, Palagi et al 2006). We examine the possible cognitive and empathic processes involved in consolation.

### **The levels of empathy**

To assess chimpanzees' empathic abilities, it is crucial to define different cognitive levels of the empathic process. Before discussing the levels of empathy, we need to clarify our stand within the multitude of its definitions (see e.g. Feshbach and Roe 1968; Hoffman 1975; Johnson et al. 1983; Batson et al. 1987; Eisenberg and Strayer 1987). We define empathy broadly, as a subject's

response to the perceived state of the other that is more appropriate to other's situation than subjects' own. This response is formed by a combination of resonance to and a cognitive representation of the other's emotional state (after Hoffman 2000 and Preston and de Waal 2002a).

The framework for the empathic process comes from developmental psychology. The development of empathic skills in humans shows empathy to be a continuum of increasing levels of complexity (e.g. Brownell and Carriger 1990, Zahn-Waxler et al. 1992; Commons et al. 1998; Hoffman 2000; Brownell et al. 2002; reviews in Eisenberg and Strayer 1987, Preston and de Waal 2002 a,b). The development from automatic to cognitively representational empathy can be roughly categorized in three levels (the number of levels obviously depends on the resolution; the three levels we explicate represents a fairly coarse division; see other examples Hoffman 2000, 2002; Commons and Wolfson 2002; Rochat 2002). (1) At the first level, present in neonatal to one-year old babies, empathy is automatic resonance to others' emotions causing the subject to obtain a similar emotional state to that of the others (Sagi and Hoffman 1976; Hatfield et al. 1993). At this primary level empathy operates as *emotional contagion* with no self-other distinction (Eisenberg and Strayer 1987). (2) Gradually, during the second year of life, children start to suppress primary emotion matching and begin to project empathy to others (Eisenberg and Strayer 1987; Zahn-Waxler et al. 1992). At this stage, empathy is connected to some perspective taking, and a child responds with sympathetic concern toward others (Zahn-Waxler et al. 1979; 1992; Eisenberg et al. 1983; Brownell et al. 2002). This level of empathy is also called quasi-egocentric empathic distress, because a child realizes the distress being the other's, not their own, but confuses the other's mental state with its own and tries to help the other by doing what would comfort him- or herself (Hoffman 2000). This phase coincides with a child's increasing capacity to understand self as an entity; by two years of age children show self-conscious emotions, categorization of self in relation to others, and mirror self recognition (Amsterdam 1972; Bertenthal and Fischer 1978; Johnson 1982; Brownell et al. 2002). Perner (1991) has described this stage as the *secondary representational level*, meaning that a child makes use of the primary representations that model

reality, but can add a representational level that differs from the direct reality-bound one. (3) With the further increasing capacity for perspective taking and the suppressing own emotions, empathy reaches the meta-representational level. In meta-representational or *cognitive empathy* the self-other distinction is fully maintained, i.e., the subject can suppress its own emotion, and represent the emotion of the other as a separate entity (Hoffman 2000; Lewis 2002). The empathic understanding can be reached by knowledge about the particular event that the other experiences and allows for a reaction appropriate to the situation of the other (Eisenberg and Strayer 1987). This level is reached by children at about four years of age, together with the ability to theorize about another's mind, to understand false beliefs and to conjecture another's emotional state in relation to their own (rev. Perner and Lang 1999).

In humans, there are yet higher cognitive levels of empathic processes. Older children (at 8-10 years) can empathize with another's condition even when it overrides the cue of the current situation (Hoffmann 2000, 2002). Adults can form empathic representations of abstract situations and they reach paradigmatic and meta-systematic levels of empathy (in which the subject understands it could be in anybody's position, yet that everyone's feelings and needs are their own: Commons and Wolfsont 2002). However, since it is not likely that chimpanzees would reach these levels of cognitive empathy, we limit the discussion to the first three levels.

### **Chimpanzee cognitive and empathic skills**

It is unclear which level of empathy chimpanzees (or other non-human primates) reach, and how it develops (see Preston and de Waal 2002a and peer commentary therein). As is apparent from the ontogeny of empathy, understanding emotions is cognitively closely linked to the Theory of Mind (Premack and Woodruff 1978) associated skills. The current state of knowledge on chimpanzee cognition places chimpanzees approximately at the secondary representational level, between a 'behaviorist mind' of primary representations and a meta-representational mind (sensu Perner 1991; Whiten 1996; Suddendorf 1998; Suddendorf and Whiten 2001; Call 2003; but see critique by

Heyes 1998; Povinelli and Vonk 2003, 2004; Povinelli and Bering 2002). Results from several batteries of experiments show that, like a two-year-old child that has reached the secondary representational level, chimpanzees show mirror self-recognition, understand what others do and do not see, what they saw in the past, intentionality in actions, and can employ their understanding of visual perspectives to gain benefits (Gallup 1970; Kitchen et al. 1996; Tomasello et al. 2003a,b; Hare et al. 2000, 2001, 2006). However, chimpanzees fail to understand prior and communicative intentions (Tomasello et al. 2003b) and cannot form metarepresentations as implied in attribution of false beliefs (Suddendorf and Whiten 2001).

Regarding emotion attribution, if chimpanzees are on the cognitive level of a secondary representational child, it suggests that chimpanzees may be able to exceed the level of primary emotional contagion but not quite reach the level of cognitive empathy. Unfortunately, experimental evidence of chimpanzees' empathic tendencies is scarce. Some evidence exists on chimpanzee understanding of the emotional meaning of facial expressions and matching these with emotionally charged video images (Parr 2001). Chimpanzees also present contagious yawning, which may reflect empathy (Anderson et al. 2004; Anderson and Matsuzawa 2006), since contagious yawning is connected to empathic tendencies in humans (Lehmann 1979; Platek et al. 2003). In contrast to the scarce experimental data, plentiful anecdotes exist about chimpanzees' allegedly empathic acts. Examples range from helping a thirsty group mate by bringing water (O'Connell 1995) and efforts to rescue another individual from danger, sometimes even with risking own life with it (Goodall 1986) to comforting distressed individuals (e.g., de Waal 1982; Goodall 1986; Boesch and Boesch-Achermann 2000). Based on a compilation of over 2000 cases of possible empathic behavior in primates it was concluded that chimpanzees are capable of cognitive empathy (O'Connell 1995). However, it is not clear how many of these cases show, or require, empathy and on which level. For instance, reconciliation between the former opponents and adopting an unrelated infant were listed as empathic behavior (O'Connell 1995), although it is not clear how these cases would require mental state representation. Furthermore, as is often pointed out,

a collection of anecdotes, even if coming from independent sources, does not exceed the evidence value of any anecdote on its own (e.g. Whiten and Byrne 1988; Heyes 1993, 1998). Overall, based on the anecdotal and experimental evidence we propose that chimpanzees may be empathic, but cannot conclude which the level of empathy they might reach.

### **Chimpanzees console each other –or do they?**

Chimpanzees frequently engage in presumably empathic behavior after aggressive conflicts (de Waal and van Roosmalen 1979; de Waal and Aureli 1996). This particular behavior, labeled 'consolation', has been taken as the flagship for chimpanzee empathy, being frequently quoted as cognitively empathic behavior (O'Connell 1995; de Waal 1996, 2005; Flack and de Waal 2000; Suddendorf and Whiten 2001; Preston and de Waal 2002 a,b; de Waal et al. 2005, Palagi et al. 2006). Consolation denotes affiliative contacts by a previously uninvolved group member to a conflict victim shortly after aggression has ceased (de Waal and van Roosmalen 1979). Since the first description of consolation by de Waal and van Roosmalen (1979) in chimpanzees of the Arnhem Zoo, the Netherlands, consolation has been recognized as a frequent post-conflict behavior of chimpanzees that occurs both in the wild and in captivity (de Waal and van Roosmalen 1979; de Waal and Aureli 1996; Wittig and Boesch 2003; Kutsukake and Castles 2004; Palagi et al. 2006; Koski and Sterck 2007). As the term suggests, consolatory contacts are presumed to benefit the recipient by calming and soothing this distressed conflict victim. Based on the presumed effect it has further been assumed that the proximate basis for consolation lays in an empathic response of the consoler (de Waal and Aureli 1996). The level of empathy in consolation has not been specified, but de Waal and Aureli (1996) hypothesized that it may operate on a cognitive level that surpasses monkey cognitive capacities. This suggestion stemmed from the absence of consolation in monkeys (reviewed by Das 2000; Watts et al. 2000; Castles 2000). In this respect, the initiator of consolatory contacts is crucial: in 'true consolation' (or consolation proper) a bystander affiliates seemingly spontaneously with the opponent, as opposed to contacts being 'solicited' or

initiated by the opponent (Verbeek and de Waal 1989). Solicited consolation, which is not likely to be empathy based, is common among monkeys and apes (Das 2000; Watts et al. 2000) whereas only chimpanzees, bonobos and low land gorillas exhibit true consolation (de Waal and Aureli 1996; Palagi et al. 2004; Mallavarapu et al. 2006; but see Call et al. 2002). Furthermore, they suggested that since "adult chimpanzees console the recipient of aggression they often do so without any sign of distress themselves..." (de Waal and Aureli 1996, p.102), chimpanzees are likely to "identify with the other's emotion without letting these emotions overwhelm their own, internal state, i.e. they maintain a distinction between their own and the other's situation" (ibid.). In other words, empathy was presumed to operate on the cognitive level.

However, the cognitive basis of consolation has never been verified, nor has the justification of the term consolation. There is no supporting evidence for the assumption that affiliative contacts to a conflict participant soothe the recipient's stress after an aggressive encounter. In fact, recent evidence on consolation behavior in captive chimpanzees suggests that consolation does not actually 'console' the recipients (Koski and Sterck 2007 / Ch 4), but that there might be a benefit for the consolers instead (Koski and Sterck in prep /Ch. 5.). Furthermore, the emotional state of the consoling chimpanzees has never been investigated, which renders the notion of their cognitive empathy hypothetical. Finally, consolation was recently found in stump-tailed macaques, when particular affiliative behaviors were analyzed separately (Call et al. 2002). Therefore, we consider a critical re-evaluation of the phenomenon known as consolation with regards to both its function and the cognitive basis to be long overdue. Below, we first review the new evidence on consolation in chimpanzees from the functional point of view and then move on to its possible empathic basis.

### **Examining consolation in chimpanzees: the function**

The term consolation contains an assumption of its function as an interaction that provides comfort for the recipient. Consequently, consolation is assumed to reduce post-conflict stress (e.g., de Waal and Aureli 1996; Aureli 1997;

Matheson 1999; Wittig and Boesch 2003; Palagi et al. 2004; Kutsukake and Castles 2004). We tested the stress reduction function in captive chimpanzees at the Arnhem Zoo (Koski and Sterck 2007). We found that consolation was equally frequently provided to conflict victims and aggressors. However, these contacts did not reduce post-conflict stress of the recipients of affiliation. The effect (or the lack thereof) was not dependent on the age or kinship of the consoler or on the type of behavior used to console. Furthermore, consolation was frequently given to individuals that showed no elevated stress after conflicts. These results imply that consolation did not actually 'console' the recipient, and that a conflict opponent's distress was not a necessary prerequisite to receive consolation. Therefore, it appears that consolation may not function to benefit the receiver in the thus far assumed way. For that reason, we have suggested to discard the term 'consolation' and to retain a functionally neutral term 'third party affiliation' until further evidence of its function is gained (Koski and Sterck 2007).

If third party affiliation ('consolation') does not benefit the recipients, it could benefit the actors. We tested whether providing affiliation would protect the bystanders from aggression by former opponents. Indeed, we found that third-party affiliation was given more frequently to those opponents that were more likely to engage in further aggression after a conflict (Koski and Sterck in prep. /Ch. 5). It was more prevalent in contexts when opponents were likely to direct further aggression to bystanders (Koski et al. submitted /Ch. 3). Furthermore, third party affiliation was given by those individuals who were at a higher risk of receiving further aggression from opponents, and giving affiliation significantly decreased the risk of receiving further aggression (Koski and Sterck in prep. /Ch. 5). Third party affiliation thus seems to function as an effective self-protection strategy from aggression by the opponents.

The 'self-protection from aggression' -function applied for the majority of affiliation. However, self-protection did not explain third party affiliation provided to aggresses by their own kin (henceforth, 'kin-affiliation'). Kin received significantly less often post-conflict aggression from opponents (Koski and Sterck in prep. /Ch. 5) and yet, they provided frequent third party aggression to aggresses (Koski and Sterck, 2007). This suggests that there are (at least) two

types of third-party affiliation in chimpanzees, one that functions as a self-protection strategy, and another, namely kin-affiliation, whose function is unclear.

Besides our studies, to our knowledge the effect of third party affiliation on the recipients has not been investigated. Therefore, the generality of our results cannot be evaluated. Furthermore, the only study we are aware of having directly addressed the protection hypothesis did not find support for the protection function of contacts between third parties and aggressors in long-tailed macaques (contacts initiated both by third parties and aggressors: Das 1998). It is therefore possible that the protection function of third party affiliation applies only to chimpanzees. Regarding kin-affiliation, affiliation by own kin to conflict opponents was also shown in stump-tailed macaques, and suggested to function as bond strengthening or support among matrilineal family members (Das 2000; Call et al. 2002). In chimpanzees, the kin relationships have less significance in the social structure than in macaques (Pusey 1979; Das 2000; Mitani et al. 2002). Nevertheless, kin-affiliation may function as support also in chimpanzees, especially in captive conditions where kinship relationships are emphasized (de Waal 1984).

### **Examining consolation in chimpanzees: the cognitive mechanisms**

To address the possibility of empathy underpinning third party affiliation, we need to evaluate the cognitively necessary processes for this behavior. The very minimum cognitive requirements for third party affiliation would be an ability to recognize conflict participants and to remember the identity when aggression has ceased (de Waal and Yoshihara 1983; Castles 2000). Since these basic abilities are an elementary part of any social species with individualized societies (cf. Byrne 1995), they are undoubtedly within the chimpanzee's cognitive reach. It is probable, however, that third party affiliation for self-protection and kin-affiliation to aggresses require additional cognitive processing.

Affiliation for self-protection is given selectively when the opponents are more likely to direct further aggression to bystanders (although the evidence for

this is weaker in aggresses: Koski et al submitted/ Ch. 3). Therefore, a bystander must 'read' the events during a conflict to know when an opponent is likely to direct further aggression. Furthermore, there are dyadic differences in the aggression frequency and hence the risk of receiving aggression is not equal for every group member. Individuals may take into account the risk of receiving aggression from particular individuals, since they give affiliation selectively to those opponents who direct aggression to them more often than to others (Koski and Sterck in prep./Ch 5.). This requires an evaluation of the own relationship with the opponents, influenced by prior interactions, kinship and possibly the relative rank position. Therefore, the risk-assessment process after observing a conflict combines the relationship evaluation with opponents and the inference of behavioral cues in the conflict. Such a strategic, self-regarding affiliative behavior does not, however, require an empathic orientation to a conflict participant's stressful situation. Insofar as comparative cognitive research should retain to the most parsimonious explanations (which is, conceptually and practically, debatable as such: e.g. Heyes 1998, Flack and de Waal 2000; Povinelli and Vonk 2004; de Waal 2005), behavior that can be explained with behavior/cue reading should not be assumed to reflect more complex cognitive processes. On the parsimony premise we therefore propose that third party affiliation for self-protection is likely not based on an empathic response to the conflict participant's emotional state.

Kin-affiliation, in contrast, seems not to be self-regarding behavior, which gives room for a possible empathic basis. Kin might be expected to show empathic behavior, since familiarity in general increases the likelihood of an empathic response (Preston and de Waal 2002a). Moreover, we found that losing a conflict increased the chance of kin-affiliation, since kin gave proportionately more often affiliation to aggresses when they were the victims of unidirectional conflicts (Koski and Sterck in prep. /Ch 5). A similar pattern was found for aggressors, as the few kin-affiliation incidences occurred proportionately more often after aggressors were likely to have lost the conflict (Koski, unpublished data), although relatives overall did not affiliate with aggressors above the baseline level (Koski and Sterck 2007). Since losing a conflict could be expected

to be a context that readily evokes an empathic response (de Waal and Aureli 1996), kin-affiliation appears as a possible candidate for empathic behavior. If kin-affiliation indeed is indeed empathic, on which empathic level does it operate?

The first, often suggested, possibility is that kin-affiliation is prompted by cognitive empathy, in which a third party cognitively represents a conflict (especially losing it) to be a stressful situation for its kin, which evokes the sympathetic concern towards the victim. In this case, empathy is realized via the understanding of the other's situation and it requires representation of other's state via perspective taking (Povinelli et al. 1992, Hoffman 2000; Preston and de Waal 2002b). The second possibility is that empathic kin-affiliation operates on the quasi-egocentric distress –level (Hoffman 2000), much like the first empathic attempts of secondary representational two-year-old children. In that, a subject has some understanding of the victim's distressed state as separate of its own and the affiliative behavior is directed to the other instead of being self-oriented. Yet, their own distress is not fully differentiated from the other's distress (Zahn-Waxler et al. 1979; Suddendorf and Whiten 2001). This secondary representational level of empathy is not realized abstractly, but instead may rely on cues associated with the distressed state (facial, vocal, and bodily cues: Suddenforf and Whiten 2001). The third possibility is that empathic response operates on the primary representational, emotional contagion level. In this case, the subject fully copies the perceived state of the conflict participant with no self-other distinction. Therefore, the empathic act would be merely an effort to seek comfort for self.

Considering that there is no evidence for chimpanzees' cognitive abilities reaching the meta-representational levels (such as understanding false beliefs and prior intentions) it is unlikely that empathy is operating on the cognitive level. Furthermore, since the first acts of empathic concern in children occur at the secondary representational level, much before the fully meta-representational mind has developed, cognitive empathy seems not to be necessary for rudimental empathic acts. On the other hand, considering the human ontogenetic data and the general cognitive level of chimpanzees, it is

quite probable that chimpanzees are capable of exceeding the primary emotional contagion level of empathy. Therefore, we hypothesize that chimpanzee empathy may operate at the secondary representational level.

To test this hypothesis, quantitative data on the third parties' emotional state prior to affiliative contacts is crucial. Specifically, by assessing whether subjects show distress upon observing another's distress we can distinguish between emotional contagion and cognitive empathy (cf. Schino et al. 2004). Unfortunately, we do not have those data, and to our knowledge, it has never been investigated in chimpanzees (despite claims in de Waal and Aureli 1996; Preston and de Waal 2002a). Furthermore, problematically enough, measuring the third parties' stress levels is probably not detailed enough a method to distinguish between emotional contagion and secondary level empathy, since in both of them individuals show some empathic distress. Currently, we have no alternative on how to distinguish between these levels. Therefore, on the parsimony premise emotional contagion cannot be excluded as a possible mechanism of kin-affiliation. Yet, the secondary representational level of empathy may be the most consistent with chimpanzees' cognitive abilities level in general. Until further knowledge in chimpanzees' empathic skills is gained, we cannot conclude whether kin-affiliation is based on emotional contagion on secondary representational empathy. We do, however, conclude that kin-affiliation is unlikely to operate on the cognitive level of empathy.

### **Concluding the case of third party affiliation**

In this article we have re-evaluated third-party affiliation in chimpanzees and adopted the most parsimonious explanations for the possible cognitive processes involved. We concluded that most of these contacts are probably not based on empathy, and if empathy is involved, that emotional contagion may suffice. Having said that, there is always the possibility that kin-affiliation, like non-kin affiliation, is not empathically driven at all. The general debate of the psychological mechanism of behavior being either mentalistic or cue-based (see references in Introduction) applies also to third party affiliation. In a conflict there are plenty of behavioral cues available (e.g., screaming, which has been

suggested to trigger consolatory contacts: Palagi et al. 2006), and thus a cognitive representation is not an absolute necessity even for kin-affiliation. By the same token, however, absence of evidence should not be interpreted as evidence of absence. Therefore, we also have to consider the possibility that kin- and non-kin associated third party affiliation both evoke cognitively empathic processes in third parties. Conceptually, gaining a benefit for self does not rule out empathic processes. Unfortunately, as is often the case in non-human cognition studies, the higher level cognitive processes are notoriously difficult to show empirically, and this is especially the case in observational studies. As long as we have no data on chimpanzees' cognitively empathic skills outside of the realm of post-conflict interactions, we have to remain careful with conclusions regarding empathy in third-party affiliation.

### **Final words on empathic chimpanzees**

We want to emphasize that it is two different questions to ask whether chimpanzees are capable of feeling empathy, and whether post-conflict third-party affiliation is based on (a level of) empathy. Despite our parsimonious approach to third party affiliation, we nonetheless, and importantly, do not want to state that chimpanzees are incapable of representing others' emotional states. Since chimpanzees seem to manage at least some of the Theory of Mind related tasks (Gallup 1970; Suddendorf and Whiten 2001; Call 2003; Tomasello et al. 2003a,b; Hare et al. 2006), and at least partly fit to the secondary representational level of human children, there is no fundamental reason to assume that emotional awareness is completely outside chimpanzees abilities (Parr 2001; Flack and de Waal 2000; Anderson and Matsuzawa 2006; Anderson et al. 2004; Matsuzawa et al. 2006). We suggest that chimpanzees' emotional awareness and empathic behavior might be best approached experimentally in other contexts than conflicts (cf. Silk et al. 2005; Jensen et al. 2006; Warneken and Tomasello 2006).

# *CHAPTER 7*

---

## FUNCTIONS, COGNITION, AND EMOTIONS – Cross-sectioning chimpanzee conflict resolution

---

Summary, discussion and conclusions



In this thesis I have studied conflict resolution in captive chimpanzees. Specifically, I investigated the occurrence and functions of various post-conflict strategies. Furthermore, I assessed the likely proximate cognitive and emotional mechanisms used in post-conflict interactions.

### **Summary of the main findings**

The first post-conflict behaviour scrutinised in this thesis was reconciliation between the conflict opponents. Reconciliation is the best known of all conflict resolution behaviours and well described in many species (see Ch 2, 3). However, the connection between the function and the underpinning mechanism of reconciliation is less well known, also in chimpanzees. In this thesis reconciliation was examined regarding both aspects. Our study supported the widely accepted function of reconciliation in relationship repair. Relationship quality (assessed by measured compatibility and inferred value) between the opponents was confirmed as the main determinant of reconciliation (Ch 2, 3). Interestingly, compatibility was assessed asymmetrically by the opponents, so that compatibility only from aggresses' perspective influenced reconciliation (Ch 3).

Anxiety was found to be the emotional mediator in reconciliation, as proposed in the integrated hypothesis (Aureli 1997). The post-conflict stress levels were elevated and the increase depended on the opponents' relationship quality (Ch 2). Reconciliation effectively decreased the stress to baseline levels (Ch 4). Only aggresses, however, experienced elevated stress after conflicts. The asymmetric stress response suggested that the damage a conflict does to the opponents' relationship is differently experienced by aggresses and aggressors. This, together with the asymmetric influence of compatibility on reconciliation, implies that aggresses may be more vulnerable to relationship damage by conflicts than aggressors.

The post-conflict behaviour consolation, which was renamed third-party affiliation (Ch 4), was the main focus of this thesis (Ch 3-6). I studied third-party affiliation with regards to its suggested function(s) and the assumed cognitive

basis. The tested functions were reduction of post-conflict stress of the receiver (i.e. consolation), substitution for reconciliation, and self-protection from further aggression for third parties. We found no support either for the stress alleviation function or for the substitute for reconciliation –function (Ch 4). Instead, we found that third parties benefit from affiliation by reducing the chance of further aggression from opponents (Ch 5). This self-protective function applied to majority of the affiliative contacts. The protection function has been previously suggested in two variants; that affiliation reduces the chance of aggression by the opponents (Das 1998; Call et al. 2002) and that affiliation reduces the spread of aggression in the group and thus indirectly reduces the chance of receiving aggression (Palagi et al. 2004, 2006). Our results supported the first but not the second variant; affiliation did not reduce the chance of an opponent engaging in further aggression in general, since the rate of further aggression did not decrease (Ch 5). Instead, third party affiliation reduced further aggression by the opponent specifically toward the affiliating individual. It has also been suggested that third-party affiliation may encourage the opponents, especially aggressors (idea stemming from side-directed affiliation during conflict: de Waal and van Hooff 1981; Das 1998). This possibility was not directly tested but seems unlikely, since the rate of further aggression did not increase after third-party affiliation (Ch 5). In sum, third-party aggression warded off further aggression but only regarding the affiliating third party, not other group members.

An exception to the self-protection function was affiliation given to aggresses by their own kin (Ch 4, 5). This 'kin-affiliation' appeared not to be connected to self-protection, since kin received further aggression from opponents significantly less often than unrelated individuals. The function of kin-affiliation remains open.

The cognitive basis of third-party affiliation has been assumed to be empathic. Specifically, it has been assumed to be cognitively empathic, implying that the affiliator maintains a cognitive distinction between the other's mind and own mind. Since we found that third-party affiliation is self-regarding behaviour, which occurs in situations that are not likely to require mental state attribution,

we concluded that self-protective affiliation is probably not empathic at any cognitive level (Ch 5, 6). Instead, self-protective third-party affiliation probably relies on an assessment of the personal interaction history with the opponent(s) and the particular circumstances of each conflict resulting in a context-dependent risk evaluation. This requires skilful behaviour- and cue reading, but no attribution of the others' mental (including emotional) states (Ch 6).

Kin-affiliation, in contrast, may have been empathy derived. Whether this indeed is the case, requires further scrutiny. If kin-affiliation has an empathic base, it is unclear whether it requires cognitive empathy; it is possible that emotional contagion or secondary representational empathy prompts the affiliative behaviour. In emotional contagion the third parties are seeking a reassuring contact to soothe themselves; in secondary representational empathy affiliation is a mixture of soothing self and soothing the other. In the absence of data we cannot conclude the level of possible empathy in kin-affiliation (Ch 5, 6).

Two other post-conflict interactions were also addressed in this thesis, namely further (or redirected) aggression by opponents and third-party aggression towards opponents (Ch 3). For these behaviours we assessed the factors that influenced their occurrence, and their occurrence in relation to other post-conflict interactions. For third-party aggression we failed to find any clear determinants (Ch 3). Surprisingly, further aggression was more frequent by aggressors than agressees, which is opposite to what is described for most species (see Ch 3). Its occurrence was determined by conflict directionality and in aggressors also by sex class. It appeared that opponents directed further aggression when they had probably won the conflict. We hypothesised that this reflects a 'winner-effect', i.e. physiological changes associated with winning a conflict that increase the willingness to engage in further fights (Ch 3). This hypothesis is to our knowledge a new one for chimpanzees; earlier it has been suggested that in macaques (and possibly other monkeys) further aggression by agressees reflects a 'loser-effect' (Kazem and Aureli 2005). In this thesis, I did not study the functions of these behaviours. Gaining information on the function(s) of further aggression for both the opponent and the recipients would

shed light on the connection between the proposed emotional mechanism and the function.

In sum, I investigated four post-conflict interactions in chimpanzees: reconciliation, third party affiliation (a.k.a. consolation), further aggression (a.k.a. redirected aggression) and third party aggression. The four post-conflict interactions occurred largely independent of one another. The function of the two aggressive post-conflict behaviours was not established, but I suggest that the mechanism of further aggression may involve a winner-effect. Chimpanzee reconciliation follows the general primate pattern; it is prompted by anxiety and functions to restore the relationship of the opponents. Chimpanzee third party affiliation yielded the most surprising results: contrary to what has been argued thus far, it does not function to console the affiliation receiving opponent, but reduces the chance of the opponent directing further aggression at the third party. The exception may be third party affiliation from kin of aggresses. This may possibly be based on empathic concern and serve the originally proposed consolatory function.

### **Third-party affiliation –why not in monkeys?**

The self-protection function of third-party affiliation in chimpanzees evokes the intriguing question of why such affiliation is nearly absent in monkeys (Das 2000, Watts et al. 2000), even though in many species of monkeys victims direct further aggression to bystanders (e.g., Aureli and van Schaik 1991a, Scucchi et al. 1988; rev. Kazem and Aureli 2005). The constraints of third-party affiliation for self-protection are probably not cognitive, since monkeys presumably are able to infer the risk of receiving aggression based on their own relationship with the opponent (Cheney and Seyfarth 1990) and on the contextual cues associated with the conflict.

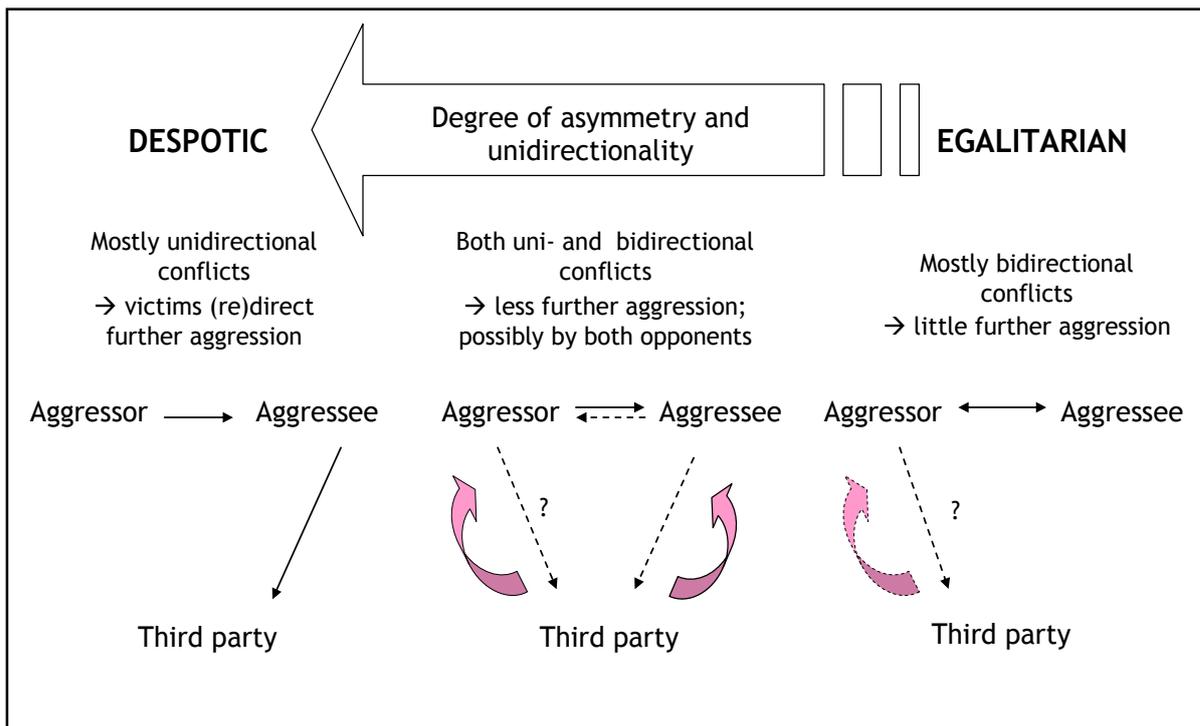
If the constraints are not cognitive, they may be social. The social constraints hypothesis (de Waal and Aureli 1996) suggested that in despotic species affiliation may be too risky and therefore it is not attempted. I hypothesise that in addition to determining the risk involved, the species dominance style influences the occurrence of further aggression. These two

factors together may predict in which species third-party affiliation for self-protection occurs.

The model goes as follows (see Figure 1). In despotic species, aggression is severe and unidirectional, and post-conflict affiliation between opponents is infrequent (reviewed in Hemelrijk 1999; Thierry 2000; van Schaik and Preuschoft 2000). In these species, victims of aggression frequently (re-)direct further aggression to third parties, and targets of further aggression are often lower ranking than the conflict victims (reviewed in Kazem and Aureli 2005). In such a system, third parties face a high risk of receiving aggression should they approach a victim and an effort to protect self by approaching and affiliating with an opponent is likely to prove unsuccessful (de Waal and Aureli 1996). In more egalitarian species bidirectional aggression becomes more prevalent, aggression is less severe and post-conflict affiliation between opponents is more frequent (Thierry 2000). In these species further aggression occurs less often (mountain gorillas: Watts 1995b; stump-tailed macaques Walker Leonard 1979, Call et al. 2002; Barbary macaques: Aureli et al. 1994; bonobos M. van Dongen pers. comm.) and at least in some cases both opponents can direct further aggression to bystanders (chimpanzees: Arnold and Whiten 2001; Ch 3). In these more egalitarian species, therefore, third parties face a smaller risk of receiving redirected aggression upon approaching and affiliating with an opponent, while they gain a potential benefit of warding off aggression by the opponents. Finally, in the most egalitarian species redirected aggression by victims may be very rare (spectacled langurs: Arnold and Barton 2001; Thomas langurs, Sterck pers. comm.; mountain gorilla females Watts 1995a). Therefore, in the most tolerant species the risk for third parties to approach an opponent is small, but there is little to gain regarding protection from further aggression. Therefore, third-party affiliation for self-protective reasons is not expected. In sum, in species where dominance style allows approaching and further aggression (by one or both opponents) is present, we might expect third-party affiliation for self-protection.

All the species that are known to present third-party initiated affiliation are relatively egalitarian and may present further aggression (chimpanzees: e.g. de Waal 1987, Boehm 1997; bonobos: Stevens et al. 2005; western low-land

gorillas: Scott and Lockard 1999; stump-tailed macaques: Thierry 2000). However, I must stress that data on this matter are limited, and especially reports on further aggression by aggressors are scarce. Furthermore, the proposed framework does not provide an all-inclusive explanation for third-party affiliation in primates. Some third-party affiliation might have a social bond strengthening function, especially when affiliation is provided by own kin (Das 2000; Watts et al. 2000; Call et al. 2002), which may also apply to kin-affiliation toward aggresses in our study. Moreover, affiliation may function as triadic reconciliation, when a conflict participant is contacted by its opponent's kin (Judge 1991). At this stage the proposed framework still evokes more questions than answers, and calls for further research.



**Figure 1.** A schematic representation of the proposed framework for further aggression and third-party affiliation in relation to the species dominance system. Thin arrows indicate the direction of aggression by/among opponents; solid ones indicating more frequent aggression, dashed ones indicating less frequent aggression. Thick arrows indicate third-party affiliation to opponents.

### **Long-term repercussions of post-conflict interactions**

In this thesis I have mostly dealt with the immediate costs and benefits associated with post-conflict interactions. In addition to those, however, there are likely to be longer term repercussions to involvement as well (e.g. de Waal and van Hooff 1981; de Waal 1982). The long term consequences of reconciliation are related to the relationship benefits. Reconciliation mitigates the damage that the conflict caused to the relationship and guarantees the continuation of benefits associated with that relationship. The long-term consequences associated with further aggression by the opponents may relate to the potential damage to the relationship with the target of aggression. If the relationship between the aggressive opponent and the target of further aggression is valuable, reconciliation is expected to occur also between them (Aureli et al. 2002). Unfortunately, we have no data on this aspect. Opponents can also seek affiliation with third parties, which was discussed less in the thesis. We found that the frequency of these 'solicited consolatory' contacts did not exceed the baseline levels of affiliation and thus deemed them 'business as usual' (Ch 3, 4). However, the baseline levels of affiliative behaviour were high during the study, which may have overshadowed the importance of post-conflict affiliation by opponents to third parties. It is possible that, although not exceeding the baseline frequency, opponents might have sought affiliative contacts after conflict for different reasons than outside of conflict context. Affiliative contacts with third parties may provide reassurance and/or encouragement for opponents and possibly also bond strengthening between interacting parties (de Waal and van Roosmalen 1979; de Waal and van Hooff 1981; Watts et al. 2000).

For third parties the options for involvement are likewise numerous. They can join the conflict by supporting one of the opponents, which is likely to entail both immediate costs (energetic, risk of aggression) and long-term consequences. Support has been found to work as a currency in the market of beneficial interactions, and can be an elementary part of collaborative relationships (e.g., de Waal 1984; 1992b; Watts 2002; Koyama et al. 2006). However, supporting one opponent places the individual into opposition of the

other one, which may damage their relationship. Again, reconciliation is expected between a supporting party and its opponent, the likelihood of which depending on their relationship. In fact, in this group supporting parties did reconcile with their opponents, although slightly less frequently than the original opponents did (Koski, unpublished data). Likewise, affiliation with an opponent can influence the relationship with the target of affiliation positively via bond strengthening, but may have negative implications for the relationship with the other opponent. This aspect was not investigated in this thesis. Finally, group members can engage as neutral mediators in a conflict or its resolution (de Waal 1982; Petit and Thierry 2000). Although not a frequent phenomenon, we did record some neutral interventions during conflicts (N=8 out of N= 696 conflicts, unpublished data). Mediation of reconciliation after conflicts was also recorded a few times, performed by one individual during the male rank reversal in the early stages of the research\*. Neutral interventions and mediation of reconciliation are conflict management strategies that are probably risky in terms of immediate danger, but potentially highly beneficial for relationships with and among other group members.

Overall, post-conflict behaviours carry possible long-term consequences for all relationships with the other group mates. This allows possible strategic employment of conflict- and post-conflicts interactions. Indeed, such strategising is described in the male-male dominance competition described as 'politics', in which also females may have relatively large impact (e.g. de Waal 1982; Goodall 1986).

### **Cognition and emotions - on the proximate mechanisms of conflict resolution**

The process of behavioural 'decisions' combines information on external stimuli with internal processes. The internal mechanisms can be divided into several inter-connected subcategories, such as neuronal substrates, the physiological

\*All mediations of reconciliation were performed by Mama, who participated very actively in conflicts during male rank reversal (see Appendix Table 2). Her mediation was often persistent and crucial in rejoining the three combating males.

and endocrinological correlates, and the psychological processes including emotions and cognition. In this study, as often in behavioural studies, only some of these aspects were addressed. Furthermore, since this study was an observational one, I do not have direct data on most of these aspects. Nevertheless, below I will make inferences of the possible mechanisms involved in four post-conflict interactions studied in this thesis, regarding their emotional, physiological and cognitive mechanisms (summarised in Table 1).

Anxiety has been suggested to be the emotional mediator for reconciliation (Aureli and Smucny 2000), but previously it has been assessed only in macaques (Aureli 1997; Kutsukake and Castles 2001). Anxiety can be measured by self-directed behaviours (Maestriperi et al 1992; Schino et al. 1996); in chimpanzees scratching is the most reliable anxiety indicator (Baker and Aureli 1997; Leavens et al. 2001). We confirmed the role of anxiety as the emotional correlate of reconciliation probably mediating the behaviour. At the physiological level, hormonal correlates of anxiety are rather well known. Especially the increase in systemic corticosteroid levels is well documented (McEwen and Sapolsky 1995; Schino et al. 1996; Whitten et al. 1998). Therefore, it is quite likely that post-conflict anxiety increased the cortisol levels of opponents (especially in aggresses). The cognitive processes required for reconciliation have been hypothesised to be rather basic; reconciliation requires at least recognising and remembering the conflict opponent until the reconciliation takes place (Castles 2000). In addition, reconciliation is dependent on the relationship attributes but whether the relationship assessment occurs also on the cognitive level in addition to the emotional one, cannot be answered on the basis of this thesis.

Third-party affiliation associated with self-protection from aggression may be preceded by some anxiety in anticipation of receiving aggression. This is, for example, evident in the elevated heart rates and rates of self-directed behaviour in macaques prior to potential further aggression (Aureli and van Schaik 1991b; Aureli et al. 1999). Therefore, if anxiety increases in the prospect of aggression, anxiety might act as a mediator for third-party affiliation, like for reconciliation. Physiologically, this would be evident in third parties' elevated cortisol levels.

**Table 1.** Possible emotional, physiological and cognitive processes in post-conflict interactions.

<b>Behaviour</b>	<b>Associated Emotion</b>	<b>Physiology/ Endocrinology</b>	<b>Cognition</b>
<b>Reconciliation</b>	anxiety	corticosteroid increase <sup>1</sup>	recognise and remember opponent <sup>2</sup>
<b>Third-party affiliation for self-protection</b>	(?) anxiety about possible aggression	(?) corticosteroid increase	risk assessment i.e., recognise and remember conflict participant, assess own relationship with them, assess the contextual probability of further aggression
<b>Third-party affiliation by kin</b>	empathic emotional contagion	skin temperature decrease <sup>3</sup>	possibly emotional state attribution; assessment of opponent losing/winning conflict
<b>Further aggression by opponents</b>	winner-effect	serotonin decrease <sup>4</sup>	decision to whom direct aggression

<sup>1</sup> Whitten et al. 1998; <sup>2</sup> Castles 2000; <sup>3</sup> Parr 2001; <sup>4</sup> Hsu et al 2006. Cognitive processes suggested are on the level of minimum requirements, which does not exclude higher order processes.

Unfortunately, we do not know whether third parties respond with anxiety to the risk of receiving further aggression as we have no data on the stress levels of third parties. Moreover, the cognitive base of third-party affiliation remains hypothetical. The cognitive process of third-party affiliation for self-protection is probably connected to the assessment of the relative risk of receiving aggression from opponents. This requires a combination of recognising the conflict opponents, assessing the own relationship with them (based on past interactions, relationship quality, and perhaps rank), and the particular conditions of the conflict to know whether further aggression is probable. The proposed process is

flexible to contextual and behavioural cues of conflicts, and to the identity of the conflict participants.

Third-party affiliation given to the aggresses by their relatives is different from the third-party affiliation for self-protective reasons (which mainly is given by non-kin individuals: see Ch 4, 5). It is possible that it reflects an empathic response, as suggested earlier for all 'consolation'. The possibility of an empathic base in kin-affiliation was strengthened by the increased prevalence of kin-affiliation when the aggressed lost the conflict (Ch 5). The emotional basis of empathy is necessarily affective resonance to the observed state of the other (Ch 6). Therefore, if empathic, kin-affiliation would evoke emotional contagion in the subject, i.e. a state similar to the opponent's emotional state. The degree of similarity in the emotional state of the third party and the conflict opponent depends on the level of cognitive process involved. At the most primary level the third parties would feel as much anxiety as the conflict victims do; at the more cognitive level the own anxiety is suppressed and the subject can understand the difference between own and other's state (Hoffmann 2000; Preston and de Waal 2002a). However, the level of cognitive involvement is unknown for chimpanzee empathy. Since I was not able to measure the third parties emotional state prior to affiliation (by measuring their anxiety), the conclusions about their emotional state and cognitive processing remain open.

Further aggression by the opponents was influenced by their winning of the conflict. This suggests that the opponents' propensity to direct further aggression to uninvolved third parties may be influenced by the emotional state connected to winning the conflict. The physiological correlates of the winner-effect are not known for primates. High serotonergic activity is associated with aggressive behaviour, and in mice winning is associated with high testosterone levels (Trainor et al. 2004). Testosterone, corticosteroids and serotonin appear to be associated with the winning experience and further aggression levels, but the details of the hormonal pathways are ambiguous (Hsu et al. 2006). The cognitive process of further aggression involves at least a 'choice' of the target of aggression, since there were dyadic differences in the aggression frequencies (Ch 5). Opponents targeted some individuals in the group more often, but the

individuals who received further aggression frequently from particular opponents were not necessarily targets of aggression from other opponents. Whether this targeting of further aggression is based on simple rules involving rank and relationship quality or is a more cognitively processed 'decision' involving strategising, cannot be resolved in this research.

To summarise, emotions were confirmed to play an important role as the underlying processes in behaviour. The role of emotions is gaining increasing interest in behavioural research (Aureli 1997; Aureli and Smucny 2000; Aureli and Schaffner 2002a,b). This is a fairly new aspect in behavioural research, and emotions as the proximate basis of behaviour deserve more attention. In addition, I suggested some possible physiological correlates of emotions and pondered on the cognitive processing associated with behaviour. Investigating the interactions between emotions, physiological and cognitive processes, and behavioural responses is important to gain a full understanding of behavioural processes. Such a cross-sectioning approach will hopefully become more widely practiced in the future.

### **Final comments**

This thesis has confirmed the notion that chimpanzee conflict and post-conflict behaviour is a complex system of multiple dimensions. Conflicts carry several behavioural options with differing consequences for each group member, and the behavioural 'decisions' are influenced by a multitude of factors. Managing such a fluent, multi-factorial system requires a large number of if-then rules that either operate separately from one another or form a hierarchical structure that allows flexibility in their employment (cf. de Waal 2003; Wittig and Boesch 2003b). Another, more cognitively demanding possibility is that chimpanzees form mental state abstractions (i.e. operate with a degree of ToM), which would allow increased flexibility in the behavioural responses to different situations. I have approached the cognitive aspects from a 'minimalist' point of view, by discussing the minimum capacities required for managing post-conflict behaviours. Nevertheless, I acknowledge that the simplest explanation is not always the most

plausible one, albeit usually the most recommendable. Andrews (2005) has pointed out that the most sceptic approach to chimpanzee cognition leads to *reductio ad absurdum* and to apply by rule the most sceptic approach to animals 'seems unfair' (Andrews 2005, p. 534). On the other hand, if anything, this thesis warns against nominal fallacy and overly generalized assumptions. Indeed, the benefit of the fiercest criticism on animal cognition is, apart from stirring the cognitive research world, in warning us against accepting easy explanations. In the quest of cognitive evolution per se, and primate (human) cognition in particular, scepticism is a good guideline to follow, while it should not render us nihilists. At its best, scepticism demands for strong evidence but allows an open mind to invent new paths. I am inclined to join others to echo that the most fruitful approach to chimpanzee—as for any species—cognition combines rigorous and repeatable experiments on different aspects of cognition, aims to see the connecting principles in them, and supports these findings with data on how these abilities are used in the animals' normal behavioural repertoire (e.g. Matsuzawa et al. 2006).

Finally, as is often the case with research, with its achievements this thesis provokes many new questions. Therefore, the plea for further studies applies also to this thesis as a whole. To assess the generality of the hypotheses posed on functions, emotions and cognition in conflict resolution in chimpanzees, repeated studies on other chimpanzee populations and other species are required.



**APPENDIX****Table 1.** The names, ages and parental information (if available) of the Arnhem Zoo chimpanzees during the study.

<b>Name (f/m)</b>	<b>Code</b>	<b>Born</b>	<b>Mother</b>	<b>Father</b>	<b>other information</b>
Mama (f)	MM	ca. 1955 (wild)	wild	wild	
Moniek (f)	Mo	7-6-1977	Mama	?	
Marka (f)	Ma	6-4-1984	Mama	?	
Morami (f)	Mr	7-2-1987	Moniek	Tarzan	
Fons (m)	FF	18-8-1975	Franje	?	
Gaby (f)	Ga	28-1-1984	Gorilla	?	
Giambo (m)	Gi	25-1-1989	Gorilla	Tarzan	
Geisha (f)	Ge	26-9-1993	Gorilla	Jing	adopted by MM
Goya (f)	Gy	13-10-1993	Gaby	Fons	
Galathea (f)	Gl	24-2-1999	Gaby	Fons	
Gizhee (f)	Gz	13-2-2003	Gaby	?	died 2003
Roos (f)	RR	23-4-1979	Krom	?	adopted by Gorilla
Roani (f)	Ro	27-11-1989	Roos	Dandy	transferred 2004
Raimee (f)	Rm	15-5-1999	Roos	Jelle	--
Jimmy (f)	SS	ca. 1960 (wild)	wild	wild	--
Jing (m)	JJ	22-3-1981	Jimmy	Dandy	
Jelle (m)	LL	6-11-1986	Jimmy	Dandy	transferred 2002
Joury (m)	Jo	23-10-1994	Jimmy	Ayo	
Sabra (f)	Sa	10-3-1986	Spin	Tarzan	adopted by SS; transferred 2005
Soona (f)	So	10-1-1996	Sabra	Ayo	transferred 2005
Saphira (f)	Sp	20-6-2001	Sabra	Jing	transferred 2005
Tepel (f)	TT	ca. 1959 (wild)	wild	wild	
Teshua (f)	Te	14-4-1986	Tepel	Fons	
Tushi (f)	Tu	21-2-1992	Tepel	Fons	
Tjobbe (m)	Tj	23-9-2003	Tepel	Giambo	
Amber (f)	Am	ca. 1968 (wild)	wild	wild	transferred 2004
Allity (f)	Al	27-12-1998	Amber	Jelle	transferred 2004
Anthe (f)	An	24-11-2002	Amber	Jelle	died 2004
Zwart (f)	ZZ	ca. 1970 (wild)	wild	wild	transferred 2002
Zola (f)	Zo	8-11-1979	Zwart	?	died 2003
Zaira (f)	Za	15-1-1983	Zwart	Dandy	
Ziswa (f)	Zs	28-12-1987	Zwart	Fons	transferred 2002
Zedoenja (f)	Zd	24-2-1994	Zwart	Fons	transferred 2002
Zombie (f)	Zm	15-3-1993	Zola	Ayo	
Zarno (m)	Zr	26-12-1997	Zola	Jing	
Zouly (m)	Zu	25-6-1993	Zaira	Fons	transferred 2004
Zwala (f)	Zw	16-4-1999	Zaira	Fons	
Zyann (m)	Zn	25-3-2003	Zaira	?	died 2003

**Table 2.** The Arnhem Zoo chimpanzee group composition during the study 2002-2006.

Ind	June 2002→	2003	2004	2005	← Aug 2006
Females					
MM	x	x	x	x	x
Mo	x	x	x	x	x
Ma	x	x	x	x	x
Mr	x	x	x	x	x
Ga	x	x	x	x	x
Gy	x (adol.)	x (adol.)	x	x	x
Gl	x (inf.)	x (juv.)	x (juv.)	x (juv.)	x (juv.)
Gz		born, died			
Ge	x (adol.)	x (adol.)	x	x	x
RR	x	x	x	x	x
Ro	x	x	x		
Rm	x (inf.)	x (juv.)	x (juv.)	x (juv.)	x (juv.)
SS	x	x	x	x	x
Sa	x	x	x		
So	x (juv.)	x (adol.)	x (adol.)		
Sp	x (inf.)	x (inf.)	x (juv.)		
TT	x	x	x	x	x
Te	x	x	x	x	x
Tu	x	x	x	x	x
Tj			x (inf.)	x (inf.)	x (inf.)
Am	x	x	x		
Al	x (inf.)	x (juv.)	x (juv.)		
An	x (inf.)	x (inf.)			
ZZ	x				
Zo	x				
Zm	x (adol.)	x	x	x	x
Zr	x (juv.)	x (juv.)	x (juv.)	x (adol.)	x (adol.)
Za	x	x	x	x	x
Zw	x (inf.)	x (inf.- juv.)	x (juv.)	x (juv.)	x (juv.)
Zn		born, died			
Zs	x				
Zd	x (adol.)				

(continued)

<b>Males</b>					
<b>JJ</b>	x beta/alpha <sup>1</sup>	x beta	x beta	x beta	x beta
<b>LL</b>	x alpha/beta				
<b>FF</b>	x gamma	x gamma	x gamma	x gamma	x gamma
<b>Gi</b>	x delta	x <b>alpha</b>	x alpha	x alpha	x alpha
<b>Zu</b>	x (adol.)	x (adol.)	x (delta) <sup>2</sup>		
<b>Jo</b>	x (adol.)	x (adol.)	x (delta)	x delta	x delta
<b>adult F</b>	17	15	17	14	14
<b>adult M</b>	4	3	5	4	4
<b>adol. F</b>	4	3	1	0	0
<b>adol. M</b>	2	2	0	1	1
<b>inf. &amp; juv.</b>	8	7 (9)	7	4	4
<b>TOTAL</b>	<b>35</b>	<b>30 (32)</b>	<b>30</b>	<b>23</b>	<b>23</b>

<sup>1</sup>Alpha position was shared by JJ and LL: no submission occurred between them and both received as often submission from other group members. A few months prior to my study LL was ranked as the alpha male (Klinkova et al 2005). <sup>2</sup> The ranks of Jo and Zu were not fully determined during their last year of adolescence.

Age classes as follows: inf.=0-3 yrs, juv.=4-7 yrs, adol.=8-9 yrs, adult= >9 yrs.



## **Chimpanzees, Conflicten en Cognitie.**

De functies en mechanismen van chimpansee conflictoplossing.

### **Algemene introductie**

De mens is verreweg de meest intelligente diersoort, ongeacht de criteria die we aanleggen voor intelligentie. Onze intelligentie verscheen echter niet *de novo*, maar evolueerde vanuit voorafgaande capaciteiten. Hoe is dat zo gekomen?

Er is het nodige onderzoek verricht om uit te vinden tot op welke hoogte geavanceerde cognitieve vermogens aanwezig zijn in andere diersoorten. Gezien onze gedeelde evolutionaire geschiedenis met apen en mensapen, concentreerden veel van deze studies zich op primaten (bv., Byrne en Whiten 1988; Cheney en Seyfarth 1990; Whiten en Byrne 1997; Tomasello en Call 1997; Matsusawa 2001; Matsuzawa et al. 2006). Gedurende de laatste jaren is de aandacht ook uitgebreid naar vogels, honden, dolfijnen en olifanten (bv., Clayton en Dickinson 1998; Lefebvre et al. 2003; Hare en Tomasello 2005; Miklosi et al. 2004; Marino 2004; Plotnik et al. 2006; Dally et al. 2006). De algemene cognitieve vermogens van primaten zijn geavanceerd vergeleken met veel andere taxa (Shettleworth 1998; Deaner et al. 2006) en primaten hebben grote hersenen in verhouding tot hun lichaamsgrootte (Harvey en Krebs 1990; Barton en Dunbar 1997; Barton en Harvey 2000; Striedter 2006). Deze grote hersenen en de geavanceerde cognitieve vaardigheden houden mogelijk verband met elkaar (bv. Byrne en Whiten 1988; 1997; Deacon 1990) en aanwijzingen voor dit veronderstelde verband zijn inderdaad gevonden (Reader en Laland 2002).

Er zijn een aantal theorieën voorgesteld om de evolutionaire sprong in de cognitieve capaciteiten van primaten te verklaren. Deze theorieën veronderstellen dat ecologische en/of sociale selectiedrukken, of, zoals onlangs voorgesteld, met de levensloop samenhangende factoren deze toename in cognitieve vermogens veroorzaakt hebben. De theorie dat leven in groepen de evolutie van cognitieve vaardigheden heeft geïnitieerd is momenteel het meest populair. Het algemene idee van de sociale-intelligentiehypothese is dat leven in

grote, geïndividualiseerde en complexe sociale groepen heeft geleid tot een selectie op toenemende cognitieve capaciteiten (Humphrey 1976; Jolly 1966; Whiten en Byrne 1988). Sociale groepen bestaan uit netwerken van verschillende soorten sociale relaties (bijv. verwantschap, coöperatie en dominantie). Wil een dier succesvol opereren in dergelijke netwerken, dan moet het rekening kunnen houden met de ingewikkelde dynamiek daarvan. Dat vergt procesmatig complexe processen. Individuen die flexibel hun eigen acties in dit netwerk uitdenken en uitvoeren, zullen voordelen kunnen behalen ten opzichte van individuen die hier niet toe in staat zijn. Ondanks enige kritische kanttekeningen (bv. van Schaik en Deaner 2003; van Schaik 2004), wordt algemeen aangenomen dat het belang van effectieve samenwerking in een spanningsvolle wisselwerking met concurrentie tussen groepsleden mogelijk de voornaamste selectiedruk vormde tot de ontwikkeling van intelligentie bij primaten (bv. Cosmides 1989; Byrne en Whiten 1997; Tomasello en Call 1997; Dunbar 2000; Reader en Laland 2002; van Schaik 2004; Kamil 2004; Zuberbühler en Byrne 2006).

De vaardigheid om andermans gedrag te voorspellen en om een ander te manipuleren en zelfs te misleiden, zou vooral voordelig zijn in soorten met een sociaal leven dat vraagt om strategisch manoeuvreren (de 'Machiavelliaanse intelligentie hypothesis': Byrne en Whiten 1988; Whiten en Byrne 1997). Het vermogen tot zulk 'Machiavelliaans' gedrag wordt ongetwijfeld vergroot indien een individu zich mentale representaties kan vormen van de mentale toestand van zijn soortgenoten. Het kunnen toeschrijven van een mentale staat aan een ander is de belangrijkste vaardigheid in het cognitieve concept Theory of Mind (ToM). ToM verwijst naar de vaardigheid te begrijpen dat de ander bedoelingen, intenties, overtuigingen en perspectieven heeft die kunnen verschillen van die van 'zelf' (Premack en Woodruff 1978). ToM omvat een aantal cognitieve vermogens, die ook los van elkaar kunnen voorkomen. In mensen ontstaat ToM geleidelijk, wat ook aangeeft dat het geen dichotome monoliet is. Sommige aspecten van ToM zouden dus aanwezig kunnen zijn in andere primaten dan de mens, zelfs als ze niet de complete, volwassen-mensen ToM bezitten. Het lijkt geen twijfel dat apen een zekere kennis hebben van hun sociale omgeving. Niettemin lijken ze niet in staat andermans mentale staat te onderkennen

(Cheney en Seyfarth 1990). Mensapen daarentegen, lijken in staat te zijn in ieder geval een beperkt aantal mentale toestanden toe te schrijven aan anderen (Tomasello et al. 2003 a,b; Call 2003; maar zie Povinelli en Bering 2002; Povinelli en Vonk 2003, 2004) en lijken dus meer met ToM geassocieerde vermogens te bezitten dan andere primaten.

Als mensapen in staat zijn bepaalde veronderstellingen te maken over de mentale toestand van een ander, dan rijst de vraag wanneer en hoe ze deze vaardigheid gebruiken. Het gebruik van sociale intelligentie heeft minder aandacht gekregen dan het bestaan ervan.

Chimpansees zijn uiterst sociale mensapen met een veelzijdig sociaal leven dat een voortdurend beroep doet op hun vaardigheid sociaal te kunnen manoeuvreren. Ze zijn daarom ook een bijzonder geschikte soort om de rol en de betekenis van sociale intelligentie in de omgang met elkaar te onderzoeken. Deze aanpak, het bestuderen van de voordelen van cognitieve vaardigheden in een sociale omgeving, onderzoekt in feite de functie van (en dus, uiteindelijk de fitness-consequenties) van sociale gedragingen. Daarnaast is het essentieel om te begrijpen welke cognitieve processen geassocieerd zijn met sociale interacties. In deze thesis heb ik deze twee aanpakken gecombineerd in het onderzoek naar conflictoplossing bij chimpansees.

### **Conflictoplossing**

Een onvermijdelijk gevolg van het leven in een groep is concurrentie om begrensde hulpbronnen. Deze concurrentie leidt tot belangentegenstellingen tussen groepsleden, die eventueel kunnen resulteren in agressieve ontmoetingen. Agressieve conflicten brengen aantoonbare kosten met zich mee in de vorm van verspilde energie, verwondingen, een verhoogd predatierisico en verslechterde relaties met groepsgenoten (en daarmee een vermindering van voordelen, zoals tolerantie bij hulpbronnen, steun en hulp van kompanen). Als er geen mechanismen zijn die escalatie van conflicten voorkomen of de schade reduceren, kunnen de kosten van het leven in een groep hoger worden dan de baten. Dit kan leiden tot de desintegratie van een groep, hetgeen ten nadele is van alle groepsleden (Aureli en de Waal 2000). De voorspelling is dat

conflictoplossing gevonden zal worden bij soorten met persoonlijke sociale relaties, die tevens op agressieve wijze concurreren om monopoliseerbare hulpbronnen. Bovendien moet deze agressie de coöperatieve relaties met groepsleden schaden en resulteren in verminderde voordelen van het samenleven voor een of beide tegenstanders in het conflict (Aureli et al. 2002; Schaffner et al. 2005). Zoals verwacht komt conflictoplossing veel voor bij sociale soorten die aan deze criteria voldoen, zoals de meest apensoorten, gedomesticeerde geiten, dolfinnen en hyena's (Schino 1998; Hofer en East 2000; Samuels en Flaherty 2000; Aureli et al. 2002; Wahaj en Holekamp 2003). Conflictoplossing ná een conflict kan plaats vinden door vriendelijk gedrag tussen de vechtende partijen, ook wel verzoening genoemd (de Waal en van Roosmalen 1979; Aureli en de Waal 2000). Bovendien kunnen groepsleden die niet bij het conflict betrokken waren deelnemen aan de conflictoplossing, bijvoorbeeld door te bemiddelen of door vriendelijk te zijn tegen een van de tegenstanders (de Waal 1982; Aureli en van Schaik 1991a; de Waal en Aureli 1996; Das et al 1998). Het patroon in conflictoplossing wordt bepaald door het soort sociale relaties dat gevonden wordt in een groep. In een groep bestaan relaties van verschillende kwaliteit, zoals verwantschap, dominantie en vriendschap. De kwaliteit van een relatie bepaalt de noodzaak om de voordelen van die relatie te behouden. Hoe belangrijker een relatie is voor de beide tegenstrevers, des te belangrijker wordt het om de schade veroorzaakt door het conflict te herstellen (Kappeler en van Schaik 1992; Cords en Thurnheer 1993; Aureli et al. 1997; van Hooff 2001; Aureli et al 2002; Watts 2006).

Het netwerk van sociale relaties van verschillende kwaliteit, de contextafhankelijke karakteristieken van gevechten en de invloed van het gedrag van de tegenstander op het eigen gedrag zijn de redenen dat conflicten en hun naweën complex zijn en cognitief veeleisend. Elk individu moet 'beslissen' (de term veronderstelt niet noodzakelijk een bewuste beslissing) of en in welke rol hij betrokken raakt in een conflict, en hij moet het effect van die betrokkenheid op zijn sociale relaties inschatten. Dit maakt conflicten ingewikkeld. In zo'n situatie zal flexibiliteit in gedrag voordelig zijn. Om die reden bieden conflicten de mogelijkheid te onderzoeken hoe individuen hun sociale intelligentie toepassen in

hun 'beslissingen'. Gedragingen voor en na een conflict leveren mogelijkwijs informatie over sociale intelligentie en zijn effect op het proximate niveau, dwz. welke cognitieve processen worden aangewend bij interacties, en op het functionele niveau, dwz. welk voordeel biedt sociale intelligentie een individu. Om deze redenen betref mijn studie conflicten en hun oplossing van chimpansees in relatie tot hun sociale intelligentie.

### **De bestudeerde soort**

#### *De ecologie en socio-ecologie van chimpansees*

De chimpansee is een hoogsociale en intelligente diersoort. Hij is daarmee een boeiend onderwerp voor een studie naar de toepassing van sociale intelligentie. Er zijn vele aanwijzingen dat chimpansees zich behoorlijk Machiavelliaans gedragen. Hun sociale gedragingen omvatten uiterst cooperative, maar ook gewiekst aandoende competitieve elementen. Hun sociale manipulaties zijn dan ook wel bestempeld als 'politiek' (de Waal 1982).

De chimpansee, *Pan troglodytes*, en de bonobo (*Pan paniscus*) zijn de twee naaste, nog levende verwanten van de mens. De evolutionaire wegen van de voorouders van beide soorten *Pan* en mens (*Homo*) scheidden zo'n 4 tot 6 miljoen jaar geleden (Groves 2001). Chimpansees leven in heel equatoriaal Afrika. Er worden momenteel vier ondersoorten onderscheiden: *P. t. verus* in West-Afrika, *P. t. vellerosus* in Nigeria, *P. t. troglodytes* in Centraal-Afrika, en *P. t. schweinfurthii* in oostelijk Centraal-Afrika. Chimpansees leven in gemeenschappen van zo'n 20 tot meer dan 100 individuen met meerdere volwassen mannetjes en vrouwtjes. De gemeenschappen hebben een losse structuur, waarin wisselende subgroepjes zich regelmatig afsplitsen en weer herenigen (Goodall 1986; Nishida 1990; Boesch 1991). Vrouwtjes zijn promiscue en paren met meerdere mannetjes. Mannetjes proberen dit tegen te gaan door het bewaken van en samenreizen met een vruchtbaar vrouwtje (Tutin 1979; Watts 1998). Niettemin zijn de mannetjes vergeleken met andere soorten seksueel betrekkelijk tolerant. Mannetjes resideren in de groep waar ze geboren zijn, terwijl vrouwtjes tijdens hun pubertijd kunnen verhuizen naar een andere gemeenschap (Pusey 1979, Boesch en Boesch-Achermann 2000). In alle

populaties onderhouden mannetjes nauwe banden met elkaar, hetgeen zich uit in de tijd die ze tezamen doorbrengen, in hun onderlinge vlooiën en steunverlening, in de verdediging van het gezamenlijke territorium en het delen van vlees (bv. van Hooff en van Schaik 1994; Watts 2002; rev. Mitani et al. 2002). De banden tussen mannetjes zijn niet alleen belangrijk voor de samenwerking tijdens de verdediging van het territorium en de jacht, maar ook bij de onderlinge concurrentie binnen de gemeenschap. Mannetjes vormen met elkaar coalities en de coalitiepartners helpen elkaar bij agressieve conflicten (o.a. de Waal 1982; Watts 2002). Deze 'politieke' netwerken zijn uiterst opportunistisch en hebben een allesbepalende rol in de strijd om de dominantiepositie (de Waal 1982). De dominantiehiërarchie van chimpanseemannetjes is duidelijk en lineair, waarbij de topdominante man een voorkeurspositie heeft bij paringen en voedsel. Deze topdominante positie wordt vaak betwist door lager-rangende mannetjes, maar wordt gehandhaafd met de steun van handlangers. Hierdoor zijn goede relaties tussen bepaalde mannetjes uiterst waardevol, maar ook instabiel. Vrouwtjes daarentegen, hebben een minder strikte en onduidelijker dominantiehiërarchie (hoewel de mate waarin die zich manifesteert varieert tussen gemeenschappen: Wrangham et al. 1992; Baker en Smuts 1994; Pusey et al. 1997; Wittig en Boesch 2003c). Dit resulteert in tolerante, stabiele maar relatief onbelangrijke relaties tussen (onverwante) vrouwtjes. Ondanks de duidelijke dominantiehiërarchie van de mannetjes, zijn de sociale betrekkingen doorgaans relatief egalitair. Dit uit zich in een grote tolerantie voor nabijheid en bezit, en in het feit dat de agressie die desondanks voorkomt veelal wederzijds (bi-directioneel) is (de Waal en Luttrell 1989, Sterck et al. 1997; Hemelrijk 1999; Thierry 2000).

#### *Cognitieve capaciteiten van chimpansees*

De cognitieve vermogens die samenhangen met de toekenning van mentale toestanden aan anderen (en dus met Theory of Mind, ToM) kunnen worden bestudeerd met specieke experimentele testen. Samengevat suggereren de resultaten van deze testen dat chimpansees sommige ToM-taken goed uitvoeren,

maar falen in andere. Chimpansees zijn in staat tot zelf-ander onderscheid; ze kunnen zichzelf namelijk herkennen in een spiegel. Ze begrijpen wat anderen wel en niet zien, herinneren zich wat hun concurrent kortgeleden zag en passen deze informatie toe ten gunste van henzelf. Deze capaciteiten suggereren een begrip van 'zelf' en het begrip dat anderen dingen kunnen zien die het individu zelf niet heeft gezien. Bovendien geven chimpansees er blijk van de bedoeling van de acties van anderen te kunnen begrijpen, en mogelijk vertonen ze een begin van bezorgdheid om anderen, hetgeen inleving in de emoties van een ander suggereert. Echter, chimpansees kunnen waarschijnlijk niet begrijpen dat anderen ideeën hebben die anders zijn dan die van henzelf, of dat hun eigen ideeën afwijken van de 'waarheid'. Desondanks is het onderwerp van de cognitieve vermogens van chimpansees controversieel. Er zijn critici, die het merendeel van de bewijzen als niet overtuigend beschouwen. Er is dus nog geen consensus tussen onderzoekers. Een deel van de onderzoekers is van mening dat chimpansees ongeveer het cognitieve niveau van een 2-jarig kind hebben, dat een deel van de ToM-taken kan volbrengen, maar niet alle (Suddendorf en Whiten 2001; Tomasello et al. 2003a; Call en Tomasello 2005; Hare et al. 2006).

### **Het doel, de opzet en de belangrijkste resultaten van deze studie**

Ik bestudeerde sociale cognitie van chimpansees in de context van conflictoplossing. Hierbij onderzocht ik het vóórkomen, de functie en de mechanismen van interacties ná conflicten. **In de eerste studie (hoofdstuk 2)** onderzocht ik de functie van verzoening. De meest geaccepteerde functie van verzoening is het herstel van de relatie met de voormalige opponent (Aureli et al. 2002). Omdat verzoening ook een risico inhoudt, zullen pogingen tot verzoening enkel ondernomen worden wanneer de baten geassocieerd met de relatie belangrijker zijn dan het risico van de poging tot verzoening. Daarom zal verzoening vaker voorkomen tussen individuen met een waardevolle relatie. Bovendien levert verzoening als direct voordeel dat het stressniveau van de tegenstanders na een conflict verlaagd wordt en de kans op hernieuwde agressie afneemt. Deze twee verklaringsniveaus zijn samengebracht in de 'Geïntegreerde

Hypothese' (Aureli 1997; Aureli en Smucny 2000), welke postuleert dat het stressniveau van de voormalige opponenten afhangt van de waarde van hun relatie. Tegenstanders met een waardevolle relatie raken meer gestresst door een conflict dan individuen met een minder belangrijke relatie. Tegenstanders zullen eerder pogen stress te verlagen als ze meer gestresst zijn. Omdat verzoening stress verlaagt, vormt stress de intermediair die leidt tot verzoenend gedrag. De 'Geïntegreerde Hypothese' is tot dusverre niet getest voor chimpanzees (Aureli 1997; Kutsukake en Castles 2001). Mijn studie onderschrijft dat verzoening relaties herstelt. De waarde van de relatie van de tegenstanders (afgeleid uit passendheid en 'aanhankelijkheid' buiten de conflictcontext) bleek een belangrijke factor voor het vóórkomen van verzoeningen (hoofdstuk 2 en 3). Stress bleek een emotionele intermediair die leidde tot verzoening, zoals verondersteld wordt in de 'Geïntegreerde Hypothese'. De stressniveaus na een conflict waren verhoogd en de hoogte bleek samen te hangen met de waarde van de relatie (hoofdstuk 2). Verzoening reduceerde de stress tot normaalwaardes (hoofdstuk 4). Echter, enkel de ontvangers van agressie, en niet de agressoren, ervoeren een verhoogd stressniveau. Deze asymmetrische stressreactie, gecombineerd met de constatering dat passendheid voor de tegensanders een asymmetrisch effect had op het voorkomen van verzoening (hoofdstuk 3), betekent dat de ontvanger van agressie mogelijk kwetsbaarder is voor beschadiging van de relatie door een conflict dan de agressor.

**De tweede studie (hoofdstuk 3)** beschouwt alle typen interacties die na een conflict (PCI) van chimpanzees kunnen voorkomen, dus niet alleen verzoeningen. De voormalige opponenten en andere groepsleden kunnen uit een aantal gedragsmogelijkheden kiezen en het is momenteel niet duidelijk op grond waarvan de keuze voor een bepaalde PCI gemaakt wordt (vgl. Wittig en Boesch 2003b). De huidige studie was opgezet om het optreden van de verschillende PCI-typen te voorspellen en de relatie tussen de verschillende PCI-typen te bepalen. Het bleek dat de vier onderzochte PCI-typen grotendeels onafhankelijk waren van elkaar. Bovendien vond ik dat een PCI-type, waarvan wordt verondersteld dat het als troost functioneert, werd gegeven als het risico op verdere agressie van een van de tegenstanders hoog was. Tenslotte bleek dat

verdere agressie vaker werd gegeven door de winnaar van het conflict. Dit suggereert dat het zogenaamde 'winnaars-effect' de emotionele basis is voor opvolgende agressie.

**De derde studie (hoofdstuk 4)** concentreert zich op 'troost'. Het begrip 'troost' wordt gebruikt voor vriendelijk gedrag van een niet bij het conflict betrokken individu naar een van de deelnemers aan het conflict. Zoals de term suggereert, werd verondersteld dat troost de stress van zijn ontvanger verlaagd. De functie(s) en mechanisme(n) van dit zogenaamde troostgedrag zijn echter vooralsnog niet duidelijk. Dit komt deels doordat het gedrag enkel bij sommige soorten mensapen werd waargenomen (de Waal en van Roosmalen 1979; de Waal en Aureli 1996; Kutsukake en Castles 2004; Palagi et al. 2004, 2006; Mallavarapu et al. 2006). Ondanks een aanzienlijke onderzoeksinspanning werd het niet gevonden bij gewone apen (overzichtartikel door Das 2000; Watts et al. 2000; maar zie Call et al. 2002; hoofdstuk 3-5). Een andere veronderstelling is dat het een vergelijkbare functie vervult als verzoening, en daarom verzoening vervangt als deze niet gegeven of verhinderd wordt (Watts et al. 2000; Wittig en Boesch 2003a). Ik vond geen steun voor deze veronderstellingen, niet voor de stressverlagende functie en niet voor de functie als vervanger van verzoening (hoofdstuk 4). Dit suggereert dat de ontvanger van troostgedrag niet op de veronderstelde wijze baat bij dit gedrag heeft, maar dat het mogelijk ten voordele is van het troostende individu. Ik suggereer dan ook om de term 'troost' niet meer te gebruiken ten faveure van de functioneel neutrale term 'derde-individu affiliatie'.

**De vierde studie (hoofdstuk 5)** vervolgt de speurtocht naar een mogelijke functie van 'derde-individu affiliatie'. Ik onderzoek of 'derde-individu affiliatie' ten voordele is van het affiliërende individu, en niet zozeer van de ontvanger, waarvan voorheen altijd gedacht werd dat deze er baat bij had. Daarbij onderzoek ik met name de mogelijkheid dat vriendelijk gedrag het derde, niet bij het conflict betrokken individu beschermt tegen opvolgende agressie van de voormalige tegenstanders. Deze hypothese was al eerder geopperd (Call et al. 2002; Palagi et al. 2004), maar was nog niet getest (met uitzondering van een niet-gepubliceerde studie over Java-apen; Das 1998). Mijn

studie is de eerste die de nieuwe zelf-beschermingsfunctie van derde-individu affiliatie onderzocht. Ik vond dat derde individuen voordeel hebben van vriendelijk gedrag naar een tegenstander, omdat het de kans op agressie verlaagt (hoofdstuk 5). Deze zelf-beschermende functie gold voor de meerderheid van de vriendelijke contacten van derden naar tegenstanders. Er zijn twee varianten van de zelf-beschermingsfunctie voorgesteld: dat vriendelijk gedrag van een derde individu de kans op agressie van een tegenstander naar dit derde individu verlaagt (Das 1998; Call et al. 2002), en dat het agressie naar alle groepsleden vermindert, en daarmee indirect ook naar het derde individu (Palagi et al. 2004, 2006). Onze resultaten ondersteunen de eerste, maar niet de tweede variant: vriendelijk gedrag verminderde niet de kans dat een tegenstander weer agressief werd (hoofdstuk 5). Vriendelijk gedrag van een derde verminderde echter wel de kans dat dit individu agressief bejegend werd door de voormalige tegenstander. Een uitzondering op de zelf-beschermingsfunctie wordt gevormd door vriendelijk gedrag van familieleden naar de ontvanger van agressie (hoofdstuk 4 en 5). Deze 'verwanten-affiliatie' dient vermoedelijk niet ter zelf-bescherming, aangezien familieleden van tegenstanders beduidend minder agressie ontvingen na een conflict dan niet verwante dieren. De functie van verwanten-affiliatie blijft vooralsnog onduidelijk. Hier zou mogelijk nog sprake kunnen zijn van een troostend effect, zoals aanvankelijk verondersteld.

**De vijfde studie (hoofdstuk 6)** beschouwt de cognitieve processen die van belang zijn bij derde-individu affiliatie. Ik richt me met name op empathie, of inlevingsvermogen, als een eventueel proces dat derde-individu affiliatie mogelijk maakt. Hierbij maak ik onderscheid tussen vriendelijk gedrag tussen verwanten en niet-verwanten, omdat familieleden er als eersten toe geneigd zouden kunnen zijn om op inlevingsgronden vriendelijk tegen elkaar te zijn. Daarnaast betoog ik dat het van groot belang is te bepalen welk cognitief niveau van inlevingsvermogen voldoende is voor derde-individu affiliatie. Ik vond dat derde-individu affiliatie veelal kan worden begrepen als zelfzuchtig gedrag, dat gevonden wordt in situaties die geen toekenning van een mentale toestand bij een ander behoeven. Er is geen reden om aan te nemen dat zelf-bescherming

iets te maken heeft met inlevingsvermogen, op welk cognitief niveau dan ook (hoofdstuk 5 en 6). In plaats daarvan berust zelf-beschermd derde-individu affiliatie waarschijnlijk op een evaluatie van het persoonlijke sociale verleden met de tegenstander(s), in combinatie met de specifieke omstandigheden van een conflict die een bijpassende inschatting van het risico van vriendelijk gedrag oplevert. Dit vereist bekwaam interpreteren van gedrag en signalen, maar geen toekenning van mentale (waaronder emotionele) toestanden aan anderen (hoofdstuk 6). Verwanten-affiliatie daarentegen is mogelijk gebaseerd op inlevingsvermogen. Of dit écht het geval is dient verder uitgezocht te worden. En ook al is verwanten-affiliatie gebaseerd op inlevingsvermogen, het blijft onduidelijk of het vereiste inlevingsniveau van een hoog cognitief niveau is. Andere vormen van inleven, zoals emotionele aanstekelijkheid en secundaire representatie, zijn ook mogelijke mechanismen die vriendelijk gedrag veroorzaken. Bij emotionele aanstekelijkheid zoeken derden vermindering van de stress die het conflict tussen hun groepsgenoten bij henzelf heeft opgeroepen; terwijl bij secundaire representatie vriendelijk gedrag een mengvorm is van kalmeren van zelf en sussen van de ander. Echter, zonder gegevens hierover kunnen we niets concluderen over het mogelijke cognitieve niveau van inlevingsvermogen bij verwanten-affiliatie bij chimpanzees (hoofdstuk 5 en 6). Alles opgeteld lijkt het er op dat de meeste vriendelijke contacten van derden met een tegenstander niet uit medeleven, maar uit eigenbelang voortkomen. Vriendelijk gedrag van verwanten van agressie-ontvangende dieren vormt mogelijk een uitzondering, en deze contacten zijn de beste kandidaten om te onderzoeken of chimpanzees zich inderdaad in kunnen leven in de stress van een ander.

Alles tezamen laat dit proefschrift zien dat conflicten en het gedrag ná conflicten van chimpanzees een complex geheel zijn dat meerdere dimensies omvat. Conflicten kunnen leiden tot verschillendsoortige reacties, die ook verschillende gevolgen hebben voor de betrokken groepsleden. De 'beslissing' welk gedrag uit te voeren wordt bepaald door meerdere factoren. Ik onderzocht vier typen gedragingen die na conflicten van chimpanzees voorkomen: verzoening, derde-individu affiliatie (ook wel 'troost' genoemd), opvolgende

agressie van een tegenstander naar een derde individu (ook wel redirectie van agressie genoemd) en agressie van een derde naar een tegenstander. Deze vier typen gedragingen zijn grotendeels onafhankelijk van elkaar. De functie van de twee typen agressie na een conflict werd niet vastgesteld, hoewel ik suggereer dat het mechanisme dat opvolgende agressie veroorzaakt beïnvloed wordt door het winnaar-effect (de emotie van de succeservaring faciliteert verdere agressie). Verzoening van chimpanzees komt overeen met het algemene patroon bij primaten. Het wordt beïnvloed door stress en angst en heeft als functie dat de beschadigde relatie van de tegenstanders hersteld wordt. Derde-individu affiliatie van chimpanzees leverde de interessantste resultaten op. Ze zijn in tegenstelling tot wat tot nog toe gedacht werd. Ik vond geen bewijs dat het vriendelijk gedrag werkt als troost voor de tegenstander. Wel vermindert het de kans dat de tegenstander agressief is naar het individu dat dit vriendelijk gedrag vertoont. Een uitzondering wordt mogelijk gevormd door derde-individu affiliatie van verwanten naar een ontvanger van agressie. Dit vriendelijk gedrag is mogelijk gebaseerd op inlevingsvermogen en vervult eventueel een troostende functie.

Emoties spelen een belangrijke bepalende rol bij alle gedragingen na een conflict. De rol die emoties spelen krijgt steeds meer aandacht in de gedragsbiologie (Aureli 1997; Aureli and Smucny 2000; Aureli and Schaffner 2002a,b). Dit is een relatief nieuw onderzoeksgebied. Emotie als een proximaat mechanisme dat gedrag beïnvloedt verdient zeker meer aandacht. Bovendien suggereer ik een aantal fysiologische correlaten van en cognitieve processen betrokken bij emoties. Onderzoek naar de onderlinge relaties en afhankelijkheid van emoties en fysiologische en cognitieve processen is noodzakelijk om gedragsprocessen te begrijpen. Ik hoop dat deze geïntegreerde benadering van gedrag in de toekomst vaker toegepast wordt.

## **Simpanssit, Konfliktit ja Kognitio.**

Simpanssien konfliktinratkaisun syyt ja mekanismit.

### **Yleinen johdanto**

Me ihmiset olemme kaikista eläimistä älykkäimpiä, riippumatta käyttämistämme älykkyyden kriteereistä. Edistynyt älykkyytemme ei kuitenkaan ilmaantunut de novo, vaan kehittyi kantamuotojemme kognitiivisista kyvyistä. Kuinka oikein päädyimme siihen, missä olemme nyt?

Runsaasti tutkimusta on tehty saadaksemme selville, millaista on muiden lajien älykkyys ja missä määrin voimme löytää edistyneitä kognitiivisia kykyjä ihmisyyden ulkopuolelta. Johtuen pitkästä yhteisestä evolutiivisesta historiastamme muiden kädellisten kanssa, kognitiiviset tutkimukset ovat suurelta osin keskittyneet apinoihin (esim. Byrne & Whiten 1988; Cheney & Seyfarth 1990; Whiten & Byrne 1997; Tomasello & Call 1997; Matsusawa 2001; Matsuzawa et al. 2006). Viime vuosina älykkyystutkimus on huomionut myös linnut, koirat, valaat, ja elefantit (esim. Clayton & Dickinson 1998; Lefebvre et al. 2003; Hare & Tomasello 2005; Miklosi et al. 2004; Marino 2004; Plotnik et al. 2006; Dally et al. 2006). Kädellisten kognitiiviset kyvyt ovat erityisen kehittyneet verrattuna moniin muihin eläinryhmiin, ja kädellisillä on myös kokoonsa nähden suhteellisen suuret aivot (Shettleworth 1998; Harvey & Krebs 1990; Barton & Dunbar 1997; Barton & Harvey 2000; Deaner et al. 2006; Striedter 2006). Suhteellisen aivojen koon oletetaankin olevan yhteydessä edistyneisiin älyllisiin kykyihin (esim. Byrne & Whiten 1988, 1997; Deacon 1990), ja tästä on saatu myös viime vuosina tutkimuksellista näyttöä (Reader & Laland 2002).

Kädellisten älykkyyden evolutiivista loikkaa on selitetty useilla teorioilla. Nämä teoriat voidaan karkeasti jakaa ekologisiin, sosiaalisiin ja, viimeisimpänä, elinhistoriallisiin. Näistä sosiaalinen teoria on nykyään ehkä laajimmin hyväksytty. "Sosiaalisen älykkyyden hypoteesi" esittää, että eläminen laajoissa sosiaalisissa ryhmissä, joissa on yksilöityneet suhteet, on asettanut valintapaineita älykkyyden kehittymiselle (Humphrey 1976; Jolly 1966; Whiten & Byrne 1988). Sosiaaliset ryhmät sisältävät erilaisten suhteiden (esim. sukulaisuus-, dominanssi- ja ystävyys-suhteiden) verkostoja, joiden

menestyksenkäs hallinta kilpailun ja yhteistyön ristipaineissa on älyllisesti vaativaa. Yksilöt, jotka kykenevät joustavaan, strategiseen käyttäytymiseen saavat etua niihin yksilöihin nähden, jotka eivät kykene käyttäytymään yhtä joustavasti. Näin ollen, tarve luovia tehokkaasti yksilöiden välisten suhteiden verkostossa on teorian mukaan ollut evolutiivinen ajava voima älykkyyden kehittymisessä. Kritiikistä huolimatta (esim. van Schaik & Deaner 2003; van Schaik 2004), useimmat tutkijat ovat yhtä mieltä siitä, että sosiaalisuuden paineet ovat olleet yksi merkittävistä tekijöistä kognitiivisuuden evoluutiossa (esim. Cosmides 1989; Byrne & Whiten 1997; Tomasello & Call 1997; Dunbar 2000; Reader & Laland 2002; van Schaik 2004; Kamil 2004; Zuberbühler & Byrne 2006).

Kyky ennustaa toisen käyttäytymistä, pettää ja manipuloida toisia on oletettavasti erityisen hyödyllistä lajeille, joiden sosiaalinen elämä asettaa paineita tämänkaltaiselle manöveroinnille (Machiavellilaisen älykkyyden hypoteesi: Byrne & Whiten 1988; Whiten & Byrne 1997). "Machiavellilainen käyttäytyminen" vaatii kognitiivista kykyä ymmärtää toisen mielikuvia, eli se vaatii Mielen Teoriaa. Mielen teoria (Theory of Mind: Premack & Woodruff 1978) tarkoittaa kykyä muodostaa mielikuvia toisen mielikuvista, eli kykyä ymmärtää toisella olevan aikeita, tavoitteita, näkökulmia ja uskomuksia. Mielen Teorian omaava yksilö ymmärtää, että toisella on "mieli", joka on erillinen subjektin omasta "mielestä". Mielen Teoria muodostuu useista osa-alueista, jotka kehittyvät varhaislapsuuden aikana eri tahtiin, ja voivat siis esiintyä erillään toisistaan (esim. Dennett 1983; Perner 1991; Zahn-Waxler et al. 1992). Vähittäinen kehitys osoittaa, että Mielen Teoria ei ole kaksijakoinen monoliitti, vaan erilaisten kognitiivisten prosessien jatkumo. Sen vuoksi onkin mahdollista, että jotkin kädellislajit voisivat omata osia Mielen Teoriasta, vaikka ne eivät kykenisikään aikuisen ihmisen Mielen Teorian tasolle. Yleisesti on havaittu, että apinat (engl. monkeys) kykenevät mm. muodostamaan abstraktioita sosiaalisesta ympäristöstään ja ovat erittäin tehokkaita oppimaan monitasoisia suhdhierarkioita, mutta ne eivät abstrahoi toisen yksilön mieltä (Cheney & Seyfarth 1990). Sen sijaan ihmisapinat (engl. apes) kykenevät ainakin joihinkin Mielen Teorian osa-alueisiin, eli omaavat jonkintasoisen kyvyn ymmärtää, että

toisella on mieli, joka on omasta itsestä erillinen entiteetti (Tomasello et al. 2003 a,b; Call 2003; katso myös Povinelli & Bering 2002; Povinelli & Vonk 2003, 2004).

Jos ihmisapinoilla on ainakin osittainen Mielen Teoria, mihin ne sitä käyttävät? Sosiaalisen älykkyyden ilmenemismuotoja on tutkittu vähemmän, kuin niiden vaatimien kognitiivisten kykyjen olemassaoloa. Tutkittaessa sosiaalisen älykkyyden ilmenemismuotoja, tutkimme ensisijaisesti strategisen käyttäytymisen funktioita (ja sitä kautta kyseisten käyttäytymisilmiöiden vaikutusta kelpoisuuteen). Toisaalta, on yhtä tärkeää ymmärtää, millaiset kognitiiviset prosessit ovat sosiaalisen käyttäytymisen taustalla. Simpanssit, älykkäinä ja erityisen sosiaalisina ihmisapinoina ovat erinomainen tutkimuskohde molemmille edellä mainituille lähestymistavoille. Tässä väitöskirjassa olen yhdistänyt funktionaalisen ja mekanistisen lähestymistavan tutkiessani simpanssien sosiaalisen älykkyyden ilmenemismuotoja. Olen lähestynyt aihetta tutkimalla simpanssien konfliktinratkaisua.

### **Konfliktinratkaisu**

Kilpailu rajallisista resursseista on sosiaalisen elämän väistämätön seuraus. Kilpailu aiheuttaa ryhmän yksilöiden välille ristiriitoja, jotka saattavat eskaloitua aggressiivisiksi konflikteiksi. Aggressiiviset konfliktit käyvät kalliiksi: konflikteihin liittyy energian hukka, haavoittumisen riski, tarkkaavaisuuden alenemisesta seuraava kasvava saalistetuksi joutumisen riski, sekä ryhmän sisäisten suhteiden vahingoittuminen (mikä puolestaan johtaa etuisuuksien, kuten liittolaisten tarjoaman avun menetykseen). Ilman eskaloitumiseen estäviä ja riidan aiheuttamien vahinkojen korjaavia mekanismeja ryhmä on vaarassa hajota, mikä olisi haitallista kaikille ryhmän jäsenille (Aureli & de Waal 2000). Näin ollen konfliktinratkaisun mekanismeja odotetaan esiintyvän sosiaalisilla lajeilla, joilla on jäsenien väliset yksilöityneet suhteet, joilla ryhmän sisäinen kilpailu aiheuttaa ristiriitoja, ja joilla aggressio vahingoittaa ryhmän sisäisiä suhteita (Aureli et al. 2002; Schaffner et al. 2005). Oletuksen mukaisesti konfliktinratkaisu on yleistä nämä ehdot täyttävillä lajeilla, kuten lähes kaikilla kädellisillä, kesyvuohilla,

delfiineillä ja täplähyeenoilla (Schino 1998; Hofer & East 2000; Samuels & Flaherty 2000; Aureli et al. 2002; Wahaj & Holekamp 2003).

Konfliktinratkaisu voi tapahtua konfliktin osapuolten välisenä ystävällisyyden osoituksena pian aggression jälkeen. Tätä käyttäytymisilmiötä kutsutaan osuvasti sovitteluksi tai sovinnonteoksi (de Waal & van Roosmalen 1979; Aureli & de Waal 2000). Myös muut ryhmän jäsenet voivat osallistua konfliktinratkaisuun, esimerkiksi toimimalla sovinnonteon välittäjinä tai osoittamalla ystävällistä käyttäytymistä opponenteja kohtaan (de Waal 1982; Aureli & van Schaik 1991a; de Waal & Aureli 1996; Das et al 1998). Konfliktinratkaisun ilmeneminen ja sen tavat riippuvat osapuolten välisen suhteen laadusta. Ryhmän yksilöiden välisten suhteiden laatu vaihtelee sen mukaan, miten paljon ja millaista hyötyä suhteesta on molemmille osapuolille. Konfliktin vahingoitettua suhdetta sen laatu määrittelee korjaamistarpeen; mitä arvokkaampi suhde on sen osapuolille, sitä akuutimmin vahingot tulee paikata, jotta suhteen tarjoamat edut säilyisivät ennallaan (Kappeler & van Schaik 1992; Cords & Thurnheer 1993; Aureli et al. 1997; van Hooff 2001; Aureli et al. 2002; Watts 2006).

Ryhmässä olevien erilaisten suhteiden verkosto, konfliktien tilannekohtaisesti muuttuvat piirteet ja ryhmän muiden jäsenten käyttäytymisen vaikutus omiin strategioihin tekevät konflikteista monitahoisia tapahtumasarjoja, joiden hallinta on kognitiivisesti haastavaa. Jokainen ryhmän jäsen tekee omat "ratkaisunsa" (termillä ei tarkoiteta tietoista päätöksentekoprosessia) konfliktiin osallistumisen suhteen, arvioiden osallistumisen hyödyt ja sen tuomat haitat. Tämän monitahoisuuden vuoksi konfliktit ja niiden ratkaisu ovat konteksteja, joissa voidaan olettaa strategisen, joustavan ja "älykkään" käyttäytymisen olevan yksilölle edullista. Konfliktit voivat tarjota tietoa siitä, miten yksilöt käyttävät sosiaalista älykkyyttään, eli miten sosiaalinen älykkyys on hyödyllistä yksilölle (→ funktionaalinen lähestymistapa), sekä siitä, mitä kognitiivisia prosesseja liittyy konfliktinratkaisuun (→ mekanistinen lähestymistapa). Tämän vuoksi olen valinnut simpanssien konfliktinratkaisun tutkimukseni kohteeksi.

### **Simpanssi tutkimuslajina**

Simpanssit ovat erittäin älykkäitä ja sosiaalisia, ja siksi erinomainen mallilaji sosiaalisen älykkyyden tutkimiseen. Simpanssien on sanottu olevan melkoisia Machiavelleja; niiden sosiaalinen dynamiikka muokkautuu ekstensiivisen yhteistyön ja kilpailun ympärille, ja simpanssien sosiaalista elämää kuvataankin usein "politiikaksi" (de Waal 1982).

#### *Ekologia ja sosioekologia*

Simpanssi (*Pan troglodytes*) ja bonobo (*Pan paniscus*) ovat ihmisen lähimmät elävät sukulaiset. Yhteinen kantamuoto Pan ja Homo -sukujen välillä esiintyi 6-8 miljoona vuotta sitten (Groves 2001). Simpanssit elävät päiväntasaajan alueen Afrikassa. Simpansseista tiedetään esiintyvän neljä alalajia: *P.t. verus* Länsi-Afrikassa, *P.t. vellerosus* Nigeriassa, *P.t. troglodytes* Keski-Afrikassa, ja *P.t. schweinfurthii* keskisessä Itä-Afrikassa. Simpanssit elävät ryhmissä, joissa on useita aikuisia naaraita ja uroksia. Ryhmien kompositio noudattelee fissio-fuusio - dynamiikkaa; ryhmän kaikki jäsenet tuntevat toisensa, mutta ne liikkuvat reviirillään muutaman yksilön pikkuryhmissä, jotka eroavat ja taas sulautuvat toisiinsa joustavasti päivän aikana (Goodall 1986; Nishida 1990; Boesch 1991). Ryhmän kokonaisuusilömäärä vaihtelee tutkimusalueittain kahdenkymmenen ja yli sadan yksilön välillä. Naaraat pyrkivät parittelemaan promiskuiteettisesti, mitä urokset rajoittavat vartioimalla naarasta hedelmällisenä aikana (Tutin 1979; Watts 1998). Simpanssiurokset jäävät syntymälaumaansa kun taas naaraat emigroituvat toisiin ryhmiin aikuisuuden kynnyksellä (Pusey 1979, Boesch & Boesch-Achermann 2000).

Urokset muodostavat toistensa kanssa voimakkaita sidoksia, joita pidetään yllä ekstensiivisen sosiaalisuuden, sukimisen ja liittoutumien avulla (esim. van Hooff & van Schaik 1994; Watts 2002; rev. Mitani et al. 2002). Urokset tekevät toistensa kanssa tiukkaa yhteistyötä, jota tarvitaan metsästyksessä ja ryhmän puolustuksessa ulkopuolisia vastaan, mutta myös ryhmän sisäisissä kilpailutilanteissa. Urosten dominanssihierarkia on selkeästi määritelty ja lineaarinen, ja kilpailu dominanssiasemasta on ankaraa. Liittoutuneet partnerit auttavat toisiaan näissä urosten välisissä kamppailuissa, jotka ovat olennainen

osa dominanssitaisteluja (esim. de Waal 1982; Watts 2002). Johtajauros pysyy asemassaan vain liittolaistensa avulla, jotka tukensa vastineeksi nauttivat erivapauksia parittelussa ja ravinnon jakamisessa. Liittoumat ovat kuitenkin luonteeltaan hyvin opportunistisia, mikä tekee urosten keskinäisistä suhteista arvokkaita, mutta epästabiileja. Tätä vastoin naaraiden hierarkia on löyhemmin määritelty ja epälineaarinen (vaikkakin naaraiden dynamiikassa esiintyy populaatioiden välistä vaihtelua: Wrangham et al. 1992; Baker & Smuts 1994; Pusey et al. 1997; Wittig & Boesch 2003c). Niinpä naaraiden suhteet ovat vähemmän arvokkaita mutta stabiileja, etenkin sukulaisuussuhteen ulkopuolella. Kokonaisuudessaan simpanssien sosiaalista dynamiikkaa voidaan luonnehtia tasa-arvoiseksi (engl. "egalitarian", vastineena tiukan nepotistiselle ja/tai despoottiselle hierarkialle), mitä heijastaa toleranssi resurssien läheisyydessä, omistuksen kunnioittaminen ja kaksisuuntaisen aggression yleisyys (de Waal & Luttrell 1989, Sterck et al. 1997; Hemelrijk 1999; Thierry 2000).

#### *Kognitiiviset kyvyt*

Mielen Teoriaan liittyviä kognitiivisia kykyjä voidaan tutkia tarkasti rajatuilla kokeellisilla paradigmoilla. Monien tällaisten kokeiden perusteella näyttää siltä, että simpanssit omaavat joitakin Mielen Teorian vaatimia kykyjä, mutta eivät yllä täyteen Mielen Teoriaan. Simpanssit mm. tunnistavat itsensä peilistä, ymmärtävät mitä toinen yksilö näkee (ja ei näe), muistavat mitä toinen näki hetki sitten, ja osaavat käyttää tätä informaatiota hyväkseen. Nämä suoritukset viittaavat ymmärrykseen "itseystestä", sekä kykyyn ymmärtää toisen näkevän jotakin muuta, kuin mitä yksilö itse näkee (ja siten ne ymmärtävät 'näkemiseen' liittyvän psykologisen tilan). Simpanssit kykenevät myös ymmärtämään toisen toiminnan olevan tarkoituksellista/tavoitteellista, vaikkeivät ymmärräkään tavoitteellisuutta toimintaa edeltävänä psykologisena tilana. Simpanssit saattavat myös ymmärtää toisen tunnetiloja ja pyrkiä auttamaan tai lohduttamaan toista. Sen sijaan simpanssit eivät ymmärrä toisella olevan ajatuksia psyykkisinä, ulospäin näkymättöminä tiloina, eivätkä näin ollen ymmärrä myöskään sitä, että toisen ajatukset poikkeavat omista, tai että omat ajatukset voivat poiketa todellisuudesta. Kaiken kaikkiaan simpanssien kognitiivisista kyvyistä kiistellään

kiihkeästi ja jotkut tutkijat pitävät todistusaineistoa puutteellisena (esim. Povinelli & Vonk 2003, 2004; Heyes 1998). Eräs viimeaikainen suuntaus kiistassa on ollut pyrkimys irrottautua monoliittisestä kysymyksestä, onko simpansseilla Mielen Teoriaa, ja pyrkiä sen sijaan tarkastelemaan kognitiivisia kykyjä yksittäin. Tämän suuntauksen perusteella näyttäisi siltä, että simpanssien kognitiiviset kyvyt ovat lähellä kaksivuotiaan ihmislapsen kykyjä (Suddendorf and Whiten 2001; Tomasello et al. 2003a; Call and Tomasello 2005; Hare et al. 2006).

### **Tutkimuksen tavoitteet, suunta ja päätulokset.**

Tässä väitöskirjassa tarkastelin simpanssien kognitiivisia kykyjä ja niiden käyttöä konfliktinratkaisun kontekstissa. Kiinnitin erityisesti huomiota konfliktin jälkeisiin käyttäytymisilmiöihin ja tutkin niiden määrittäviä tekijöitä, funktioita ja mekanismeja.

**Ensimmäisessä osatyössä (luku 2)** tutkin sovinnonteon funktiota. Sovinnontekoa on tutkittu useilla kädellisillä, ja sen yleisesti hyväksytty funktio on konfliktin vahingoittaman suhteen korjaaminen (Aureli et al. 2002). Sovinnontekoon liittyy myös riskejä, ja siksi sovintoa tulisi yrittää vain silloin, kun sen tuomat hyödyt ovat suuremmat kuin yrityksen riskit. Näin ollen, sovinto on yleisintä silloin, kun osapuolten keskinäinen suhde on niille molemmille arvokas. Suhteen korjaamisen lisäksi sovinnonteko tarjoaa välittömiä etuja, kuten konfliktista aiheutuneen stressin ja muiden ryhmän jäsenten osoittaman vihamielisyyden vähentyminen. Nämä kaksi hyödyn tasoa yhdistyvät 'integroidussa hypoteesissa', joka esittää, että konfliktin aiheuttama stressi riippuu opponenttien suhteen laadusta (Aureli 1997; Aureli & Smucny 2000). Jos osapuolten välinen suhde on molemmille arvokas, aiheuttaa sen vahingoittuminen suurempaa stressiä, kuin jos suhde on vähemmän tärkeä. Koska sovinnonteko vähentää tätä stressiä, toimii stressi välittävänä emotionaalisenä mekanismina sovinnonteon prosessissa. Integroitua hypoteesia on testattu tähän mennessä vain makakeilla (Macaca spp.: Aureli 1997; Kutsukake and Castles 2001), joten osatyöni tarkoituksena oli testata sitä simpansseilla.

Tulokset tukivat integroitua hypoteesia. Sovinnon ilmeneminen riippui opponenttien suhteen laadusta (määritelty mitatun yhteensopivuuden ja estimoidun arvon kautta) (luvut 2,3). Myös stressitason nousu riippui opponenttien suhteen laadusta, ja stressi laski pian sovinnonteon jälkeen takaisin perustasolle (luku 4). Siten voidaan sanoa, että stressi toimii sovinnon mekanismina (luku 2) ja että sovinnon funktio on konfliktin vahingoittaman, tärkeän suhteen korjaaminen. Yllättävä havainto oli, että vain konfliktin altavastaajat kokivat konfliktin jälkeistä stressiä. Lisäksi suhteen laatu arvioituna vain altavastaajien näkökulmasta vaikutti sovinnon tekemiseen. Tämä viittaa siihen, että konfliktin aiheuttama vahinko suhteelle koetaan epäsymmetrisesti opponenttien välillä.

**Toinen osatyö (luku 3)** on yleiskatsaus konfliktin jälkeisiin tapahtumiin. Sekä konfliktin opponentit että muut ryhmän jäsenet tekevät valintoja konfliktiin ja sen jälkiselvittelyyn osallistumisesta. Osallistumisen mahdollisuudet ovat lukuisat, ja on epäselvää, mitkä tekijät vaikuttavat päätöksentekoon (vrt. Wittig and Boesch 2003b). Tutkimuksen tarkoitus oli selvittää, mitkä konfliktin piirteet vaikuttavat kunkin konfliktin jälkeisen käyttäytymisilmiön esiintymiseen. Lisäksi pyrin selvittämään, miten konfliktin jälkeiset tapahtumat vaikuttavat toisiinsa. Lisäksi määritin kunkin käyttäytymisilmiön tärkeimmät vaikuttajat. Osin tulokset tukivat aiempia tutkimuksia. Ensimmäinen päätulos oli se, että neljästä tutkitusta käyttäytymisilmiöstä lähes kaikki ilmenivät toisistaan riippumatta. Lisäksi havaitsin, että "lohdutukseksi" (consolation: de Waal & van Roosmalen 1979) nimetty ilmiö on yhteydessä jatkoaggression riskiin; jos opponentit olivat aikeissa jatkaa aggressiivista käyttäytymistään suunnaten aggression muihin ryhmän jäseniin, suuntasivat muut jäsenet opponentteja kohtaan suhteellisesti enemmän "lohdutusta". Viimeisimpänä päätuloksena mainittakoon ns. voittajavaikutus (eli voittamisen aiheuttaman tunteen vaikutus alttiuteen aloittaa lisää konflikteja) jatkettun aggression mekanismina. Voittaja- ja häviövaikutus konfliktin seurauksena tunnetaan monilla muilla eläinryhmillä, mutta kädellisillä niitä ei ole juurikaan tutkittu. Yleisemmällä tasolla tutkimus vahvisti käsitystä konfliktinratkaisun moniulotteisuudesta.

**Kolmas osatyö (luku 4)** keskittyi tarkastelemaan "lohdutusta". Lohdutuksella tarkoitetaan kolmannen, konfliktin ulkopuolisen osapuolen ystävällistä käyttäytymistä konfliktiin osallistujia kohtaan (de Waal & van Roosmalen 1979). Huolimatta merkityksellisestä termistä lohduttamisen funktiot ja mekanismit ovat jokseenkin tuntemattomat. Pitkälti tämä johtuu siitä, että useimmilta tutkituilta kädellislajeilta tämä ilmiö puuttuu; vain ihmisapinoiden tiedetään lohduttavan toisiaan (ihmisapinat: de Waal & van Roosmalen 1979; de Waal & Aureli 1996; Kutsukake & Castles 2004; Palagi et al. 2004, 2006; Mallavarapu et al. 2006; apinat: rev. Das 2000; Watts et al. 2000; ks. myös Call et al. 2002). Termin mukaisesti lohdutuksen oletetaan tarjoavan emotionaalista tukea vastaanottajalleen, eli sen tulisi vähentää vastaanottajan stressiä ja ahdistusta. Tämän lisäksi on ehdotettu, että lohdutus olisi korvaava ilmiö sovinnolle, jos sovinnonteko on liian riskialtista (Watts et al. 2000; Wittig & Boesch 2003a). Tässä tutkimuksessa ei löytynyt tukea kummallekaan näistä oletuksista. Lohdutus ei vähentänyt vastaanottavien opponenttien stressiä, eikä sen ilmenemisestä sovinnon korvaajana ollut näyttöä (luku 4, 3). Tulokset viittaavat siihen, että lohdutuksen funktio ei olekaan tarjota hyötyä sen saajalle, kuten on tähän mennessä oletettu, vaan mahdollisesti sen antajalle. Tulosteni perusteella ehdotin, että ilmiötä kutsuttaisiin neutraalilla termillä "kolmannen osapuolen ystävällisyys".

**Neljäs osatyö (luku 5)** jatkoi edellisen työn jäljillä, etsien lohduttamisen funktiota. Tutkin, voiko kolmannen osapuolen ystävällinen käytös tarjota hyötyä antajalle itselleen. Erityisesti tarkastelin mahdollisuutta, että ystävällinen käytös suojaa antajaansa opponenttien taholta tulevalta aggressiolta. Tämä "suojaushypoteesi" on esitetty aiemminkin kahdessa muodossa: a) se tarjoaa välittömän suojan antajalleen, mutta ei muille ryhmän jäsenille (Das 1998; Call et al. 2002) tai, että b) se suojaa antajaa aggressiolta välillisesti, vähentäen aggression leviämistä ryhmässä (Palagi et al. 2004). Kumpaakaan näistä hypoteesin muodoista ei ole testattu aiemmin. Tulokseni tukivat suojaushypoteesin ensimmäistä muotoa. Tutkimukseni on siis ensimmäinen, joka testasi ja löysi funktion "kolmannen osapuolen ystävällisyydelle". Ystävällisyys vähensi merkittävästi subjektiin, mutta ei muihin ryhmän jäseniin kohdistuvan

aggression riskiä, ja ystävällisyys kohdistettiin spesifisti niihin yksilöihin, joilla oli taipumus kohdistaa aggressiota muihin ryhmän jäseniin. Näin ollen voidaan sanoa, että oletettu lohduttaminen onkin itsekästä, itsesuojelullista toimintaa. Poikkeuksen tälle itsekkäälle ystävällisyydelle muodosti sukulaisten keskinäinen ystävällisyys. Erityisesti konfliktin altavastaajat saivat sukulaisiltaan ystävällistä huomiota, ja tämän ei voitu osoittaa johtuvan itsesuojelullisista tarkoituksesta (luku 4,5). Sukulaisten osoittaman ystävällisyyden funktiota ei tässä työssä löydetty.

**Viides osatyö (luku 6)** tarkasteli kolmannen osapuolen ystävällisyyden kognitiivisia mekanismeja. Erityisesti tarkastelin mahdollisuutta, että ystävällisyys pohjautuu empatiaan. On pitkään oletettu, että empatia, ja erityisesti kognitiivinen empatia, on tämän käyttäytymisilmiön kognitiivinen perusta. Teoriaa on tukenut se, että ihmisapinoiden uskotaan kykenevän kognitiivisesti empaattiseen vasteeseen kun taas apinoilta tämä kyky puuttuu. Koska kolmannen osapuolen ystävällisyys ei kuulu apinoiden repertuaariin, on esitetty sen olevan kognitiivisesti niille liian vaativaa. Työssä tarkastelen ensin empatiaa prosessina ja erittelen sen eri kognitiiviset tasot. Tutkiessani mahdollisuutta, että kolmannen osapuolen ystävällisyys pohjautuu kognitiiviseen empatiaan, erotan sukulaisten tarjoaman ystävällisyyden ja itsesuojelullisen ystävällisyyden toisistaan, koska niiden funktiot eroavat toisistaan (luku 3,4,5). Sukulaisten tiedetään oletusarvoisesti reagoivan herkemmin empaattisesti kuin ei-sukulaisten. Koska sukulaisten tarjoama konfliktinjälkeinen ystävällisyys ei luultavasti sisällä suoraa omaa etua, on mahdollista, että se pohjautuu empaattiseen vasteeseen. Mikäli sukulaisten tarjoama ystävällisyys on empaattista, on tärkeää määritellä empatian kognitiivinen taso. On luultavaa, että simpanssit eivät kykene arvioimaan toisen emotionaalista tilaa täysin irrallaan omasta emotionaalisesta vasteestaan. Esitän, että simpanssien empatia on mahdollisesti tasoltaan ns. pseudoegoistista empatiaa, jossa sekoittuvat oman itsen ja toisen lohduttaminen. On myös mahdollista, että niiden empaattinen vaste toimii primitiivisemmin ns. emotionaalisen tartunnan kautta, jossa subjekti ei ymmärrä kognitiivisesti toisen tunteita vaan kopioi suoraan toisen tunnetilan itseensä. Tutkimukseni ei kykene testaamaan, kumpi näistä mahdollisuuksista on

todennäköisempi. Esitän kuitenkin, että täysin eriytynyt kognitiivisen empatian taso, jossa omat ja toisen tunteet ovat täydellisesti eriytettyinä, ei ole simpanssille todennäköinen. Tämä taso vaatii kognitiivisia kykyjä, joita tämänhetkisen tietämyksen valossa simpanssit eivät omaa.

Suurin osa tästä empaattisena pidetystä "lohduttamisesta" ei kuitenkaan näytä pohjautuvan empatiaan. Näin ehdotan, koska käyttäytymiselle on osoitettavissa suora oma hyöty, kun taas empatiaan pohjaava käytös (so. *sympatia*) on lähtökohtaisesti toisen hyödyn huomioonottavaa. Toiseksi, riskialttiin kontekstin arviointi ei kognitiivisesti vaadi toisen tunteiden ymmärtämistä, vaan aggressioriskin arviointiin riittää tilanneriippuvan riskin ja oman suhdehistorian opponentin kanssa huomioon ottaminen. Tämä tutkimus on ensimmäinen, joka asettaa kyseenalaiseksi vuosikymmenien uskomuksen simpanssien empaattisesta lohduttamisesta. Tutkimukseni varoittaa tekemästä ontoille oletuksille perustuvia yleistyksiä ja peräänkuuluttaa empatian kognitiotasojen arvioinnin tärkeyttä eläinten kognitiivisuuden tutkimisessa.

### **Yhteenveto**

Tutkimukseni on osoittanut, että simpanssien konfliktinhallinta ja -ratkaisu on monitahoinen järjestelmä. Ryhmän yksilöillä on lukuisia vaihtoehtoja tarjolla konfliktin osallistumisen suhteen, joista jokaisella on omat seurauksensa. Käyttäytymisstrategioiden valintaan vaikuttavat monet tekijät samanaikaisesti. Rajasin tutkimukseni neljään konfliktinjälkeiseen ilmiöön: sovinnontekoon, "lohduttamiseen", jatkettuun aggressioon sekä kolmannen osapuolen aggressioon. Nämä neljä konfliktin jälkeistä käyttäytymisvaihtoehtoa ovat suurimmaksi osaksi toisistaan riippumattomia, ja kuten siis voidaan olettaa, niiden ilmenemistä määräävät tekijät eroavat toisistaan. Aggressiivisten interaktioiden osalta tutkin vain niiden ilmenemistä. Tältä osin merkittävimmäksi tulokseksi nousi voittajavaikutuksen tärkeys jatkettun aggression mekanismina. Sovinnonteko seuraa muilla kädellisillä todettuja periaatteita: sen mekanismina toimii konfliktin jälkeinen stressi, ja sen funktio on korjata konfliktin vahingoittama suhde ennalleen. "Lohdutuksena" tunnettu käyttäytymisilmiö oli työni suurin yllättäjä. Vastoin ennakkokäsityksiä se ei näyttänyt tarjoavan

oletettuja etuja vastaanottajilleen, vaan sitä vastoin toi suoran ja merkittävän edun tekijöilleen. Nimesin ilmiön kolmannen osapuolen tarjoamaksi ystävällisyydeksi, ja ehdotin sille itsesuojelun funktiota. Mahdollinen poikkeus tähän on sukulaisten välinen ystävällisyys, jolle ei löydetty funktiota. Sukulaisystävällisyys saattaa pohjata empaattiseen vasteeseen, kuten on aiemmin ehdotettu kaikelle "lohduttamiselle". Yleisesti ottaen tunteiden osoitettiin olevan merkittäviä mekanismeja käyttäytymisessä. Emootioiden rooli käyttäytymisen välittäjinä on suhteellisen uusi tutkimusalue, joka ansaitsee lisää tutkimuksellista huomiota (Aureli 1997; Aureli & Smucny 2000; Aureli & Schaffner 2002a,b). Lisäksi työssäni esitin joitakin fysiologisia tunnetilojen korrelaatteja, ja pohdin käyttäytymisen kognitiivisia mekanismeja. Emootioiden, fysiologian ja kognition vuorovaikutusten tutkiminen on tärkeätä ymmärtääksemme käyttäytymisilmiöiden mekanismeja paremmin. Lisäksi eläinten käyttäytymistä tutkittaessa olisi toivottavaa yhdistää mekanistinen taso funktionaaliseen tutkimukseen. Tutkimukseni kaltainen läpileikkausmenetelmä toivottavasti lisääntyy tulevaisuuden käyttäytymistutkimuksessa.

## REFERENCES

- Adang OMJ, Wensing JAB, and van Hooff JARAM. 1987. The Arnhem Zoo colony of chimpanzees. *Int. Zoo Yb.* 26, 236-248.
- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227-267.
- Amsterdam BK 1972. Mirror self-image reactions before age of two. *Dev. Psychobiol.* 5, 297-305.
- Anderson JR 1984. Monkeys with mirrors: Some questions for primate psychology. *Int. J. Primatol.* 5, 81-98.
- Anderson JR and Matsuzawa T 2006. Yawning: an opening to empathy? In: *Cognitive Development in Chimpanzees*. Matsuzawa T, Tomonaga M and Tanaka M (Eds). Springer-Verlag, Tokyo. Pp. 233-245.
- Anderson JR, Myowa-Yamakoshi M, Matsuzawa T 2004. Contagious yawning in chimpanzees. *Proc. R. Soc. Lond. B.* (suppl.) 271, S468-470.
- Andrews K 2005. Chimpanzee Theory of Mind: looking in all the wrong places? *Mind & Language* 20, 521-536.
- Apperly IA, Samson D and Humphreys GW 2005. Domain specificity and theory of mind: evaluating neuropsychological evidence. *Trends Cogn. Sci.* 9, 572-577.
- Arnold K and Whiten A 2001. Post-conflict behaviour of wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Behaviour* 138, 649-690.
- Arnold K and Barton RA 2001. Postconflict behaviour on spectacled leaf-monkeys (*Trachypithecus obscurus*) II Contact with third parties. *Int. J. Prim.* 22, 267-286.
- Arnold K and Whiten A. 2003. Grooming interactions among the chimpanzees of the Budongo Forest, Uganda: tests of five explanatory models. *Behaviour* 140, 519-552.
- Aureli F 1992. Post-conflict behaviour among wild long-tailed macaques (*Macaca fascicularis*). *Behav. Ecol. Sociobiol.* 31, 329-337.
- Aureli F 1997. Post-conflict anxiety in nonhuman primates: the mediating role of emotion in conflict resolution. *Aggr. Behav.*, 23, 315-328.
- Aureli F and van Schaik CP 1991a. Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*): I. The social events. *Ethology* 89, 89-100.
- Aureli F and van Schaik CP 1991b. Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*): II. Coping with the uncertainty. *Ethology* 89, 101-114.
- Aureli F and de Waal FBM 1997. Inhibition in social behaviour in chimpanzees under high-density conditions. *Am. J. Primatol.* 41, 213-228.
- Aureli F and de Waal FBM 2000. (eds.) *Natural Conflict Resolution*. University of California Press, Berkeley. 409 p.

- Aureli F and Smucny D 2000. The role of emotion in conflict and conflict resolution. In: Aureli F, de Waal FBM, editors. *Natural Conflict Resolution*. University of California Press. Pp. 199-224.
- Aureli F and Schaffner CM 2002a. Empathy as a special case of emotional mediation of social behavior. *Behav. Brain Sci.* 25, 23-24.
- Aureli F and Schaffner CM 2002b. Relationship assessment through emotional mediation. *Behaviour* 139, 393-420.
- Aureli F, van Schaik CP, and van Hooff JARAM. 1989. Functional aspects of reconciliation among captive long-tailed macaques (*Macaca fascicularis*). *Am. J. Primatol.* 19: 39-51.
- Aureli F, Cozzolino R, Cordishi C, and Scucchi S 1992. Kin-oriented redirection among Japanese macaques: an expression of a revenge system? *Anim. Behav.* 44, 283-291.
- Aureli F, Das M, Verleur D, and van Hooff JARAM. 1994. Post-conflict social interactions among Barbary macaques (*Macaca sylvanus*). *Int. J. Primatol.* 15, 471-485.
- Aureli F, Das M, and Veenema HC 1997. Differential kinship effect on reconciliation in three species of macaques (*Macaca fascicularis*, *M. fuscata*, *M. sylvanus*). *J. Comp. Psychol.* 111, 91-99.
- Aureli F, Preston S and de Waal FBM 1999. Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): A pilot study. *J. Comp. Psychol.* 113, 59-65.
- Aureli F, Cords M and van Schaik CP 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Anim. Behav.* 64, 325-343.
- Baker KC and Smuts BB 1994. Social relationships of female chimpanzees: Diversity between captive social groups. In *Chimpanzee Cultures*. RW Wrangham, WC McGrew, FBM de Waal and P Heltne (eds.) Harvard University Press.
- Baker KC and Aureli F. 1997. Behavioural indicators of anxiety: an empirical test in chimpanzees. *Behaviour* 134, 1031-1050.
- Bard KA. 2002. Developmental processes in empathy. *Behav. Brain Sci.* 25, 25-26.
- Baron-Cohen S, Leslie AM and Frith U 1985. Does the autistic child have a 'theory of mind'? *Cognition* 21, 37-46
- Barr R and Hayne H. 1999. Developmental changes in imitation from television during infancy. *Child Dev.* 70, 1067-1081.
- Barrett L, Henzi P, and Dunbar RIM. 2003. Primate cognition: from 'what now?' to 'what if?' *Trends Cogn. Sci.* 7, 494-497.
- Barton RA and Dunbar RIM 1997. Evolution of the social brain. In *Machiavellian intelligence II. Extensions and evaluations*. A Whiten and RW Byrne (eds.). Cambridge University Press, Cambridge. Pp. 240-261
- Barton RA and Harvey PH 2000. Mosaic evolution of brain structure in mammals. *Nature* 405, 1055-1058.
- Batson C.D., Fultz J. and Schoenrade P.A. 1987. Distress and empathy: two qualitatively distinct vicarious emotions with different motivational consequences. *J. Personal.* 55, 19-39.
- Bergman TJ, Beehner JC, Cheney DL and Seyfarth RM 2003. Hierarchical classification by rank and kinship in baboons. *Science* 302, 1234-1236.

- Berenthal BI and Fischer KW 1978. The development of self-recognition in the infant. *Dev. Psychol.* 14, 291-311.
- Bland JM and Altman DG 1995. Calculating correlation coefficients with repeated measures observations: part 1- correlation within subjects. *Br. Med. J.* 310, 446.
- Boehm C 1997. Egalitarian behaviour and the evolution of political intelligence. In *Machiavellian intelligence II. Extensions and evaluations*. A. Whiten and R.W. Byrne (eds). Cambridge University Press, Cambridge. Pp. 341-364.
- Boesch C 1991. The effect of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117, 220-242.
- Boesch C 1996. Social grouping in Tai chimpanzees. In: *Great Ape Societies*. WC McGrew, T Nishida, and L. Marchant (eds.). Cambridge University Press, Cambridge. Pp. 101-113.
- Boesch C and Boesch-Achermann H 2000. *The chimpanzees of the Tai Forest. Behavioural ecology and evolution*. Oxford University Press, Oxford.
- Bräuer J, Call J and Tomasello M. 2005. All great ape species follow gaze to distant locations and around barriers. *J Comp Psychol.* 119, 145-154
- Brosnan SF, Schiff HC, and de Waal FBM. 2005. Tolerance for inequity may increase with social closeness in chimpanzees. *Proc. R. Soc. B.* 272, 253-258.
- Brownell CA and Carriger MS 1990. Changes in cooperation and self-other differentiation during the second year. *Child Dev.* 57, 275-286.
- Brownell CA, Zerwas S and Balaram G 2002. Peers, cooperative play and the development of empathy in children. *Behav. Brain Sci.* 28-29.
- Byrne RW 1995. *The thinking ape: evolutionary origins of intelligence*. Oxford: Oxford university press.
- Byrne RW 2002. Social and technical forms of primate intelligence. In: *Tree of origin. What primate behavior can tell us about human social evolution*. FBM de Waal (ed.). Harvard University Press. Pp 145-172.
- Byrne RW and Whiten A 1988. *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans*. Oxford Clarendon Press.
- Byrne RW and Whiten A 1990. Tactical deception in primates: The 1990 database. *Primate Rep.* 27, 1-101.
- Byrne RW and Whiten A 1992. Cognitive evolution in primates: Evidence from tactical deception. *Man* 27, 609-627.
- Byrne RW and Whiten A 1997. Machiavellian intelligence. In: *Machiavellian intelligence II: Extensions and evaluations*. Whiten A and Byrne RW (eds). Cambridge University Press. Pp. 1-23
- 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: 515-523.
- Call J 2003. Beyond learning fixed rules and social cues: abstraction in the social arena. *Phil. Trans. R. Soc. Lond. B.* 358, 1189-1196.
- Call J and Tomasello M. 1999. A nonverbal false-belief task: the performance of children and great apes. *Child Dev.* 70, 381-395.
- Call J and Tomasello M 2005. What chimpanzees know about seeing revisited: an explanation of a third kind. In: *Joint attention: Communication and other*

- minds*. N. Eilan, C Hoerl, T. McCormack and J Roessler (eds.). Oxford University Press, Oxford.
- Call J, Hare BA and Tomasello M. 1998. Chimpanzee gaze in an object-choice task. *Anim. Cogn.* 1, 89-99.
- Call J, Aureli F and de Waal FBM 1999. Reconciliation patterns among stumptailed macaques: a multivariate approach. *Anim. Behav.* 58:165-172.
- Call J, Aureli F. and de Waal FBM 2002. Post-conflict third party affiliation in stumptailed macaques. *Anim. Behav.*, 63, 209-216.
- Call J, Hare B, Carpenter M and Tomasello M 2004. 'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action. *Dev. Sci.* 7, 488-498.
- Casperd JM. 1997. The evolution of reconciliation within the primate order. [Ph.D. dissertation]. University of Liverpool.
- Castles DL 2000. Triadic versus dyadic resolutions: Cognitive implications. In: *Natural conflict resolution*. F Aureli and FBM de Waal. (eds.) Berkeley, California, University of California Press. Pp. 289-291.
- Castles DL and Whiten A 1998a. Post-conflict behaviour of wild olive baboons. I Reconciliation, redirection and consolation. *Ethology*, 104, 126-147.
- Castles DL and Whiten A 1998b. Post-conflict behaviour of wild olive baboons. II. Stress and self-directed behaviour. *Ethology* 104, 148-160.
- Chapais B, Savard L and Gauthier C 2001. Kin selection and the distribution of altruism in relation to degree of kinship in Japanese macaques (*Macaca fuscata*). *Behav. Ecol. Sociobiol.* 49, 493-502.
- Chase ID, Bartolomeo C, and Dugatkin LA 1994. Aggressive interactions and inter-contest interval: how long do winners keep winning? *Anim. Behav.* 48, 393-400.
- Cheney DL and Seyfarth RM 1989. Further aggression and reconciliation among vervet monkeys, *Cercopithecus aethiops*. *Behaviour* 110, 258-275.
- Cheney DL and Seyfarth RM 1990. *How monkeys see the world*. Chicago University Press.
- Cheney DL and Seyfarth RM. 1991. Truth and deception in animal communication. In: *Cognitive ethology: the minds of other animals*. CA Ristau (ed.). Erlbaum.
- Clayton NS and Dickinson A 1998. Episodic-like memory during cache recovery by scrub jays. *Nature* 395, 272-274.
- Clutton-Brock TH and Harvey PH 1980. Primates, brains and ecology. *J. Zool. Lond.* 190, 309-323.
- Commons ML and Wolfsont CA 2002. A complete theory of empathy must consider stage changes. *Behav. Brain Sci.* 25, 30-31.
- Commons ML, Trudeau EJ, Stein SA, Richards FA and Krause SR 1998. The existence of developmental stages as shown by the hierarchical complexity of tasks. *Dev. Rev.* 8, 237-278.
- Cooper MA, Bernstein IS, Hemelrijk CK 2005. Reconciliation and relationship quality in Assamese macaques (*Macaca assamensis*). *Am. J. Primatol.* 65: 269-282.
- Cords M 1992. Post-conflict reunions and reconciliation in long-tailed macaques. *Anim. Behav.* 44, 57-61.
- Cords M. 1993. On operationally defining reconciliation. *Am. J. Primatol.* 29, 255-267.

- Cords M 1997. Friendships, alliances, reciprocity, and repair. In: *Machiavellian intelligence II: Extensions and evaluations*. Whiten A and Byrne RW (eds). Cambridge University Press. Pp. 24-49.
- Cords M and Killen M. 1998. Conflict resolution in human and nonhuman primates. In: *Piaget, Evolution and Development*. Langer J, Killen M (eds). Mahwah, New Jersey: L. Erlbaum. Pp.193-219.
- Cords M and Aureli F. 2000. Reconciliation and relationship qualities. In: Aureli F, de Waal FBM, editors. *Natural Conflict Resolution*. University of California Press. Pp. 177-198.
- Cords M and Thurnheer S. 1993. Reconciliation with valuable partners by long-tailed macaques. *Ethology* 93, 315-325.
- Côté SD and Festa-Bianchet M 2001. Offspring sex ratio in relation to maternal age and social rank in mountain goats (*Oreamnos americanos*). *Behav. Ecol. Sociobiol.* 49, 260-265.
- Dally JM, Emery NJ, and Clayton NS 2006. Food-caching Western scrub-jays keep track of who was watching when. *Science* 312, 1662-1665.
- Das M 1998. *Conflict management and social stress in long-tailed macaques*. PhD diss. Utrecht University
- Das M 2000. Conflict management via third parties. In: *Natural conflict resolution*. Aureli F and de Waal FBM (eds). University of California Press. Pp. 263-280.
- Das M, Penke Zs and van Hooff JARAM 1997. Affiliation between aggressors and third parties following conflicts in long-tailed macaques (*Macaca fascicularis*). *Int. J. Primatol.* 18, 157-179.
- Das M, Penke Z, and van Hooff JARAM 1998. Postconflict affiliation and stress-related behavior of long-tailed macaque aggressors. *Int. J. Primatol.* 19, 53-71.
- Deacon TW 1990. Fallacies of progression in theories of brain-size evolution. *Int. J. Primatol.* 11, 193-236.
- Deaner RO, Nunn CL and van Schaik C 2000. Comparative tests of primate cognition: different scaling methods produce different results. *Brain. Behav. Evol.* 55, 44-52.
- Deaner RO, Barton RA and van Schaik CP 2003. Primate Brains and life histories: renewing the connection. In *Primate Life Histories and Socioecology*. PM Kappeler and ME Pereira (eds). Chicago University Press, Chicago. Pp. 233-265.
- Deaner RO, van Schaik CP and Johnson V 2006. Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evol. Psychol.* 4, 149-196.
- Dennett D 1983. Intentional systems in cognitive ethology: The "Panglossian paradigm" defended. *Behav. Brain Sci.* 6, 343-390.
- Dunbar RIM 1988. *Primate Social Systems*. Billing & Sons Ltd, Worcester.
- Dunbar RIM 1991 Functional significance of social grooming in primates. *Folia Primatol.* 57, 121-131.
- Dunbar RIM 1992. Neocortex size as a constraint on group size in primates. *J. Human Evol.* 20, 469-493.
- Dunbar RIM. 1993. The functional significance of social grooming in primates. *Folia Primatol.* 57: 121-131.
- Dunbar RIM 1995. Neocortex size and group size in primates: A test of the hypothesis. *J Human Evol.* 28, 287-296.

- Dunbar RIM 2000. Causal reasoning, mental rehearsal and the evolution of primate cognition. In: *The evolution in cognition*. CM Heyes and L Huber (eds). Massachusetts Institute of Technology Press, Cambridge, Massachusetts. Pp. 205-220.
- Eisenberg N and Strayer J (eds.) 1987. *Empathy and its development*. Cambridge University Press.
- Eisenberg N, Lennon R and Roth K 1983. Prosocial development: a longitudinal study. *Dev. Psychol.* 19, 846-855.
- Feshbach ND and Roe K. 1968. Empathy in six- and seven-year-olds. *Child Dev.* 39, 133-145.
- Flack JC and de Waal FBM 2000. Any animal whatever. Darwinian building blocks of morality in monkeys and apes. *J. Consc. St.* 7, 1-29.
- Flavell JH 2000. Development of children's knowledge about the mental world. *Int. J. Dev.* 24, 15-23.
- Flavell JH 2004. Theory-of-Mind development: retrospect and prospect. *Merrill-Palmer Quart.* 50, 274-290.
- Fuentes A, Malone N, Sanz C, Matheson M and Vaughan L 2002. Conflict and post-conflict behavior in a small group of chimpanzees. *Primates* 43, 223-235.
- Gallup GG Jr. 1970. Chimpanzee self-recognition. *Science* 167, 86-87.
- Gallup GG Jr. 1998. Self-awareness and the evolution of social intelligence. *Behav. Proc.* 42, 239-247.
- Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of behaviour*. Cambridge, MA: Belknap Press of Harvard University Press.
- Groves C. 2001. *Primate taxonomy*. Washington DC: Smithsonian Inst Pr. 350 p.
- Hatfield E, Cacioppo JT and Rapson RL. 1993. Emotional contagion. *Curr. Dir. Psychol. Sci.* 2, 96-99.
- Hare B. 2001. Can competitive paradigms increase the validity of social cognitive experiments on primates? *Anim. Cogn.* 4, 269-280.
- Hare B and Tomasello M 2004. Chimpanzees are more skillful in competitive tasks than in cooperative cognitive tasks. *Anim. Behav.* 68, 571-581.
- Hare B and Tomasello M 2005. Human-like social skills in dogs? *Trends Cogn. Sci.* 9, 439-444.
- Hare B, Call J, Agnetta B, and Tomasello M 2000. Chimpanzees know what conspecifics do and do not see. *Anim. Behav.* 59, 771-785.
- Hare B, Call J and Tomasello M. 2001. Do chimpanzees know what conspecifics know? *Anim. Behav.* 61, 139-151.
- Hare B, Call J and Tomasello M 2006. Chimpanzees deceive human competitor by hiding. *Cognition* 101, 495-514.
- Harvey PH and Krebs JR 1990. Comparing brains. *Science* 249, 140-146.
- Hatfield E, Cacioppo JT and Rapson RL 1993. Emotional contagion. *Curr. Dir. Psychol. Sci.* 2, 96-99.
- Hauser MD 1997. Minding the behaviour of deception. In: *Machiavellian intelligence II. Extensions and evaluations*. A Whiten and RW Byrne (eds.) Cambridge University Press, Cambridge. Pp. 112-143.
- Hauser MD 2000. Homologies for numerical memory span? *Trends Cogn. Sci.* 4, 127-128.
- Hauser MD 2005. Our chimpanzee mind. *Nature* 437, 60-63.

- Hemelrijk CK 1999. An individual-oriented model of the emergence of despotic and egalitarian societies. *Proc R. Soc. Lond. B.* 266, 361-369.
- Heyes CM 1993. Anecdotes, training, trapping and triangulating: do animals attribute mental states? *Anim. Behav.* 46, 177-188.
- Heyes CM 1995. Self-recognition in primates: further reflections create a hall of mirrors. *Anim. Behav.* 51, 1533-1541.
- Heyes CM 1998. Theory of mind in nonhuman primates. *Behav. Brain Sci.* 21, 101-148.
- Heyes CM and Huber L (eds.) 2000. *The evolution of cognition*. MIT Press, Cambridge, MA.
- Hirata S and Matsuzawa T 2001. Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). *Anim. Cogn.* 4, 285-2295.
- Hofer H and East ML 2000. Conflict management in female-dominated spotted hyenas. In: *Natural Conflict Resolution*. Aureli F, de Waal FBM. (eds.) University of California Press, Berkeley. Pp. 232-234.
- Hoffman ML 1975. Developmental synthesis of affect and cognition and its implications for altruistic motivation. *Dev. Psychol.* 11, 607-622.
- Hoffman ML 2000. *Empathy and moral development. Implications for caring and justice*. Cambridge University Press.
- Hoffman ML 2002. How automatic and representational is empathy, and why. *Behav. Brain Sci.* 25, 38-39.
- van Hooff JARAM. 1973a. The Arnhem Zoo chimpanzee consortium: An attempt to create an ecologically and socially acceptable habitat. *Int. Zoo Yb* 13. p 195-203.
- van Hooff JARAM. 1973b. A structural analysis of the social behaviour of a semi-captive group of chimpanzees. *European Monogr. Soc. Psychol.* 4. p 75-162.
- van Hooff JARAM 2001. Conflict, reconciliation and negotiation in non-human primates: the value of long-term relationships. In: *Economics in Nature. Social dilemmas, mate choice and biological markets*. R Noë, JARAM van Hooff and P Hammerstein (eds.). Cambridge University Press, Cambridge. Pp. 67-90.
- van Hooff JARAM and van Schaik CP 1994. Male bonds: affiliative relationships among nonhuman primate males. *Behaviour* 130, 309-337.
- Hsu Y and Wolf L 1999. The winner and loser effect: integrating multiple experiences. *Anim. Behav.* 57:903-910.
- Hsu Y, Earley RL and Wolf L 2006. Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. *Biol. Rev.* 81, 33-74.
- Humphrey NK 1976. The social function of intellect. In: *Growing points in ethology*. PPG Bateson and RA Hinde (eds.). Cambridge, Cambridge University press. Pp. 303-307.
- Itakura S 2001. The level of self-knowledge in nonhuman primates: from the perspective of comparative cognitive science. In: *Primate origins of human cognition and behaviour*. T. Matsuzawa (ed.). Springer-Verlag Tokyo. Pp.313-329.
- Inoue-Nakamura N 2001. Mirror self recognition in Primates: an ontogenetic and a phylogenetic approach. In: *Primate origins of human cognition and behaviour*. T. Matsuzawa (ed.). Springer-Verlag Tokyo. Pp. 297-312.

- Jensen K, Hare B, Call J, and Tomasello M 2006. What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proc. R. Soc. Lond. B.* 273, 1013-1021.
- Johnson DB 1982. Altruistic behaviour and the development of self in infants. *Merrill-Palmer Quart.* 28, 379-388.
- Johnson JA, Cheek JM and Smither R 1983. The structure of empathy. *J. Pers. Soc. Psychol.* 45, 1299-1312.
- Jolly A 1966. Lemur social behaviour and primate intelligence. *Science* 152, 501-506.
- Judge PG 1991. Dyadic and triadic reconciliation in pigtail macaques (*Macaca nemestrina*). *Am. J. Primatol.* 23, 225-237.
- Kamil AC 2004. Sociality and the evolution of intelligence. *Trends Cogn. Sci.* 8, 195-197.
- Kappeler PM and van Schaik CP 1992. Methodological and evolutionary aspects of reconciliation among primates. *Ethology* 92, 51-69.
- Kavaliers M, Choleris E, and Colwell DD 2001. Brief exposure to female odors 'emboldens' male mice by reducing predator-induced behavioral and hormonal responses. *Horm. Behav.* 40, 497-509.
- Kazem AJN and Aureli F 2005. Redirection of aggression: multiparty signaling within a network? In: *Animal Communication Networks*. P.K McGregor (ed.). Cambridge University Press. Pp. 191-218.
- Kitchen A, Denton D and Brent L 1996. Self-recognition and abstraction in the common chimpanzee studied with distorting mirrors. *Proc Natl Acad Sci, USA.* 93, 7405-7408.
- Klinkova E, Hodges JK, Fuhrmann K, de Jong T and Heistermann M. 2005. Male dominance rank, female mate choice and male mating and reproductive success in captive chimpanzees. *Int. J. Primatol.* 26, 357-384.
- Koski SE and Sterck EHM 2007. Triadic post-conflict affiliation in captive chimpanzees: does consolation console? *Anim. Behav.* 73, 133-142.
- Koski SE, Koops K and Sterck EHM 2007. Reconciliation, relationship quality and post-conflict anxiety: testing the Integrated Hypothesis in captive chimpanzees. *Am. J. Primatol.* 69, 158-172.
- Koyama NF 2000. Conflict prevention before feeding. In: Aureli F and de Waal FBM, editors. *Natural Conflict Resolution*, University of California Press, Berkeley. Pp. 130-132
- Koyama NF 2001. The long-term effects of reconciliation in Japanese macaques (*Macaca fuscata*). *Ethology*, 107, 975-987.
- Koyama N, Caws C and Aureli F 2006. Interchange of grooming and agonistic support in chimpanzees. *Int. J. Primatol.* 27, 1293-1309.
- Krebs JR and Dawkins R 1984. Animal signals: Mind reading and manipulation. In *Behavioural ecology: An evolutionary approach*. JR Krebs and NB Davies (eds.). Blackwell Scientific Publ., Oxford. Pp. 380-401.
- Kudo H and Dunbar RIM. 2001. Neocortex size and social network size in primates. *Anim. Behav.* 62, 711-722.
- Kummer H 1978. On the value of social relationships to non-human primates: a heuristic scheme. *Soc. Sci. Inform.* 17, 687-705.
- Kutsukake, N. 2003. Assessing relationship quality and social anxiety among wild chimpanzees using self-directed behaviour. *Behaviour*, 140, 1153-1171.

- Kutsukake N and Castles DL 2001. Reconciliation and variation in post-conflict stress in Japanese macaques (*Macaca fuscata fuscata*): testing the intergrated hypothesis. *Anim. Cogn.* 4, 259-268.
- Kutsukake N and Castles DL 2004. Reconciliation and post-conflict third-part affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates* 45, 157-165.
- Leavens DA and Hopkins WD 1998. Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Dev. Psychol.* 34, 813-822.
- Leavens DA, Aureli F, Hopkins WD and Hyatt CW 2001. Effects of cognitive challenge on self-directed behaviors by chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* 55, 1-14.
- Leavens DA, Hopkins WD and Thomas RK 2004 Referential communication by chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 118, 48-57.
- Leavens Da, Russell JL and Hopkins WD 2005. Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Dev.* 76, 291-306.
- Lefebvre L, Whittle A, Lascaris E and Finkelstein A 2003. Feeding innovations and forebrain size in birds. *Anim. Behav.* 53, 549-560.
- Lehmann HE 1979. Yawning: a homeostatic reflex and its psychological significance. *Bull. Meninger Clin.* 43, 123-136.
- Leslie AM. 1987. Pretense and representation in infancy: The origins of "theory of mind". *Psychol. Rev.* 94, 412-426.
- Lewis M 2002. Empathy requires the development of self. *Brain Behav. Sci.* 25, 42.
- Lukas D, Reynolds V, Boesch C and Vigilant, L 2005. To what extent does living in groups mean living with kin? *Molec. Ecol.*, 14, 2181-2196.
- McEwen BS and Sapolsky RM 1995. Stress and cognitive function. *Curr. Opinion Neurobiol.* 5, 205-216.
- Maestriperi G, Schino G, Aureli F and Troisi A. 1992. A modest proposal: Displacement activities as indicators of emotions in primates. *Anim. Behav.* 44, 967-979.
- Mallavarapu S, Stoinski TS, Bloomsmith MA, and Maple TL. 2006. Postconflict behavior in captive Western Lowland gorillas. *Am. J. Primatol.* 68, 789-801.
- Marino L 2004. Dolphin cognition. *Curr. Biol.* 14, R910-911.
- Matheson M 1999. Social contact following severe aggression in Rhesus macaques (*Macaca mulatta*): A new test of the consolation hypothesis. *Int. J. Primatol.* 20, 961-974.
- Matsuzawa T 2001. *Primate origins of human cognition and behaviour*. Springer-Verlag Tokyo, Tokyo.
- Matsuzawa T, Tomonaga M and Tanaka M (eds.) 2006. *Cognitive Development in Chimpanzees*. Springer-Verlag, Tokyo. Pp. 233-245.
- Miklosi A, Topal J, and Csanyi V 2004. Comparative social cognition: what can dogs teach us? *Anim. Behav.* 67, 995-1004.
- Milton K. 1988 Foraging behaviour and the evolution of intellect in monkeys, apes and humans. In: *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans*. Byrne RW and A Whiten (eds.) Oxford, Clarendon Press. Pp. 285-305.

- Mitani, JC, Watts, DP, Pepper, JW and Merriwether, DA 2002. Demographic and social constraints on male chimpanzee behaviour. *Anim. Behav.* 64, 727-737.
- Nishida T. 1979. The social structure of chimpanzees of the Mahale Mountains. In: *The Great Apes*. Hamburg DA, McCown ER, (eds). Menlo Park CA. Benjamin/Cummings. Pp 73-122.
- Nishida T. (ed.) 1990. *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*. University of Tokyo Press, Tokyo.
- Nishida T, Takasaki H and Takahata Y 1990. Demography and reproductive profiles. In *The chimpanzees of the Mahale Mountains: Sexual and life history strategies*. T Nishida (ed.). University of Tokyo Press, Tokyo. Pp. 63-97.
- Noë R and Sluijter AA 1995. Which adult male savanna baboons form coalitions? *Int J Primatol* 16, 77-105.
- Noë R., de Waal FBM and van Hooff JARAM 1980. Types of dominance on a chimpanzee colony. *Folia Primatol.* 34, 90-110.
- Noldus Information Technology, Wageningen, the Netherlands, 2003.
- O'Connell S.M. 1995. Empathy in chimpanzees: Evidence for Theory of Mind? *Primates*, 36, 397-410.
- Onishi K. and Baillargeon R. 2005. Do 15-month-old infants understand false beliefs? *Science* 306, 255-258.
- Palagi E 2006. Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): Implications for natural social systems and interindividual relationships. *Am. J. Phys. Anthropol.* 129, 418-426.
- Palagi E, Cordoni G, and Borgonini Tarli S 2006. Possible roles of consolation in captive chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* 129, 105-111.
- Palagi E, Paoli T, and Borgonini Tarli S. 2004. Reconciliation and consolation in captive bonobos (*Pan paniscus*). *Am. J. Primatol.* 62, 15-30.
- Parr LA. 2001. Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglodytes*). *Anim. Cogn.* 4, 223-229.
- Parr LA 2002. Understanding other's emotions: From affective resonance to empathic action. *Behav. Brain Sci.* 25, 44-45.
- Pepper JW, Mitani JC and Watts DP. 1999. General gregariousness and specific social preferences among wild chimpanzees. *Int. J. Primatol.* 20, 613-32.
- Perner J 1991. *Understanding the representational mind*. Cambridge, Massachusetts, MIT press.
- Perner J and Lang B 1999. Development of theory of mind and executive control. *Trends Cogn Sci.* 3, 337-344.
- Petit O and Thierry B 1994. Reconciliation in a group of guinea baboons. In: *Current primatology. Vol 2: Social development, learning and behavior*. JJ Roeder, B Thierry, JR Anderson, N Herrenschildt (eds.). Strasbourg University of Louis Pasteur. Pp. 137-145.
- Petit O and Thierry B 2000. Do impartial interventions in conflicts occur in monkeys and apes? In: *Natural conflict resolution*. Aureli F and de Waal FBM (eds). University of California Press. Pp. 267-269
- Platek SM, Critton SR, Myers TE and Gallup GG 2003. Contagious yawning: the role of self-awareness and mental state attribution. *Cogn. Brain Res.* 17, 223-237.
- Plotnik JM, FBM de Waal and Reiss D. 2006. Self-recognition in an Asian elephant. *Proc. Natl. Acad. Sci.* 103, 17053-17057.

- Povinelli D 1987. Monkeys, apes, mirrors and minds: The evolution of self-awareness in primates. *Human Evol.* 2, 493-509.
- Povinelli DJ and Eddy TJ 1996. What young chimpanzees know about seeing. *Monogr. Soc. Res. Child. Dev.* 61 (247).
- Povinelli DJ and Bering JM 2002. The mentality of apes revisited. *Curr. Dir. Psychol. Sci.* 11, 115-119.
- Povinelli, DJ and Vonk J 2003. Chimpanzee minds: suspiciously human? *Trends Cogn. Sci.* 7, 157-160.
- Povinelli DJ and Vonk J 2004. We don't need a microscope to explore the chimpanzee's mind. *Mind & Language*, 19, 1-28.
- Povinelli DJ, Nelson KE, and Boysen ST. 1990. Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). *J Comp Psychol.* 104, 203-210.
- Povinelli DJ, Nelson KE and Boysen ST 1992. Comprehension of role reversal in chimpanzees: Evidence of empathy? *Anim. Behav.* 43, 633-640.
- Premack D and Woodruff G 1978. Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* 1, 515-526.
- Premack R 1988. 'Does the chimpanzee have a theory of mind?' revisited. In: *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans*. RW Byrne and A Whiten (eds.) Oxford Clarendon Press. Pp. 160-179.
- Preston S and de Waal FBM 2002a. Empathy: its ultimate and proximate bases. *Behav. Brain Sci.* 25, 1-72.
- Preston and de Waal 2002b. The communication of emotions and the possibility of empathy in animals. In: *Altruism and Altruistic love: science, philosophy and religion in dialogue*. Post SG, Underwood LG, Schloss JP, and Harbut WB (eds.) New York: Oxford Univ Press. 2002. Pp. 284-308.
- Preuschoft S and van Schaik CP. 2000. Dominance and communication. Conflict management in various social settings. In: Aureli F, de Waal FBM, editors. *Natural Conflict Resolution*, University of California Press, Berkeley. Pp. 77-105.
- Preuschoft S, Wang X, Aureli F, and de Waal FBM 2002. Reconciliation in captive chimpanzees: a re-evaluation with controlled methods. *Int. J. Primatol.* 23, 29-50.
- Pusey A. 1979. Intercommunity transfer of chimpanzees in Gombe National Park. In: *The Great Apes* D. Hamburg & E. McCown (eds.), pp. 456-479. Menlo Park, California, B Cummings.
- Pusey A, Williams, J, and Goodall J 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277, 828-831.
- Reader SM and Laland KN 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl. Acad. Sci.* 99, 4436-4441.
- Ruffman T and Perner J 2005. Do infants really understand false belief? *Trends Cogn. Sci.* 9, 462-463.
- Rochat P 2002. Various kinds of empathy as revealed by the developing child, not the monkey's brain. *Behav. Brain Sci.* 25, 45-46.
- Sagi A and Hoffman ML 1976. Empathic distress in newborns. *Dev. Psychol.* 12, 175-176.

- Samuels A and Flaherty C 2000. Peaceful conflict resolution in the sea? In: *Natural Conflict Resolution*. Aureli F, de Waal FBM (eds). University of California Press, Berkeley. Pp. 229-231.
- Schaffer CM and Caine NG. 2000. The peacefulness in cooperatively breeding primates. In: *Natural Conflict Resolution*. Aureli F, de Waal FBM (eds). University of California Press, Berkeley. Pp. 155-169.
- Schaffner CM and Aureli F 2004. Problems and solutions for conflict management in fission-fusion societies. *Folia Primatol.* 75(S), 146.
- Schaffner CM, Aureli F, and Caine NG 2005. Following the rules: why small groups of tamarins do not reconcile conflicts. *Folia Primatol.* 76, 67-76.
- van Schaik CP and Deaner RO 2003. Life history and cognitive evolution in primates. In: *Animal Social Complexity: Intelligence, culture and individualized societies*. FBM de Waal and Tyack PL (eds.). Harvard University Press. Pp. 5-25.
- van Schaik CP 2004. *Among orangutangs: red apes and the rise of human culture*. Cambridge, The Belknap Press of Harvard University Press.
- Schino G. 1998. Reconciliation in domestic goats. *Behaviour* 135, 343-356.
- Schino G. 2000. Beyond the primates – expanding the reconciliation horizon. In: Aureli F, de Waal FBM, editors. *Natural Conflict Resolution*, University of California Press, Berkeley. p. 225-242.
- Schino G, Geminiani S, Rosati L and Aureli F 2004. Behavioral and emotional response of Japanese macaque (*Macaca fuscata*) mothers after their offspring receive an aggression. *J. Comp. Psychol.* 118, 340-346.
- Schino G, Perretta G, Taglioni AM, Monaco V and Troisi A 1996. Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety*, 2, 186-191.
- Schucchi S, Cordishi C, Aureli F, Cozzolino R 1988. The use of redirection in a captive group of Japanese monkeys. *Primates* 29, 229-236.
- Seyfarth RM. 1981. Do monkeys rank each other? *Behav Brain Sci* 4, 447-448
- Shettleworth SJ 1998. *Cognition, Evolution, and Behaviour*. Oxford University Press, Oxford.
- Siegel S, Castellan NJ. 1988. *Nonparametric statistics for the behavioural sciences*. 2<sup>nd</sup> ed. McGraw-Hill, New York.
- Silk JB. 1996. Why do primates reconcile? *Evol. Anthropol.* 5: 39-42.
- Silk JB, Alberts SC, and Altmann J. 2003 Social bonds of female baboons enhance infant survival. *Science* 302, 1231-1234.
- Silk JB. 2002. Using the 'F'-word in primatology. *Behaviour* 139, 421-446.
- Silk JB, Cheney DL and Seyfarth RM 1999. The structure of social relationships among female savannah baboons in Moremi Reserve, Botswana. *Behaviour* 136, 679-703.
- Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS, Lambeth SP, Mascaró J, and Schapiro S. 2005. Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437, 1357-1359.
- Skipper RA, Jr. 2004. Perspectives on the animal mind. *Biol. Phil.* 19, 483-487.
- Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW and Struhsaker TT. (eds.) 1987. *Primate Societies*. University of Chicago Press, Chicago.
- Sterck EHM, Watts DP and van Schaik CP 1997. The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.* 41, 291-309.

- Sterelny K 2000. Primate worlds. In *The evolution in cognition*. CM Heyes and L Huber. (eds.) MIT Press, Cambridge, MA. Pp.143-162.
- Stone V and Gerrans P 2006. Does the normal brain have a theory of mind? *Trends Cogn. Sci.* 10, 3-4.
- Striedter GF 2006. Précis of principles of brain evolution. *Behav. Brain Sci.* 29, 1-36.
- Suddendorf T 1998. Simpler for evolution: Secondary representation in apes, children and ancestors. *Behav. Brain Sci.* 21, 131.
- Suddendorf T and Whiten A 2001. Mental evolution and development: evidence for secondary representation in children, great apes and other animals. *Psychol. Bull.* 127, 629-650.
- Suddendorf T 1999. The rise of the metamind. In *The Descent of mind: Psychological perspectives on hominid evolution*. MC Corballis and SEG Lea (eds.). Oxford University Press, London. Pp. 218-260.
- Sugiyama Y and Koman J 1979. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* 20, 513-524.
- Takeshita H, van Hooff JARAM. 2001. Tool use by chimpanzees (*Pan troglodytes*) of the Arnhem Zoo community. In: *Primate Origins of Human Cognition and Behaviour*. Matsuzawa T (editor. Springer, Tokyo.
- Thierry, B. 1985. Patterns of agonistic interactions in three species of macaque (*Macaca mulatta*, *M. fascicularis* and *M. tonkeana*). *Aggress. Behav.* 11, 223-233.
- Thierry B 2000. Covariation of conflict management patterns across Macaque species. In: *Natural Conflict Resolution*. Aureli F. and de Waal FBM (eds.) University of California Press, Berkeley. Pp. 106-128.
- Tomasello M 1999. *The cultural origins of human cognition*. Harvard University Press, MA.
- Tomasello M 2000. Two hypotheses about primate cognition. In *The evolution in cognition*. CM Heyes and L Huber (eds). Massachusetts Institute of Technology Press, Cambridge, Massachusetts. Pp. 165-183.
- Tomasello M and Call J. 1997. *Primate Cognition*. Oxford: Oxford University Press.
- Tomasello M and Rakoczy H 2003. What makes human cognition unique? From individual to shared collective intentionality. *Mind & Language* 18, 121-147.
- Tomasello M, Call J, and Hare B 1998. Five primate species follow visual gaze of conspecifics. *Anim. Behav.* 55, 1063-1069.
- Tomasello M, Hare B and Agnetta B. 1999. Chimpanzee follow gaze direction geometrically. *Anim. Behav.* 58, 769-777.
- Tomasello M, Call J and Hare B 2003a Chimpanzees versus humans: it's not that simple. *Trends Cogn. Sci.* 7, 239-240.
- Tomasello M, Call, J and Hare B 2003b. Chimpanzees understand psychological states – the question is which ones and to what extent. *Trends Cogn. Sci* 7, 153-156.
- Trainor BC, Bird IM and Marler CA 2004. Opposing hormonal mechanisms of aggression revealed through short-lived testosterone manipulations and multiple winning experiences. *Horm. Behav.* 45, 115-121.
- Veenema HC, Das M, Aureli F. 1994. Methodological improvements for the study of reconciliation. *Behav. Process.* 31, 29-38.

- Verbeek, P. & de Waal, F.B.M. 1997. Postconflict behaviour of captive brown capuchins in the presence and absence of attractive food. *Int. J. Primatol.* 18, 703-726
- Vigilant L, Hofreiter M, Siedel H and Boesch C 2001. Paternity and relatedness in wild chimpanzee communities. *Proc. Natl. Acad. Sci.* 98, 12890-12895.
- de Vries H. 1993. The rowwise correlation between two proximity matrices and the partial rowwise correlation. *Psychometrika* 58: 53-69.
- de Waal FBM. 1982. *Chimpanzee Politics: Power and Sex among Apes*. New York: Harper & Row.
- de Waal FBM 1984. Sex differences in the formation of coalitions among chimpanzees. *Ethol. Sociobiol.* 5, 239-255.
- de Waal FBM. 1986. The integration of dominance and social bonding in primates. *Q. Rev. Biol.* 61: 459-479.
- de Waal FBM 1987. Dynamics of social relationships. In: *Primate Societies*. Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW and Struhsaker TT. (eds.) University of Chicago Press, Chicago. Pp. 421-429.
- de Waal FBM 1989. *Peacemaking among primates*. Cambridge: Harvard University Press.
- de Waal FBM. 1992a. Appeasement, celebration, and food sharing in the two *Pan* species. In: *Current Topics in Primatology*. Nishida T, McGrew WC, Marler PR, Pickford M, de Waal FBM, (eds). Tokyo, University of Tokyo Press. Pp. 37-50.
- de Waal FBM. 1992b. Coalitions as part of reciprocal relations in the Arnhem chimpanzee colony. In: *Coalitions and Alliances in Humans and Other Mammals*. Harcourt AH, de Waal FBM. (eds.) Oxford University Press, New York. Pp. 233-257.
- de Waal FBM. 1993. Reconciliation among primates: a review of empirical evidence and unresolved issues. In: Mason WA and Mendoza SP, editors. *Primate Social Conflict*, State Univ. of New York Press. p.111-144.
- de Waal FBM 1996a. *Good Natured: The origins of right and wrong in humans and other animals*. Cambridge, MA, Harvard University Press.
- de Waal FBM 1996b. Conflict as negotiation. In: *Great Ape Societies*. WC McGrew, L Marchand and T Nishida (eds.). Cambridge University Press, Cambridge. Pp 159-172.
- de Waal FBM 2003. Social syntax: The if-then structure of social problem solving. In *Animal Social Complexity. Intelligence, Culture and Individualized societies*. FBM de Waal and PL Tyack (eds). Harvard University Press, Cambridge MA. Pp. 230-248.
- de Waal FBM 2005. *Our Inner Ape. A leading primatologist explains why we are who we are*. Penguin books Ltd. NY.
- de Waal FBM and Roosmalen A 1979. Reconciliation and consolation among chimpanzees. *Behav. Ecol. Sociobiol.* 5, 55-66.
- de Waal FBM and van Hooff JARAM 1981. Side-directed communication and agonistic interactions in chimpanzees. *Behaviour* 77, 164-198.
- de Waal FBM, Yoshihara D. 1983. Reconciliation and redirected affection in rhesus monkeys. *Behaviour* 85: 224-241.

- de Waal FBM and Luttrell LM 1989. Toward a comparative socioecology of the genus *Macaca*: different dominance styles in rhesus and stump-tail macaques. *Am. J. Primatol.* 19, 83-109.
- de Waal FBM and Aureli F 1996. Consolation, reconciliation and a possible difference between macaques and chimpanzees. In: *Reaching into thought. The minds of great apes*. AE Russon, KA Bard and ST Parker (eds.) Cambridge, Cambridge Univ Press. Pp. 80-110.
- de Waal FBM, and Aureli F 1997. Conflict resolution and distress alleviation in monkeys and apes. In: *The Integrative Neurobiology of Affiliation*. Carter CS, Kirkpatrick B, Lenderhendler I (eds). New York, Annals of New York Academy of Sciences. p. 317-328.
- de Waal FBM, Dindo M, Freeman CA and Hall MJ 2005. The monkey in the mirror: hardly a stranger. *Proc. Natl. Acad. Sci* 102, 11140-11147.
- Wahaj SA and Holekamp KE. 2003. Conflict resolution in the spotted hyena. In *Animal Social Complexity. Intelligence, Culture and Individualized societies*. FBM de Waal and PL Tyack (eds). Harvard University Press, Cambridge MA. Pp. 249-259.
- Walker-Leonard J. 1979. A strategy approach to the study of primate dominance behaviour. *Behav. Process.* 4, 155-172.
- Warneken F and Tomasello M 2006. Altruistic helping in human infants and young chimpanzees. *Science* 311, 1301-1303.
- Watts DP. 1995a. Post-conflict social events in wild mountain gorillas (Mammalia, Hominoidae). I. Social interactions between opponents. *Ethology* 100, 139-157.
- Watts DP. 1995b. Post-conflict social events in wild mountain gorillas (Mammalia, Hominoidae). II Redirection, side direction and consolation. *Ethology* 100, 158-174.
- Watts DP. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour* 139, 343-370.
- Watts DP 2006. Conflict resolution in chimpanzees and the valuable-relationships hypothesis. *Int. J. Primatol.* 27, 1337-1364.
- Watts DP, Colmenares F and Arnold K 2000. Redirection, consolation and male policing. How targets of aggression interact with bystanders. In: *Natural conflict resolution*. Aureli F and de Waal FBM (eds). University of California Press
- Wellman HM, Cross D, and Watson J 2001. Meta-analysis of Theory-of-mind development: the truth about false belief. *Child Dev.* 72, 655-684.
- Whiten A 1996. Imitation, pretence and mindreading: Secondary representation in comparative primatology and developmental psychology? In: *Reaching into thought. The minds of great apes*. A.E. Russon, K.A. Bard & S.T. Parker (eds.). Cambridge, Cambridge Univ. Press. Pp. 300-324.
- Whiten A 1997. The Machiavellian mindreader. In *Machiavellian intelligence II. Extensions and evaluations*. A Whiten and RW Byrne Cambridge University Press, Cambridge. pp 145-173.
- Whiten A and Byrne RW 1988. Tactical deception in primates. *Behav. Brain Sci.* 11, 233-273.
- Whiten A and Byrne RW 1997. *Machiavellian intelligence II. Extensions and evaluations*. Cambridge University Press, Cambridge.
- Whitten PL, Stavisky R, Aureli F and Russell E 1998. Response of fecal cortisol to stress in captive chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* 44, 57-69.

- Wimmer H and Perner J 1993. Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition* 13, 103-128.
- Wittig RM and Boesch C. 2003a. The choice of post-conflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour* 140, 1257-1559.
- Wittig RM and Boesch C. 2003b. "Decision-making" in conflicts of wild chimpanzees (*Pan troglodytes*): an extension of the Relational Model. *Behav. Ecol. Sociobiol.* 54, 491-504.
- Wittig RM and Boesch C 2003c. Food competition and linear hierarchy among female chimpanzees of the Tai National Park. *Int. J. Primatol.* 24, 847-867.
- Wittig RM and Boesch C. 2005. How to repair relationships – reconciliation in wild chimpanzees. *Ethology* 111, 736-763.
- Wrangham RW. 1986. Ecology and social relationships in two species of chimpanzee. In: *Ecological aspects of social evolution: Birds and mammals*. Rubenstein DI and Wrangham RW (eds). Princeton University Press, Princeton, N.J. Pp. 352-378.
- Wrangham RW, Clark AP and Isabirye-Basuta G 1992. Female social relationships and social organisation of Kibale Forest chimpanzees. In *Topics in primatology. Vol 1: Human origins*. T Nishida, WC McGrew, PR Marler, M Pickford, FBM de Waal (eds). University of Tokyo Press, Tokyo. Pp 81-98.
- Zahn-Waxler C., Radke-Yarrow M. and King R.A. 1979. Child rearing and children's prosocial initiations toward victims of distress. *Child Devel.* 50, 319-330.
- Zahn-Waxler C, Radke-Yarrow M, Wagner E and Chapman M. 1992. Development of concern for others. *Dev. Psychol.* 28, 126-136.
- Zuberbühler K and Byrne RW. 2006. Social cognition. *Curr. Biol.* 16, R786-790.

## Acknowledgements

There are so many people to whom I am thankful for their contribution -- personal and/or scientific -- to this thesis. First and foremost, I thank Liesbeth Sterck and Jan van Hooff for inviting me for to study those incredible creatures that chimpanzees are, and for being by my side every step of the way. Jan, thank you for your wisdom, guidance, commentaries and great support. I thank Johan Bolhuis for being my second promoter; many thanks for great discussions and encouragement throughout the years. Liesbeth, you have been my main supervisor, and as that the best I could ever hope for. You have unfalteringly supported me no matter what, and never failed to give me whatever personal or scientific backing up I needed. You have taught me a lot and been a good friend as well. Extra thanks for not letting me give it up when things got hairy, and also for the super hard work you put in at the end phase of my thesis work! It has been stimulating, fun, educating, warm, and caring –thank you for it all! I'm happy to know our collaboration continues.

The last couple of years were greatly enriched by the new ensemble BeCSoS, and I want to thank all the people who gathered together to discuss behaviour and cognition of social systems (and anything that loosely fitted the topic); Liesbeth, Maaïke, Valerie, Zjef, Han, Henk, Rita, Brigitte, Margot, Marusha, Jorg, and Karlijn. I think our gang is a great support network both scientifically and mentally! Of course, everybody at the department (past and present) deserves huge thanks for the gezelligheid and for being great colleagues: Johan, Liesbeth, Simon, Matt, Ulf, Han, Thijs, Marie-José, Zjef, Ido, Eleni, Frouke, Serge, Maaïke, Miranda, Karlijn, Annet, Brigitte, Sharon, Margot, Jorg, Marusha, Renee and Bert. Han, I'm enormously grateful for your help. Your efforts for my and my students' benefit never cease to humble me. Boys – cheers for the fun & beers! Maaïke, Brigitte and Sharon, thanks for your friendship! The new kids on the block—Jorg, Marusha and Margot—it's great that we overlapped and got to hang out. And all of you together: it has been good, thanks very much.

Thanks and a big hand to Liesbeth, Jan and Kat for translating my Summary to Dutch and to Femke Bulten at B&V for making my beautiful cover.

A major part of my work was done at the Burger's Zoo. I am deeply grateful that I was allowed to conduct my research there. Everybody at the zoo provided me an excellent working place, and I thank each and every staff member for that! A few people deserve extra thanks: Wineke, thanks for always being willing to help out, to provide info or whatever it was that I asked from you. All the keepers, Jackie, Maurice, Tjerk, Herjo, Inge, Koen, and the rest: thank you so much. The chimps don't know how great people they have taking care of them! You always were good company and great people to work with. Thanks also for teaching me the chimps, even when it seemed to take forever ☺. Tjerk and Maurice, my boys, extra hugs for being such great friends! You guys kept me going even on hard days. And Tjerk, you were there for me also when things got tough... Thanks so much!!

This work would not have been possible without my students: Maurice, Kat, Evelien, Marlies, Catharine, Olaf, Ron, Laura, Manuel, Rick, Margot, Mariken, Alice, Jurgen, Erica, Saskia, Hanneke, and Marjolein. Thank you all for the hard work and commitment. Marlies and Cath, you both stepped in when I needed you the most. Thanks girls, you really saved my day!

Which takes me to friends and how important they all have been to my sanity. To you communally: Thank You. Annet, Cath, Margot, Tjerk – you guys belong to

this list as well. Marijn and Victor, thanks for being there for me in my Arnhem times, and sorry for making you worry much too often! Martin, thanks for keeping me up when I desperately needed that. Valerie, Kristo, Lotta, and Job: you guys are hugely important to me, thanks for being such great friends!! Lotta, I'm so happy that we have re-established our friendship after a wee break. Kristo—little did I know that we are to become such good friends... after the many years we've known each other only now we truly know each other. Thanks Luv, for it all!

Friends in Finland have remained vitally important. I won't go naming the entire biology-circle there, as you guys are numerous. Let's just say that every time I meet a part of that bunch, it feels like I never left. That's quite something. Extra special thanks go to Minttu, Anu, Miiu, Sara, Paa, Saara, Marianne, Jon, Laura H., Sally, Inari, Jukka P., Paavo, Jano – I'm truly amazed how friendships can take so much distance without being damaged at all! Miiu and Minttu, you both have been my super darling friends for a long time, and I love you very dearly. Johanna, you have been there practically forever. It's been too long since we hung out and I miss you so much. And then, in no particular order: Atte, Laura V., Sanni, Kikka -- what can I say? You're my best friends, thru thick and thin. You all mean more than anything to me... thank you for your love, support, warmth, crazy fun, honesty, and the trust that no matter what, you are in my life. I love you all. Kikka, an extra special one for you. No 'thanks' can ever cover it all and I'm left speechless. You know how much you mean to me.

Family, the backbone of one's life, deserves my biggest thanks for being the safe harbor at all times. Marjatta, kiitos elämänmittaisesta tuestasi ja kaveruudestasi. Pekka, on hienoa olla paitsi siskontyttösi, myös ystäväsi! Riitta ja Heidi, lempparitäti ja -serkku, kiitos ystävydestänne! Thanks to my Dutch family, Kat, Irma, Melissa, Roelof and Maja. Anything they say about in-laws is so not true!! Thanks for being a great extension to my family bonds. And then, Kat, my partner, thank you for Everything. For you have given it to me; endless love, support, understanding, unfaltering belief in me even when I lost it myself, all the fun. Perhaps most importantly, you have given me hope. With hope comes freedom, with freedom comes happiness. With that happiness I am looking forward to all the expeditions future has in store for us! Thank you for the best years of my life –yet!

Isä, kirjani on omistettu sinulle, sillä kaikesta antamastasi ehkä hienointa on opettamasi arvostus kirjoja, kirjallisuutta ja lukemista kohtaan. Ilman sitä en olisi nyt tässä. Ja sitten, äiti, jälleen sanat loppuvat. Miten voi kiittää ihan kaikesta? Elämänmittaisesta rajattomasta tuesta, ymmärryksestä ja rakkaudesta, mitä ilman en olisi minä, enkä tässä tänään. Kiitos.

## **Curriculum Vitae**

I, Sonja Elena Koski, was born on the 14<sup>th</sup> of December 1973 in Helsinki, Finland. I spent my first school years in Hämeenlinna, a small town with plenty of forest around. I moved back to Helsinki to attend Kallio High School (1989-1992), which taught performing arts in addition to the regular Finnish curriculum. When at the graduation I received an award for 'a biology enthusiast', I realised that rather than becoming a dancer, I would become a biologist. I then started my biology studies in Helsinki University (1993), initially as a student of animal physiology, with ecology and molecular biology as minors. During my undergraduate years I enjoyed various field courses and jobs of, for instance, catching voles and lemmings, radio-tracking stoats, and measuring tree saplings. In my studies I wanted to combine behaviour and physiology, which led me to my first research project in Leiden University in 1997. I spent eight months in Leiden under the supervision of Carel ten Cate and Mechteld Ballintijn studying the effects of testosterone on Collared doves' vocalizations. During those months I heard about monkey research in Indonesia, and soon I found myself packing up for a rainforest. In 1998-1999 I spent ten unforgettable months in Sumatra studying Thomas langurs' vocalizations, and stayed afterwards in Utrecht for another half a year. The project became my MSc research, being supervised by Serge Wich and Liesbeth Sterck. Little did I know then that the group in Utrecht was to become my future home!

Being now permanently hooked by behavioural research and primates, I changed my major from physiology to ecology, and obtained my MSc degree (with plenty of extra studies on genetics, biochemistry and physiology) at Helsinki University in November 2000. In April 2002 I returned to Utrecht to study chimpanzee cognition, and since then I have been observing, wondering and marvelling chimpanzees. This thesis is the result of these years.

Next, I will continue studying chimpanzees aiming to unravel the mysteries of their individual personalities.