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Post-conflict Strategies Among Captive Chimpanzees and Bonobos: Testing the Role of Dyadic and Triadic Affiliations

Dissertação apresentada à Universidade de Coimbra para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Evolução e Biologia Humanas, realizada sob a orientação científica da Professora Doutora Eugénia Cunha (Universidade de Coimbra), da Professora Doutora Cláudia Sousa (Universidade Nova de Lisboa) e do Professor Doutor Josep Call (Instituto Max Planck de Antropologia Evolutiva).

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Abstract:

Life in groups often entails conflicts. It is believed that natural selection acted on gregarious animals to evolve mechanisms for conflict resolution. Most of these have been demonstrated in the living primates (prossimians, monkeys and apes). Since its first study over 30 years ago, conflict resolution strategies have developed into more complex descriptions with several possible proximate functions proposed. What we now know as post-conflict strategies include reconciliation (dyadic post-conflict affiliation) and consolation (triadic post-conflict affiliation). Presently there are four hypotheses on the proximal functions of reconciliation (the valuable-relationship hypothesis, the uncertainty-reduction hypothesis, the integrated hypothesis and the benign intent hypothesis) and three hypotheses regarding also the proximal functions of consolation (the consolation hypothesis, the self-protection hypothesis and the relationship repair hypothesis). Most predictions regarding triadic affiliations seem to fall on two categories: victim-oriented motivations for affiliation (or empathic) and bystander-oriented motivations for affiliation (or selfish). Taking this perspective, an empathy-based integrated hypothesis of triadic affiliations is propose together with an alternative selfish-based integrated hypothesis of triadic affiliations for further studies. Both strategies have, on some degree, been demonstrated in the primate literature. For these predictions this research took chimpanzees and bonobos as its subjects. While chimpanzees have been well studied, bonobos remain largely unexplored. Triadic affiliations are a complex phenomenon and its various proximate functions have not been fully explored. A total of 102 PC-MC pairs were observed in the chimpanzees and 20 PC-MC pairs in the bonobos. Some of the results tested showed an inverse tendency contrary to the predictions made. The chimpanzees had a group CCT=22,3% and group TCT=53,3% while the bonobos had a group CCT=21,4% and group TCT=43,7%. Direct comparisons among chimpanzees and bonobos may provide a powerful method of testing phylogenetic hypotheses. Since we humans share so much with these African apes it is important to investigate what sets them apart, as a species, from each other and ultimately what sets us apart from them.

Keywords: *Pan troglodytes*; *Pan paniscus*; post-conflict behaviour; reconciliation; consolation.

Resumo:

Viver em grupos, muitas vezes, envolve, conflitos. Acredita-se que a selecção natural actuou em animais gregários de forma a que evoluíssem mecanismos para a resolução de conflitos. Muitos destes têm sido confirmados nos primatas actuais (prossímios, antropóides e grandes símios). Desde o seu primeiro estudo há mais de 30 anos, as estratégias de resolução de conflitos foram desenvolvendo descrições mais complexas com várias possíveis funções proximais propostas. O que presentemente conhecemos como estratégias pós-conflito, afiliações diádicas pós-conflito (reuniões entre dois oponentes) e afiliações triádicas pós-conflito (interacções amigáveis entre a vítima e um espectador). Actualmente, conhecem-se quatro hipóteses principais acerca da função proximal das afiliações diádicas (hipótese da relação valiosa, hipótese da redução de incerteza, hipótese integrada e a hipótese das intenções benignas) e três hipóteses principais das afiliações triádicas (hipótese da consolação, hipótese da auto-protecção, e a hipótese do restauro da relação). A maioria das previsões respeitando as afiliações triádicas aparentam enquadrar-se em duas categorias: motivações para afiliação orientadas para a vítima (ou afiliação empática), e motivações para afiliação orientadas para o espectador (ou afiliação egoísta). Utilizando esta perspectiva, uma organização teórica foi proposta de forma a testar futuramente, uma hipótese integrada empática e a hipótese integrada egoísta. Ambas as estratégias foram, a determinado nível, demonstradas na literatura primatológica. Para esta previsão este estudo teve como sujeitos chimpanzés e bonobos. Enquanto que os chimpanzés têm sido bastante estudados, os bonobos permanecem maioritariamente por explorar. As afiliações triádicas são um fenómeno complexo e as suas várias funções proximais não foram completamente examinadas. Alguns dos resultados obtidos mostraram-se contrários a previsões feitas. Um total de 102 pares de PC-MC foi obtido para os chimpanzés e 20 pares de PC-MC para os bonobos. Os chimpanzés exibiram um CCT grupal = 22,3% e um TCT grupal = 53,3% enquanto que os bonobos exibiram um CCT grupal = 21,4% e um TCT grupal = 43,7%. Comparações directas entre chimpanzés e bonobos podem promover um método vigoroso de teste de hipóteses filogenéticas. Uma vez que nós humanos partilhamos tanto com estes grandes símios africanos, é essencial averiguar o que os distingue, como espécie, uns dos outros e em último caso, o que nos distingue a nós deles.

Palavras chave: *Pan troglodytes*; *Pan paniscus*; comportamento pós-conflito; reconciliação, consolação.

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CHAPTER 1

Conflict Resolution: A Theoretical Framework

1. Introduction

The research on animal and human aggression has always had difficulty in ascertaining its causations first and foremost because aggression has no single etiology regardless of species considered, consequently, its research has had difficulty in producing an unitary concept (McKenna, 1983; Blanchard & Blanchard, 2003; Sousa & Casanova, 2006). In animals, aggression is considered part of a behavioral repertoire called agonistic behavior, a term first coined by Scott and Fredericson in 1951 during their research on mice and rats. Agonistic behaviors involve threat, aggression and submission (McGlone, 1986), as a result not all agonistic behavior inevitably involves aggression. Konrad Lorenz (1964) argued in his controversial book "*On Aggression*", that aggressive behaviors were due to an internal build-up of aggressive instinctive drives and that these only emerged in the same species being distinct from predation but ultimately ensuring survival. More than 50 years later the most recent theories now integrate, more or less, genetic and hormonal with learning and environmental models (Anderson & Bushman, 2002; DeWall et al., 2011; *but see* Ferguson & Dyck, 2012).

So what is the phenomenon uniting two sea anemones releasing their attack polyps on another and two children fighting each other in a playground? A simple answer is conflict: the first an internally perceived conflict and the second the subsequent external conflict arising/or not from the actions following the first. An internal conflict being acted upon brings about external conflict (by means of threats or aggression), as do any accidental or spontaneous acts of aggression. Then, what behavioral mechanisms are there to deal with such events of intragroup conflict? Enter conflict resolution.

Sociality in the order of primates is often explained as an adaptation. This order represents socially complex species with differing dominance hierarchies as well as regular patterns of group belonging and intergroup transference (Whiten & Byrne, 1997). Some possible factors regarding their gregariousness have been extensively studied in terms of benefit and these include: avoidance, detection and defence against predators; vantages in detection of resources in foraging; avoidance of threat of conspecifics by limiting the risk of infanticide (Chapman & Chapman, 2000).

There are however some costs, namely acts of aggression as earlier mentioned. Indeed, life in groups frequently generates competition and conflict among members of the same group. This can take form in struggle over food, mating partners, social partners or access to resources (Mason & Mendonza, 1993). Thus conflict, as a general term, will occur whenever individuals interact with incompatible objectives. Resolution then decreases or eliminates the incompatibility (Judge, 2005). Faced with this inevitability, many species of non-human primates have developed an effective mechanism towards the resolution of conflicts and conflict management. Some of these strategies include post-conflict dyadic affiliations (de Waal & van Roosmalen, 1979; Preutschoff *et al.,* 2002; Koski *et al.,* 2007), post-conflict triadic affiliations (Palagi *et al.,* 2004; Fraser *et al*., 2008; Koski & Sterck, 2009) and sometimes, avoidance (Watts, 1995a; Sommer *et al.,* 2002). The present research delves mainly in reconciliation and triadic affiliation in primates particularly in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), the strategies they employ in conflict resolution and the possible functions of such interactions and other possible factors previously unattended.

1.1 Reconciliation – Dyadic Post-Conflict Affiliation

The first systematic study of conflict resolution was done with chimpanzees in the Arnhem Zoo Colony by Frans de Waal and Angeline van Roosmalen and published in 1979. The term reconciliation was used and was defined as a friendly or peaceful contact between opponents shortly after a conflict[1]. Such interactions have now included grooming, embracing, kissing or genital contact (de Waal & van Roosmalen, 1979; de Waal, 1986; Preuschoft *et al.,* 2002; Wittig and Boesch, 2003).

Since then, this type of post-conflict affiliation now described in close to 50 primate species (Aureli *et al*., 2012). Most of these refer to old world monkeys such as macaques (*M. fascicularis; M. arctoides; M. sylvanus*) (Cords, 1992; Call *et al.*, 1999; Majolo *et al.*, 2005), baboons (*Papio cynocephalus; P. anubis*) (Silk *et al*., 1996;

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[1] Even though these behaviours had been observed independently by a number of primatologists across a few species like wild chimpanzees, baboons and langurs (van Lawick-Goodall, 1968b; Seyfarth, 1976; McKenna, 1978) with different terminologies such as appeasement or reassurance, it was first with de Waal & van Roosmalen (1979), coining the terms reconciliation and consolation, that research was carried out systematically.

Meishvilli *et al.,* 2005), colobine monkeys (*Presbytis entellus; Rinopithecus bieti)* (Sommer *et al.*, 2002; Gruter, 2004) but there have been also studies focusing on new world monkeys, like capuchins (*Cebus apella; C. capucinus*) (Weaver & de Waal, 2003; Leca *et al.*, 2002) and even prossimians as brown lemurs (*Eulemur fulvus*) (Norscia & Palagi, 2011) and sifakas (*Propithecus verreauxi*) (Palagi *et al.,* 2008). Among great apes the chimpanzee has been the most widely studied species (*Pan troglodytes*) (Preutschoft *et al.*, 2002; Watts, 2006; Koski *et al.*, 2007) followed by the gorilla (*Gorilla gorilla*) (Watts, 1995a; Cordoni *et al*, 2006; Mallavaparu *et al.*, 2006;) and lastly by the bonobo (*Pan paniscus*) (Palagi *et al.*, 2004; van Dongen *et al.*, 2008). Presently there seems to be no evidence of occurrences of reconciliation in orangutans, though conflict interventions by unrelated third parties have been observed in captivity (*Pongo pygmaeus*) (see: Zucker, 1987; Tajima & Kurotori, 2010).

Reconciliation (or peaceful post-conflict interaction) is mostly a dyadic phenomenon, and so, despite differences in their motives for reconciling, both former opponents need to take part for the post-conflict reunion to occur (Aureli & Schaffner, 2006). It was first anticipated by de Waal & van Roosmalen (1979) that the function of reconciliation might serve as an important socially homeostatic function citing Mason (1964) on the calming effects bodily contact has on primates. This thinking goes back to the experiments by Harlow & Zimmermann (1958) with infant rhesus macaques seeking physical contacts from a surrogate cloth mother. Its implications for humans were then developed into Bowlby's (1969) attachment theory. Over the years, hypotheses regarding the functions of reconciliation and its underlying motivations have surfaced in the scientific community; some of these are discussed below.

1.1.1. The Valuable Relationship Hypothesis

Basing themselves on Hans Kummer's classic paper (Kummer, 1978), de Waal and Yoshihara (1983) suggested that friendly interactions between former opponents serve to restore a relationship disturbed by the previous conflict. Reconciliation would reduce the likelihood of further aggression and restore tolerance between former opponents. Accordingly there will be a tendency to reconcile depending on the quality of the relationship in the dyad, which will be more likely if the relationship value is high (thus, the opponents have more to lose if they do not repair the relationship) (Aureli, 1997; Romero *et al.,* 2008). Ideally three components of relationship quality have to be tested, according to Cords and Aureli (2000): value, security and compatibility. These have been measured mostly by observing events of grooming (Koski *et al.,* 2007), agonistic support (Preushoft *et al*., 2002), proximity (Kutsukake & Castles, 2004). Though not all variables have been tested in conjunction (Fraser *et al.,* 2010), evidence for this hypothesis has been seen in long-tailed macaques (Cords, 1992), Japanese macaques (Koyama, 2001), gorillas (Watts, 1995a), chimpanzees (Wittig & Boesch, 2005; Watts, 2006) and bonobos (Palagi *et al.,* 2004).

1.1.2. The Uncertainty-Reduction Hypothesis

This second hypothesis implies that the use of behavioural signals allow for the reconciliation to happen thus reducing the uncertainty that follows agonistic interactions. It emphasises a physiological component as it proposes that the recipient of aggression should be more aroused and the reconciliation would function to reduce its anxiety, allowing a quicker cessation of the stress response and preventing the adverse consequences of a long-lasting activation (Aureli *et al*., 1989; Aureli & van Schaik, 1991). It was during observations of long-tailed macaques that this hypothesis first gained strength (Aureli et al., 1989), by which the authors made the first attempt to access the physiological effects of aggressive interactions. This was done through monitoring self-directed behaviours associated with stress (self-scratching, self-grooming, and yawning) after the conflict. They found out the rates of such behaviours were higher following a conflict and declined rapidly when affiliative contact occurred. This has been also demonstrated in olive baboons (Castles & Whiten, 1998) and assamese macaques (Cooper *et al.,* 2005).

1.1.3. The Integrated Hypothesis

This hypothesis joins the assumptions of the valuable relationship hypothesis and the uncertainty-reduction hypothesis, in that it predicts that post-conflict affiliative interactions between former opponents should: 1) repair a relationship damaged by aggression amongst individuals who share a more valuable relationship, therefore being in their interest to reconcile in the first place; 2) decrease the post-conflict uncertainty and stress of former combatants (Aureli, 1997). So a “key prediction” of this hypothesis is that sufferers of aggression undergo more stress after conflicts with individuals with whom they share a valuable relationship (Aureli, 1997; Kutsukake & Castles, 2001). It has been tested with significant results in Japanese macaques (Kutsukake & Castles, 2001), bonnet macaques (Cooper *et al*., 2007), Barbary macaques (Mcfarland & Majolo, 2011) and in chimpanzees (Koski *et al.,* 2007).

1.1.4. The Benign Intent Hypothesis

According to this hypothesis, reconciliation is first and foremost a mean of communication (Aureli & Shaffner, 2006). It was first brought to attention by Silk (1996), and proposes an alternative and more proximal explanation to the function of reconciliation. It suggests that such peaceful post-conflict interactions are honest signals indicating that the conflict is over and that the intentions are now benign (Silk, 1998; 2000). Silk supports these claims with observational data from wild baboon females. She confirmed that female’s interest in handling infants of their former opponents had an influence: there was greater chance of reconciling (through the form of grunting) if the opponents were carrying infants than otherwise (Silk, 1996; 2000). Cords and Aureli (1996) voiced criticism of this hypothesis arguing that it was not really an alternative view but that it is complementary to the function of relationship maintenance. Since then this hypothesis has resurfaced in at least one study involving facial expressions in chimpanzees as a way of explaining their function in various social situations (Waller & Dunbar, 2005).

1.2. Consolation - Triadic Post-Conflict Affiliation

Triadic affiliations are a matter of some confusion and disagreement. They first came under the name of consolation in de Waal’s and van Roosmalen’s seminal paper (de Waal and van Roosmalen, 1979). The problem with consolation (and reconciliation for that matter) is, like the authors first acknowledged, that it remains a functional label rather than an operational one. It is defined as a post-conflict interaction in which and uninvolved bystander initiates friendly contact with the victim of aggression thus consoling her. So the reconciliation dyad becomes a triad. The problem emerges in ascertaining the function of this contact, that is, is it really consoling or is it something else altogether?

The consolation phenomenon has been proposed to be indicative of a possible cognitive distinction between great apes and macaques. Indeed it was suggested that, in chimpanzees, the expression of consolatory behaviour could be related to either dominance style of the species or to a seemingly more developed empathy in comparison to monkeys (de Waal & Aureli, 1996). But there have been consistent observations in monkeys of uninvolved bystanders initiating contacts after aggression. So consolation seems to have undergone another label transformation: it integrates part of what are now, in a broader behavioural sense, called "bystander" or "third-party" (triadic) affiliations which may have a consolatory value or not. Defined has such, these interactions have now been observed in stump-tailed macaques (Call *et al*., 2002), baboons (Wittig *et al*., 2007), mandrills (Schino & Marini, 2012) and Barbary macaques (Mcfarland & Majolo, 2012). These interactions may fall into two categories; the affiliation can be solicited by the recipient (Verbeek & de Waal, 1997) or unsolicited (de Waal, 1993), the unsolicited being the most appropriate interaction defining consolation behaviour.

There are three main hypotheses now form our understanding of the function and cognitive constructs of bystander affiliation; these are the consolation hypothesis, the self-protection hypothesis and the relationship repair hypothesis. These follow below.

1.2.1. The Consolation Hypothesis

This was the first hypothesis devised by de Waal and van Roosmalen (1979), but was not actually tested using more accurate methods until much later. It postulates that the bystander affiliation will lessen the recipient's[2] stress caused by the conflict (Romero & de Waal, 2010; Fraser *et al*., 2009), thus, arguing that the bystander's motivation for its association is supposed to be empathetic and should enhance the bond between the bystander and the recipient (Wittig & Boesch, 2010). According to

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[2] The recipient of aggression (Wittig & Boesch, 2010) can also be called victim (Romero *et al.,* 2010) or agressee (Koski *et al.,* 2007). These terms are used interchangeably in this study.

this view it should then not be surprising to find that, for the most times, the bystander will already be strongly bonded[3] with the recipient (Aureli & Schaffner, 2006). Ironically, the first study to actually test this hypothesis in chimpanzees did it in the same Zoo where de Waal and Roosmalen first proposed it almost 30 years earlier and found no evidence that bystander affiliation in fact reduces stress in the recipient (Koski & Sterck, 2007). Nonetheless, evidence was found in a later study also involving these species (Fraser *et al*., 2008). In bonobos, third party affiliation has been found to occur (Palagi *et al*., 2004), but this hypothesis was only recently tested. The results have failed to show a significant decrease in self directed behaviours with Clay & de Waal (2013), however Palagi and Norscia (2013) shifting the methodology to focus on when consolation occurred compared to when no affiliation occurred found significant results for this hypothesis[4].

1.2.2. The Self-protection Hypothesis

This second hypothesis proposes that, in order to avoid becoming the target of redirected aggression[5], the bystander will offer affiliation to the recipient. Such behaviour is believed to reduce the likelihood of the bystander of becoming the target of further aggression by the recipient. In addition, it postulates affiliative behaviours being shown more by individuals who are frequent targets of aggression (Koski & Sterck, 2007, 2009). This was first suggested by observations on stump-tailed macaques by which most contacts involved socio-sexual behaviours. These were unlikely to decrease stress and were not given by the recipient's kin (Call *et al.*, 2002). Evidence for this hypothesis was found in chimpanzees (Koski & Sterck, 2009) and mandrills (Schino & Marini, 2012) were bystanders were less likely to become targets of redirected aggression if they affiliated with the recipient of aggression after a conflict.

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[3] This bonding can sometimes be kin related (Kutsukake & Castles, 2001) or friendship based (de Marco *et al*., 2010).

[4] Studies researching this hypothesis have compared rates of self directed behaviours in the victim before bystander affiliation occurred with rates of self directed behaviours after bystander affiliation occurred in the same PC. Palagi and Norscia (2014) research was done including self directed behaviours as a whole (before and after pooled) and compared them with events where no affiliation occurred, thus comparing distinct PCs.

[5] Studies have shown that is likely that the victim sometimes redirects aggression towards uninvolved group members (Aureli & van Schaik, 1991; Aureli et al. (1993).

1.2.3. The Relationship Repair Hypothesis

Finally, the third hypothesis stipulates that consolation serves as a substitute for reconciliation when the latter fails to happen. It predicts that when the risks of renewed aggression are high, a bystander will offer affiliation in order to repair the opponent's relationship and reduce the aggression (Wittig & Boesch, 2003; 2010; Palagi *et al.*, 2006). This should happen mostly if the bystander has a close bonding with the aggressor, the rationale being that if the recipient could not reconcile with its former opponent, the bystander will serve has a proxy (Fraser *et al.,* 2009). There have been some findings supporting indirectly this hypothesis in bonobos (Palagi *et al*., 2004) and chimpanzees (Fraser *et al*., 2008; Palagi *et al.,* 2006a). They found that in the absence of reconciliation, affiliation by a third party was more likely to take place.

1.2.4. Other kinds of triadic affiliations

Sometimes, bystander affiliations towards the aggressor can happen also. These may be "*qualitatively different*" and should be "*investigated separately*" (Romero *et al.*, 2011). They have been found in hamadryas baboons (Romero *et al*., 2008) and in chimpanzees (Romero & de Waal, 2010) and in many macaque species (See also Das, 2000, for a review). The proposed hypotheses for explaining these interactions, thought, are mostly identical to the abovementioned with the focus switching from the recipient to the aggressor: stress reduction; self-protection; relationship repair (Romero *et al.*, 2011).

Throughout this thesis, dyadic affiliations will refer to unsolicited and solicited affiliations of between the victim and the aggressor and triadic affiliations will refer to unsolicited and solicited affiliations (consolation proper) between the victim and the bystander (see Fig. 1 for a illustration covering all known post-conflict interactions).

1.3. Overview of Conflict Resolution Research in Pan

Recent comparisons of the genome sequences of chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and humans (*Homo sapiens*) show that the latter differ approximately by 1.3% from both chimpanzees and bonobos and these two are more closely related with a difference of 0.4% in their genomes (Prüfer *et al*., 2012). It has also been suggested that chimpanzees and bonobos share a more recent common ancestry with humans than with gorillas (Goodman *et al*., 1998). The last common ancestor of humans and chimpanzees is dated at around 5-7 million years ago and the split with chimpanzees and bonobos occurred 2 million years ago (Fisher *et al*., 2011). Mental properties such as self-recognition (Anderson & Gallup, 2011), theory of mind (Herrmann *et al*., 2010) and empathy (de Waal, 2008) which are recognizably human have been attributed to them. Direct comparisons between chimpanzees (see Box 1) and bonobos (see Box 2) can potentially provide a powerful method of testing hypotheses regarding the evolutionary processes which moulded behavioural traits between the species (Hare *et al.*, 2009). Since we share so much with these African apes it is important to investigate what sets them apart, as a species, from each other and ultimately what sets us apart from them.

Of all the African great apes, bonobos (*Pan paniscus*) and gorillas (*Gorilla* sp.) have been the least studied, with the chimpanzee (*Pan troglodytes*) being the most widely investigated. Whilst most studies mainly focused on reconciliation, there has been a growing scientific interest regarding triadic affiliations in primates.

The studies involving bonobos namely Palagi *et al.* (2004) suffer from a small sample size (5 adult individuals) which is understandable as there are fewer bonobos in captivity than chimpanzees, although this has been addressed with the studies of Clay & de Waal (2013). Also, while these authors did present evidence for triadic post-conflict affiliation in the species, they did not find evidence for the stress reduction (consolation) hypothesis. In the first study there were no reports of self-directed behaviours in the recipient of aggression: if these behaviours decreased or increased followed by affiliation or in the absence of it, respectively (Palagi, 2004) or if they showed an increase before and a decrease after affiliation (Palagi & Norscia, 2013). While the self protection hypothesis (Koski & Sterck, 2009) has now been tested for bonobos (Palagi & Norscia, 2013) no evidence was found for it, additionally, the grooming exploitation hypothesis (McFarland & Majolo, 2012) has not yet been tested. There is still much to learn from the post conflict strategies employed by this species.

On the other hand, studies focusing on post-conflict resolution in chimpanzees are, in comparison, plentiful, be it in captivity (e.g., de Waal & van Roosmalen, 1979; Preuschoft *et al*., 2002; Fuentes *et al*., 2002, Koski *et al*., 2007; Fraser et al., 2010) or in the wild (e.g., Arnold & Whiten, 2001; Wittig & Boesch, 2003; Kutsukake & Castles, 2004; Watts, 2006). Though triadic post-conflict affiliations remain still an emergent research topic, these have passed the period of being described into a period of hypothesis testing in captivity (Palagi *et al.*, 2006a; Koski & Sterck, 2007; Fraser *et al*., 2008; Koski & Sterck, 2009; Romero & de Waal, 2011) and in the wild (Wittig & Boesch, 2003; Kutsukake and Castles, 2004; Wittig & Boesch, 2010). However, there are variations in the criteria used in these studies (Fraser *et al*., 2010) as such they would benefit further if a more standardized criteria were utilized. An added comprehensive evaluation of post-conflict behaviours is therefore needed paired with a concern for a continuation of longitudinal research regarding conflict resolution (with more attention given to triadic affiliations) and well as novel predictions for new emerging hypotheses.

1.4 The Matter of Studies in Captivity

In captivity, the animals have always food available this being one of the main variables accounting for the differences in behaviour when compared to their wild counterparts; the other is the lack of predation. Captive enclosures limit the foraging behaviours, and with an increase of leisure time, it is assumed that both chimpanzees and bonobos will be more concentrated in social life (de Waal, 1982; de Waal, 1989; Stanford, 1998). It is not unreasonable then to think these factors will also have an effect on the social model of captive communities. Moreover, the medical attention given to both species in captivity will greatly contribute to the extension of their lives (Conlee & Boysen, 2005). In such conditions, as they allow controlling some variables otherwise uncontrollable, the study for these animals should produce more information about their behaviour in lesser time, when compared to the constraints of the observations in the wild. Regarding the possibility of post-conflict reunions bein an artefact of captivity, Aureli *et al.* (2002) gave four arguments against it: first, some of the captive groups were kept in large enclosures so the animals can easily avoid each other; second, the frequency of post-conflict interactions in some groups were not changed when the same group was moved to smaller confinements; third, studies done in the wild showed evidence for post-conflict affiliations; fourth, the author had the knowledge of having studied the same species (*Macaca fascicularis*) in both captivity and wild and found similar behaviour in both conditions. Colmenares (2006) further argued that whole wild versus captivity dichotomy in regards to conflict resolution was potentially meaningless as an explanatory variable. This is mainly because captive populations may vary within themselves being it in ecological factors (e.g., temperature, amount and complexity of space, resource distribution) or social settings (e.g., group size and structure, kin relations), which is also true for wild populations. While in theory individuals in wild populations may avoid each other after a conflict resulting in decreased group cohesion, external forces such as risk of predation or intergroup competition may function to keep that cohesion making it comparable to captive populations (Sommer, 2002).

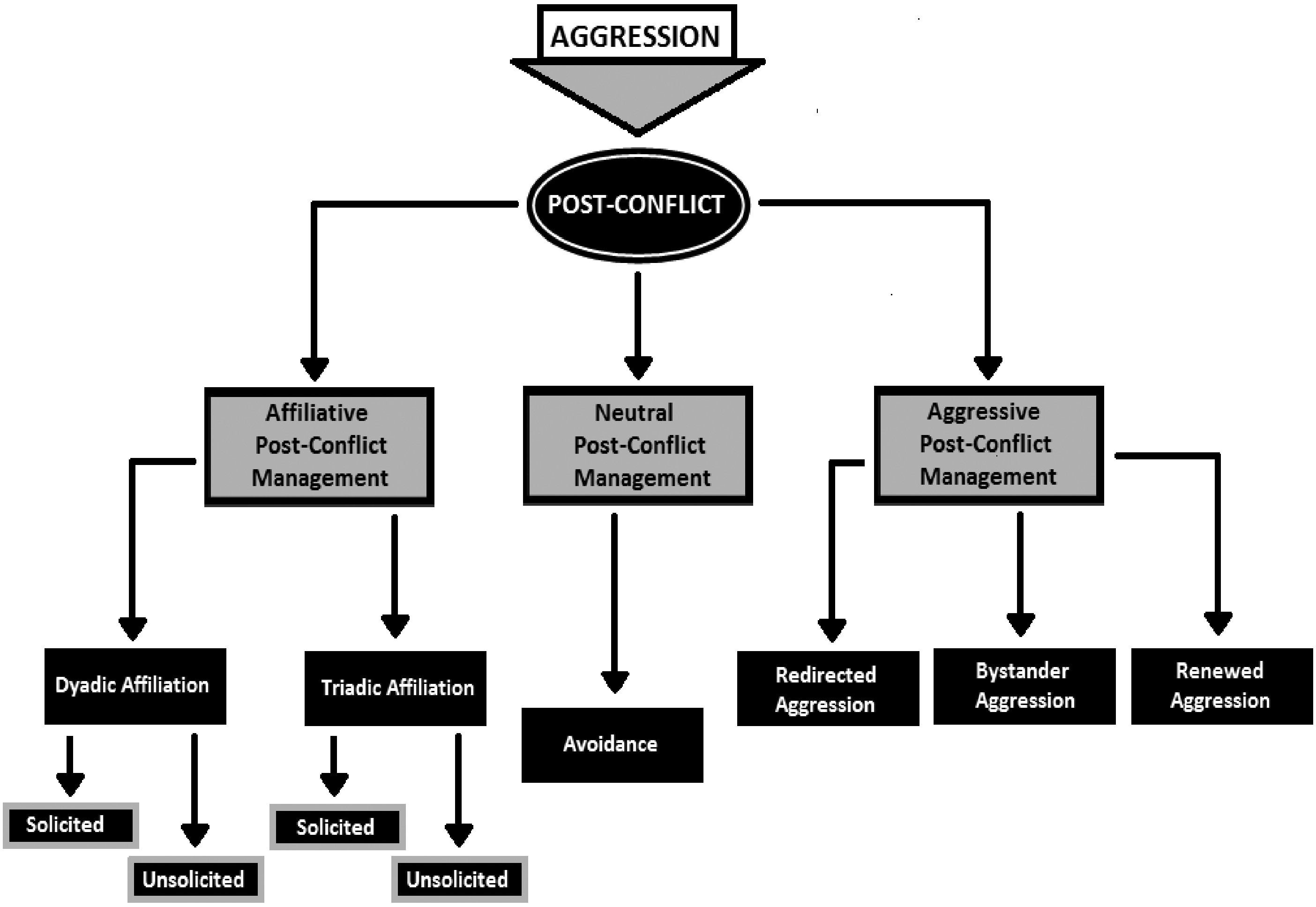

Fig. 1 - Diagram adapted from Wittig and Boesch (2003) depicting all possible outcomes of a conflict. Here consolation is seen as a sub-group of triadic affiliations (unsolicited). Both dyadic affiliations (solicited and unsolicited) can carry the functional label of reconciliation.

CHAPTER 2

Research Predictions

2. Research Predictions

2.1. Triadic Affiliations: An Integrated Hypothesis?

In the reconciliation research there have been attempts to test an integrated hypothesis with somewhat positive results in chimpanzees (Koski *et al.,* 2007). With regards to triadic affiliations, if we join the consolation hypothesis with the relationship repair hypothesis we can also come up also with an integrated hypothesis in the triadic post-conflict dynamics. So far, this has not been fully tested in chimpanzees and not at all in bonobos. The predictions could be as follows:

1a) It is not unlikely that social organization of the species will carry an added weight on the post-conflict interactions. Usually in chimpanzees the males often form stronger affiliative relationships (de Waal, 1982), in the bonobos it is the females that form stronger relationships (Kano, 1992). So chimpanzee male bystanders will be more attracted[6] to male agressees than otherwise and female bonobo bystanders will be more attracted to female agressees than otherwise;

2a) Occurrences of triadic affiliations should be higher if reconciliation failed to occur, thus serving as substitute for them (Wittig & Boesch, 2010);

3a) If triadic affiliations do console, it should be expected that self directed behaviours (self-scratching, self-grooming) in the recipient of aggression to be reduced in the aftermath of affiliation in comparison to occasions where third party affiliation does not occur (Fraser et al., 2008);

4a) The bystander, in most cases, should be strongly affiliated with the recipient of aggression (Aureli & Schaffner, 2006) the rationale being that even with the possibility of redirected aggression it would be unlikely for it to befall on a friend or kin than it would with less bonded individual;

5a) Taking a hint from the view of reconciliation as a means of communications (Silk, 1996) it should be expected that in the context of triadic affiliations, solicited affiliations should occur more frequently than unsolicited ones, with varying degrees of proximity and affinitive quality depending on the individuals.

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[6] Attracted is defined here in a broader sense: the bystander will have an underlying preference, correlating the sexes with the value of the relationship, to approach and emit affiliative behaviours to the previous recipient of aggression.

2.2. Alternative Predictions: A Selfish Perspective

Other predictions outside the integrated hypothesis abovementioned can also be made, whereas the first regarded bystander interactions in a more victim-oriented or empathic lens, these predictions may fall on a more bystander-oriented or selfish perspective. Most of these have not been tested in either chimpanzees or bonobos:

1b) Bystanders, particularly the ones that are repeated victims of aggression, should offer affiliation more frequently in order to protect themselves from redirected aggression (Koski & Sterck, 2009);

2b) As suggested with Barbary macaques (Macfarland & Majolo, 2012) it is possible that the third party is selfishly motivated, seizing an opportunity after the conflict to exploit grooming from the recipient of aggression;

3b) If reconciliation does decrease stress levels (Fraser *et al.*, 2008) then one expects likewise a diminishing in redirected aggression by the recipient of aggression, thus affiliation offered by bystanders should increase if conflicts are reconciled because uncertainty and risk of aggression are reduced;

4b) If the aggression originates from bluff displays it is less likely there will be reconciliations than otherwise (Fraser *et al.,* 2010). Triadic affiliations should also be less likely to take place in such conditions.

2.3. The Chimpanzee-Bonobo Psychological Divide

Having made such predictions, what is there to be said about how will chimpanzees and bonobos differ in their post-conflict strategies? It might be too simplistic to cluster each species to either a more “empathic integrated hypothesis” or a more “selfish integrated hypothesis” as there are other important variables with a greater degree of influence on conflict resolution than phylogeny alone. Once more, as suggested by Colmenares (2006) the ecological settings (amount and complexity of space, resource abundance and distribution) and the social settings (group size and composition, genealogical structure and group structure, social relationships) have to be considered. These may account for some of the variation in the literature on triadic affiliations in chimpanzees as there seem to be regional or “cultural”[7] strategies

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[7] This statement implies, like some authors have suggested (de Waal & Johanowicz, 1993; Weaver & de Waal, 2003; Kempes, 2009) that post-conflict strategies have a social learning component to them.

depending on the population being studied: self protection (Arnhem Zoo: Koski & Sterck, 2009); relationship repair (Mahale: Kutsukake & Castles, 2004; Taï: Wittig & Boesch, 2010); stress reduction (Chester Zoo: Fraser & Aureli, 2008; Yerkes Primate Center, Romero et al., 2010). So far, the literature on bonobos suggests that stress reduction and relationship repair serve as the main function of triadic affiliations (Palagi *et al.,* 2004). So again, what can we expect to find if we compare both species' post-conflict strategies?

There have been few comparative studies of chimpanzees and bonobos in most domains of research; this is partly because bonobos were the last ape known to science, because its shortage of numbers in captivity and also due to its remote habitat (de Waal, 1997). This presents a problem when one tests phylogenetic hypothesis regarding human evolution since there is a shortage of data. The collective data now tells us that while bonobos and chimpanzees are highly similar to each other in many aspects their behaviour differs in significant ways (Boesch *et al*., 2002). We know that chimpanzees show high forms of both intragroup and intergroup aggression; be it for dominance rank, fight for resources and for female submission (Goodall, 1986; Watts & Mitani, 2002; Muller *et al.,* 2007), excluding the intergroup variable, these also apply in captivity (de Waal, 1989). In contrast, bonobos do not compete strongly for dominance or form male alliances (which are also typical of chimpanzees) and are seen to be more subordinate to females. Stevens *et al*. (2006) observing several captive groups of bonobos noted that unlike chimpanzees where male-male coalitions are prevalent, female-female coalitions were the most prevalent support pattern as opposed to male-male or male-female coalitions. In fact, while bonobos show less aggression than chimpanzees, groups of female bonobos have been observed to attack and seriously injure males (Stevens *et al*., 2006; Hohmann & Fruth, 2011). Still, all present data indicates that bonobos show fewer severe levels of aggression when compared to its sister species (Hare *et al.,* 2012). Truthfully, bonobos remain playful all through their adulthood initiating play and using play faces significantly more than chimpanzee adults (Palagi, 2006). This reflects on their conflict strategies where Palagi *et al.* (2006b), found that bonobos often cope with competition and social tension with play and sociosexual behaviours as a way of appeasement and reassurance in tense situations. Rilling *et al.* (2011) recently found that bonobos possess more grey matter in areas (including the right dorsal amygdala and right anterior insula) which are implicated in perceiving distress in others, as well as others (larger pathways linking the amygdala to ventral anterior cingulated cortex) which are implicated in mediating aggressive impulses. These findings further support earlier of these species more tolerant and somewhat egalitarian nature. Herrmann *et al*. (2010) who did the first experimental study comparing the cognitive skills of both *Pan* species, found that while chimpanzees were more skilful at solving tasks requiring tool use and understanding physical causality, bonobos were more skilful at solving tasks related to theory of mind and understanding social causality.

De Waal & Aureli (1996) argued that unsolicited triadic affiliations (consolation behaviours) should be more common in egalitarian societies (like in the chimpanzees) than in despotic societies (like in the macaques). While there have been observations of bystander affiliation with the recipient in some macaque species like stump tailed macaques (Call *et al*., 2002) or tonkean macaques (de Marco *et al.,* 2010) these are deemed more tolerant and egalitarian in comparison to often labelled despotic rhesus macaques (Matheson, 1999) and Japanese macaques (Majolo *et al.,* 2005) in which any post-conflict bystander consolatory behaviour on both species remains yet to be seen. So taking this reasoning a little further we can consider both *Pan* species to be egalitarian since there is a high occurrence of both reconciliation and triadic affiliations among them. Then, in light of the known psychology of chimpanzee-bonobo, it now seems plausible to make these predictions:

1c) Motivations for triadic affiliations will be varied among the two species but somewhat more empathetically based in the bonobo. This is additionally supported from the findings of Palagi *et al.* (2004) where no redirection of aggression was found limiting the motivational shifts for affiliation;

2c) There should be a lesser occurrence of conflicts in bonobos since they show more levels of tolerance, and conflict prevention mechanisms (Palagi *et al.,* 2006b) paired with a greater tendency for reconciliation and triadic affiliation in comparison to chimpanzees;

3c) Chimpanzees (particularly males) should have a greater tendency for conflicts than bonobos while still reconciling and consoling;

4c) Socio-sexual behaviours will be higher in bonobo triadic affiliations than in chimpanzee triadic affiliations (where embraces and kisses should be more common);

5c) As males are more strongly affiliated in the chimpanzees they may as well be more strongly motivated to offer affiliation to a male recipient of aggression than a female, likewise as female bonobos are more strongly affiliated with each other than with a male they should be strongly motivated to offer affiliation to a female recipient than a male;

6c) Since male bonobos retain a strong relationship with their mothers (Surbeck *et al.,* 2011), there may be a greater tendency for bonobo mothers (if they have not previously intervened in the conflict) to console their kin.

Box 1 - The Chimpanzee (*Pan troglodytes*): Social Organization and Behaviour

The majority of the information regarding this species behaviour in the wild comes from several long-term field studies such as the Gombe National Park (Goodall, 1986), Mahale National Park (Nishida, 2011), Taï Forest National Park (Boesch & Boesch-Achermann, 2000) and Bundogo Field Station (Reynolds, 2005) and Bossou (Matsuzawa *et al*., 2011.). In the wild, chimpanzees live in fission-fusion communities that vary between 20 and 150 individuals. In each of these communities, the individuals form temporary factions (or parties), which fluctuate in size and composition by the duration of the day (Goodall, 1986; Mitani *et al.,* 2010). Males are the philopatric sex and, generally, are more social than females (Wrangham & Smuts, 1980; Goodall, 1986). These species lives in a linear and transitive dominance hierarchy between the males, associated to high levels of aggression, displays and alliance formation (Nishida, 1983; Watts, 1998; Mitani *et al.,* 2000). High territoriality is also recognized in this species; males tend to be highly affiliated and are known to patrol their home range borders, attacking and, sometimes mortally wounding extracommunity individuals, with the exception of fertile females (Goodall, 1986; Wrangham, 1999; Nishida, 2011). In relation to other great apes they are a particularly promiscuous species in their sexual system, being that most mating happens in mixed encounters where one or more ovulating females copulate several times with multiple males (Matsumoto-Oda, 1999; Mitani *et al.,* 2002), though a best-male strategy is sometimes employed where females tend to chose their partners while ovulating (Stumpf & Boesch, 2004). It is known that chimpanzees incorporate meat in their diet: hunting as been described in all known populations (Teleki, 1973; Stanford, 1999; Boesch & Boesch-Achermann, 2000), the main prey being the red colobus monkey (Stanford, 1999). Chimpanzee populations also show signs of cultural variation with distinct group traditions and for some time are recognized to engage in tool-use such as nut-cracking, termite-fishing and leaf-sponging (McGrew, 1992; 2004).

Box 2 - The Bonobo (*Pan paniscus*): Social Organization and Behaviour

The bulk of information we now know about wild bonobos comes mainly from two field sites: Wamba Station (Kano, 1992) and Lomako (White, 1996), though new findings are being recorded at Lui Kotale National Park (Hohmann & Fruth, 2003a). Bonobos, the closest relatives to the chimpanzee, have a similar fission-fusion social structure. Their communities range from 25 to 75 individuals thought there are estimates of communities up to 125 individuals (Elsacker *et al.,* 1995 *in* de Waal, 1997). The information on party composition of both Wamba and Lomako showed that bonobos form larger and more stable and mixed parties (White, 1988; Kano, 1992), in relation to chimpanzees in Gombe (Goodall, 1986) and Taï (Boesch & Boesch-Achermann, 2000). In contrast to the chimpanzee, the bonobo society is regarded as more egalitarian in relations between the sexes (Furuichi, 1997). Like chimpanzees, male bonobos are the philopatric sex (Kano, 1992), though females establish stronger relationships with other females whether these are resident (Idani, 1991) or immigrant (Furuichi, 1989). Such relationships are affiliative and not necessarily of kin (Kano, 1992). As a result, while individual females do not outrank males, they create coalitions among them and can bring out submissive behaviour in males (Furuichi, 1989). Dominance rank among males is strongly influenced by the presence of their mothers in the community (Inhobe, 1992a; Furuichi, 1989). Though aggression is much reduced in the bonobo than in the chimpanzee, the label "peaceful" is misleading: both hostile and peaceful intercommunity encounters were observed, half of those involve aggression of some sort (Kano, 1992). In the community, aggression among males and between sexes is less intense, and conflicts are often settled in a non-agonistic way (Furuichi & Ihobe, 1994). This might be because bonobos often engage in sexual interactions serving purposes other than reproduction. It can function as appeasement, social status, reconciliation and stress reduction (de Waal, 1997). These interactions, as defined by Kano (1992) are: G.G. rubbing; mounting; rump contact and penis fencing. De Waal (1995) describes even further contacts: ventro-ventral, ventro-dorsal, opposite, genital massage, oral sex, and mouth kiss. Similarly to its sister species, the bonobo engages in hunting. Forest antelopes and flying squirrels are thought to be the main prey (Ihobe, 1992b; Hohmann & Fruth, 1993), but recently at Lui Kotale, there were reports of monkeys being caught (Surbeck & Hohmann, 2008) with meat sharing afterwards. Cannibalism was also observed in the wild for the first time in bonobos at Lui Kotale (Fowler & Hohmann, 2010). Despite the fact that they are not recognized as frequent tool users in the wild, bonobos have been observed using leafs to what has been called rain hats, (Ingmanson, 1996), and also leaf sponges and fly whisks (Hohmann & Fruth, 2003b).

CHAPTER 3

The Chimpanzee Group:
Methods, Results and Discussion

3.1. Research Methodology

3.1.1. Study Subjects & Housing

This study was carried out on a group of West African chimpanzees (*Pan troglodytes verus*) all born in captivity (see Fig1. for details). The chimpanzee group was comprised of 16 individuals (3 adult males, 9 adult females, 2 adolescent males and 1 adolescent female plus 1 male infant). The group was housed at the Wolfgang Köhler Primate Research Center in the Leipzig Zoo, Germany since 2001. They had access to sleeping rooms (approx. 150m²), semi-natural indoor area (approx. 400m²), and outdoor enclosure (approx 4000 m²) both with many places for climbing (see Fig3). They were fed a variety of fruits and vegetables, occasionally supplemented by meat, eggs and yoghurt and had access to water *ad libitum*. Enclosures were equipped with environmental enrichment such as artificial termite mounds. Additional enrichment materials were provided for each subject every afternoon. The chimpanzee group was stable throughout the study ending when 2 new females were added in September.

3.1.2. Observational Methods

Data was collected on both the A-Chimps and the Bonobos, alternately, mornings and afternoons from March to September of 2013, in a combined total of 720 hours, 360h for the A-Chimps. All agonistic interactions between individuals were collected when visible by sampling all occurrences. Additional data on affilliative interactions (grooming, play, contact sitting) was gathered carried out at 5-min intervals (Altmann 1974).

Agonistic interactions were defined as any interaction involving aggressive behavioral patterns such as threat, charging display, brusque rush, chase, slap, pull, hit, trample or bite and involving submissive behavioral patterns and vocalizations such as bared teeth, whimper, screaming and urination (van Lawick-Goodall, 1968a; van Hoof, 1973). The identities of the opponents were recorded. A three stage scale of aggressive intensity was used borrowing elements from Palagi *et al.* (2006) Koski *et al.* (2007) and Fraser *et al.* (2008). Stage 1 (low) involved threat, chase-fleeing without physical contact, stage 2 (medium) involved physical contacts such as hit, slap, pull,

Fig 2. The A-Chimps Group.

Fig. 3a. The A-Chimp Group Indoor Enclosure.

Fig. 3b. The A-Chimp Group Outdoor Enclosure.

brusque rush, and stage 3 (high) involved physical contacts such as trample and/or bite. All of these should be followed at least by bared teeth expressions whimpers, screams and urination by the victim respectively but not exclusively. If interactions displaying patterns from the stage 1 (no physical contacts) did not make the victim display any submissive behaviors they were not coded as an aggressive conflict.

Conflicts were also categorized based on directionality with unidirectional, meaning aggression from the aggressor to the victim and bidirectional, meaning aggression exchanged from between the two opponents. Whenever polyadic conflicts occurred (more individuals joined the conflict) the aggressor-victim dyad with the most intense aggressive patterns was chosen for the post-conflict observations.

The context of the conflicts was also categorized. For this study six categories of context were included: 1) Bluff display, 2) Rough play, 3) Food, 4) Greeting, 5) Object competition and 6) Unknown. The amount of categories was somewhat greater than in previous studies on conflict resolution but all of them show a degree of fluctuation[8]. This more detailed analysis was chosen with the intent of better describing the situations in which conflicts occurred.

In order to differentiate whether opponents and bystanders tended to engage in affiliative interactions sooner after a conflict than in a control setting the Post-Conflict/Matched-Control method (PC/MC for short) introduced by de Waal and Yoshihara (1983) was used, where the focal animal was followed for 10 minutes and all self directed behaviors and interactions it had with other group members were recorded. If the conflict was resumed within 2 minutes the PC was cancelled starting only after the last aggressive pattern of the conflict event.

Self directed behaviors were recorded as a measure of anxiety in the Post-Conflict (Koski et al 2007; Fraser et al 2008) these were separated in duration of self-grooming and the frequency of self-scratching (a new scratching bout was assigned when scratching resumed after >5 seconds). All PC observations were conducted on both the victim and the aggressor with exception to situations in which, for technical

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[8] Authors such as Koski (2007) have simplified agonistic interactions arising in two categories: feed and non-feed, while Fraser et al (2010) have made distinctions from conflicts arising in bluff-displays or not arguing that these would have an effect in post-conflict affiliations, de Waal and Hoesktra (1980) categorized five possible contexts (play, infant protection, annoyance, social competition and object competition), whereas Palagi et al. (2004) took into account play and feeding contexts.

reasons, the recording of both elements at the same time was not possible. In these cases, preference was given to the observation of the recipient of the aggression/victim.

Affiliative interactions occurring in the PC were defined as any interaction from or towards the victim involving affiliative behavioral patterns such as gentle touch, embrace, hold out hand invitations, kissing and contact sitting (de Waal, 1986; Goodall, 1986), also included were behaviors such as mating and mounting though less common (de Waal, 1992 *in* Mason & Mendonza, 1993 p.124). If the victim approached either the aggressor or the bystander in the PCs it was coded as a solicited affiliation, if the victim was approached by either aggressor or the bystander it was coded as an unsolicited affiliation.

The PC was matched with a control observation (MC) on the same individual at the same time of the previous conflict on the next possible day within 7 days in the absence of a previous conflict 10 minutes before the start of the control. The outdoor enclosure was divided into two sectors based on the activity and cohesion of the group, the indoor enclosure was counted as a third sector. Within these all individuals were visible and audible to each other with MC only starting when opponents were in the same sector. Only when these conditions met was the MC started.

3.1.3 Data Analysis

A total of 102 PC-MC pairs on adults and adolescents were recorded (28 pairs for reconciliation, 31 pairs for triadic affiliation 13 pairs were both reconciliation and triadic affiliation occurred). For both reconciliation and triadic affiliation PC-MC pairs were labeled as "attracted" if the affiliation between opponents or between the victim and bystander occurred earlier in the PC than the MC, or just in the PC and labeled as "dispersed" if the affiliation occurred earlier in the MC than the PC, or just in the MC and labeled neutral if the affiliation occurred at the same time in both PC and MC or in neither. Any cases were reconciliation occurred together with triadic affiliation were coded separately in order to control for potentially confounding effects in cases were only reconciliation or triadic affiliation occurred. Agonistic supporters were considered as conflict participants and not as possible bystanders.

Relationship Quality. A weighted grooming network using UCINET 6 was made to visualize the grooming interactions (Fig. 4), relationship quality was assessed by the frequency grooming events among dyads, following Preutschof *et al.* (2002) as its study comprised a similar group size and grooming frequency. Two individuals were close when grooming events were >5 times, medium when dyads groomed 1-5 times and low if there were no grooming events. Conflict allies were also recorded when present, high supporters were individuals who aided another individual more than once, medium supporters aided once and low frequency supporters were never observed aiding in a conflict.

Post-Conflict Affiliations. The minimal number required of PC-MC pairs per focal animal was one. In order to evaluate reconciliation at the individual level the CCT method (corrected conciliatory tendency) was utilized (Veenema *et al.*, 1994) defined as "(Attracted Pairs minus Dispersed Pairs) divided by total pairs". For each individual the CCT was calculated, from which a mean CCT was obtained of the whole group. To test of triadic affiliations and its subset, consolation, the TCT method (triadic conciliatory tendency) introduced by Call *et al.* (2002) as a variation of the CCT method was used also defined as "(Attracted Pairs minus Dispersed Pairs) divided by total pairs" but substituting opponents for victim and bystander. Again, for each individual a TCT was calculated, from which a mean TCT was obtained for the whole group. Both individual CCTs and TCTs were compared via Wilcoxon Signed-Ranks test following the procedures suggested by Siegel and Castellan (1988) when N>15 an asymptotic test was used and when N_<15 an exact test was used.

To measure the stress levels in the PC-MC periods, rates of self-scratching (bouts per minute) and duration of self-grooming (seconds per minute) were recorded as in previous studies (Koski et al., 2007; Fraser et al., 2008). Individual means on the rates of self-scratching and durations of self-grooming per minute on PCs without dyadic or triadic affiliation were compared with individual mean levels of self-scratching and self-grooming during the entirety of the subsequent MC. A Wilcoxon Signed-Ranks test was used to compare the rates of self directed behaviors in the PC with their respective controls in the MC. A Friedman's test was conducted alternatively to test the Consolation Hypothesis, with a post-hoc Dunnett's test.

To find out which gender of bystander tended to offer the most affiliation to whom a Cochran's Q test was used including 4 classes of dyads (male-male, male-female, female-male, female-female) with a post-hoc Cochran's Q test on the two dyads of most interest. A Fisher's Exact test was conducted to test which sex dyad occurred more frequently in triadic affiliations.

TABLE 1. Frequency and Percentage of the Directionality of Grooming of each member of the study group

Group Member	Grooming Given Freq.	Grooming Given %	Grooming Received Freq.	Grooming Received %
Robert (RO)	89	9,13	104	10,38
Frodo (FR)	70	7,18	158	15,77
Lome (LM)	149	15,28	38	3,79
Lobo (LB)	30	3,08	10	1,00
Kofi (KO)	17	1,74	73	7,29
Natasha (NA)	33	3,38	92	9,18
Corrie (CO)	131	13,44	30	2,99
Riet (RI)	60	6,15	82	8,18
Fraukje (FK)	72	7,38	93	9,28
Tai (TA)	32	3,28	52	5,19
Sandra (SA)	117	12,00	45	4,49
Kara (KA)	56	5,74	63	6,29
Dorien (DO)	37	3,79	26	2,59
Ulla (UL)	60	6,15	24	2,40
Swella (SW)	22	2,26	112	11,18
Total	975	100,0	1002	100,0

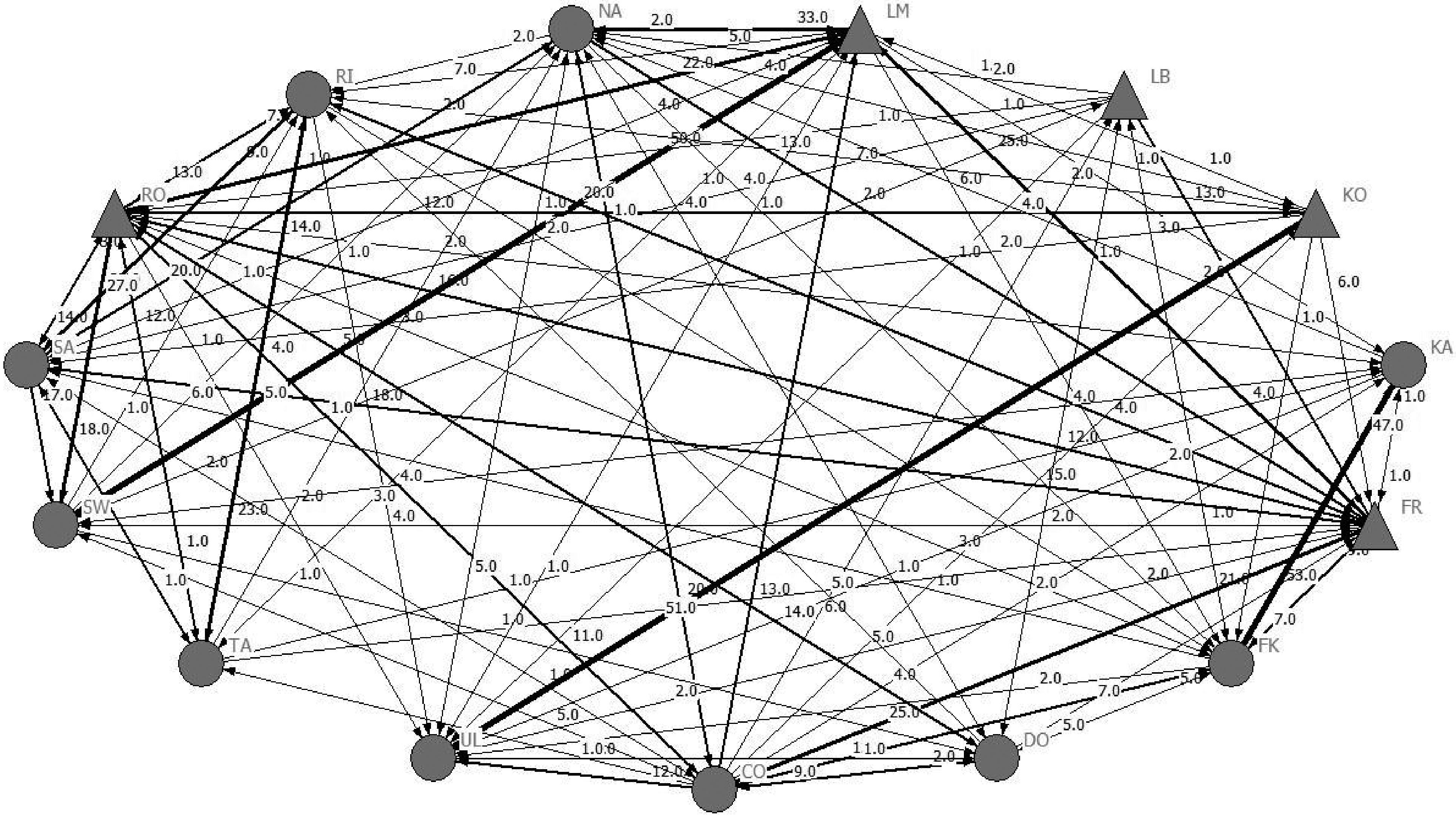

Fig. 4 A weighted grooming network of the A-Chimps (triangles=males; circles=females).

3.2. Results

Occurrence of Post-conflict Affiliations. The number of attracted, dispersed and neutral pairs were calculated for each of the 15 individuals. Regarding dyadic affiliations, the mean proportion of attracted pairs was significantly greater than the mean proportion of dispersed pairs indicating that the opponents were reconciling (attracted = 40,8% ± 24,3% SD; dispersed =16,3% ± 14,4% SD; Wilcoxon Signed Ranks Test per individual Z= -2,738, N=15, P=0.005, two-tailed exact sig). The mean CCT for the whole group calculated from individual CCTs was 22,3% ± 22,3 SD[9]. Regarding triadic affiliations the mean proportion of attracted pairs was also significantly greater than that of dispersed pairs showing that victim-bystander were affiliating (attracted = 57,24% ± 16,9 SD; dispersed = 0%; Wilcoxon Signed Ranks Test per individual Z= -3,068, N=12, P<0.001, two-tailed exact sig). The mean TCT for the whole group also calculated from individual TCTs was 53,3% ± 10,7 SD. There were also significant results for consolation (unsolicited bystander affiliations with the victim), the mean proportion of pairs was calculated (attracted= 45.14% ± 14.59 SD; dispersed = 0 %; Wilcoxon Signed Ranks Test per individual Z= -2,844, N=10, P=0.002, two-tailed exact sig). This result was confirmed by the time-rule method where most affiliations occurred in the first minutes of the PC: 58,5% of dyadic affiliations occurred in the first 3 minutes, 77,3% of triadic affiliations occurred in the first minute and of these triadic affiliations, consolation occurred 77,1% in the first minute (see Fig5abc).

Prediction 1a) Triadic affiliations occur more frequently among chimpanzee males. A Cochran's Q test was conducted to ascertain if significant differences existed in male-male female-male, male-female and female-female dyads. A further post-hoc Cochran's Q test was done on the MM/MF dyads with significant results (c^2= 9,143, N=45, P=0.002). Surprisingly, the tendency was inverse; females tended to offer the most affiliation or be affiliated to by the male victims (Fig. 8).

Prediction 2a) Triadic affiliations take place additionally if dyadic affiliations have failed to occur. In order to test this prediction a Fisher's Exact Test was

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[9] The Standard deviation is high because there were negative values derived from the LB_FR dyad in which LB tended to show a high frequency of dispersal following observed conflicts. Also in the CO_FR dyad, CO tended to affiliate with FR (repeated greetings) very frequently in the MC. Negative values have been represented also in Fuentes *et al.* (2002) as well as Puga-Gonzalez *et al.* (2014).

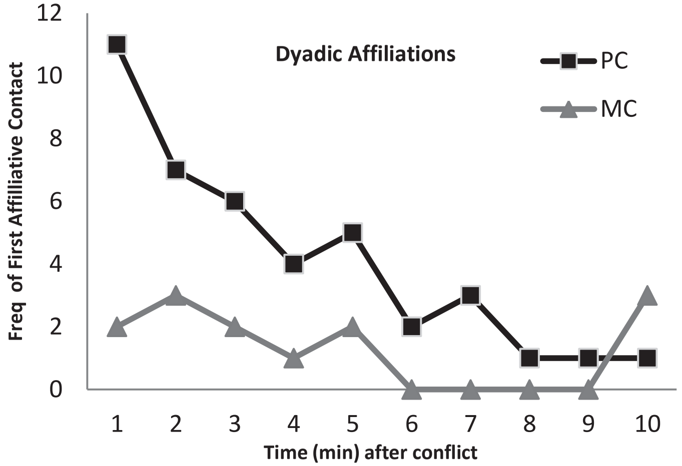

Fig 5a - Distribution of the first affiliative contacts between opponents across time (pooled data from both solicited and unsolicited affiliations).

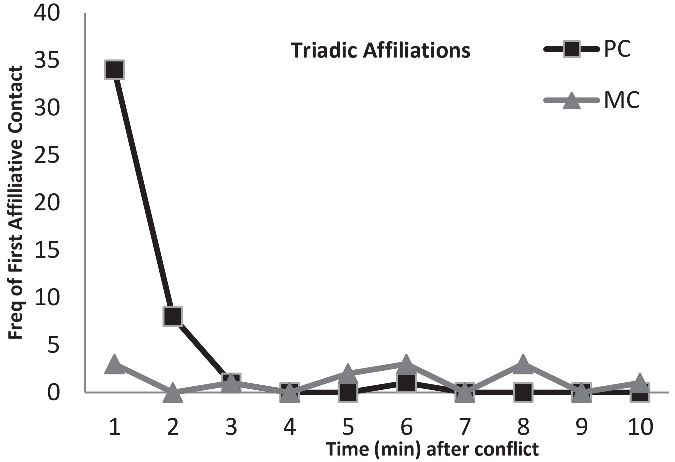

Fig 5b - Distribution of the first affiliative contacts between victims and bystanders across time (pooled data from both solicited and unsolicited affiliations).

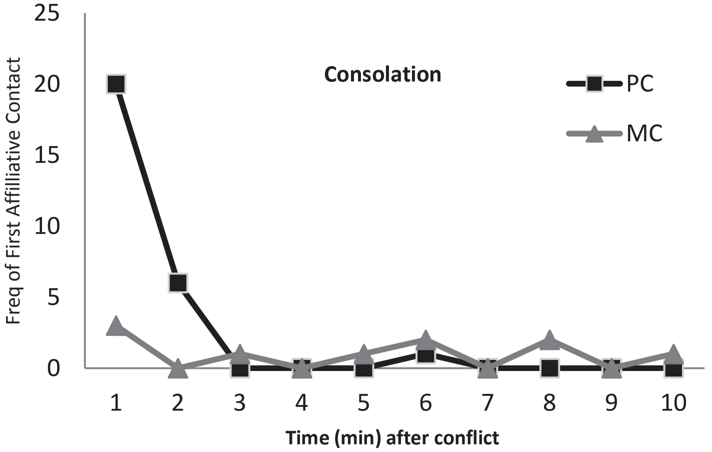

Fig 5c - Distribution of the first affiliative contacts between victims and bystanders across time (unsolicited affiliations).

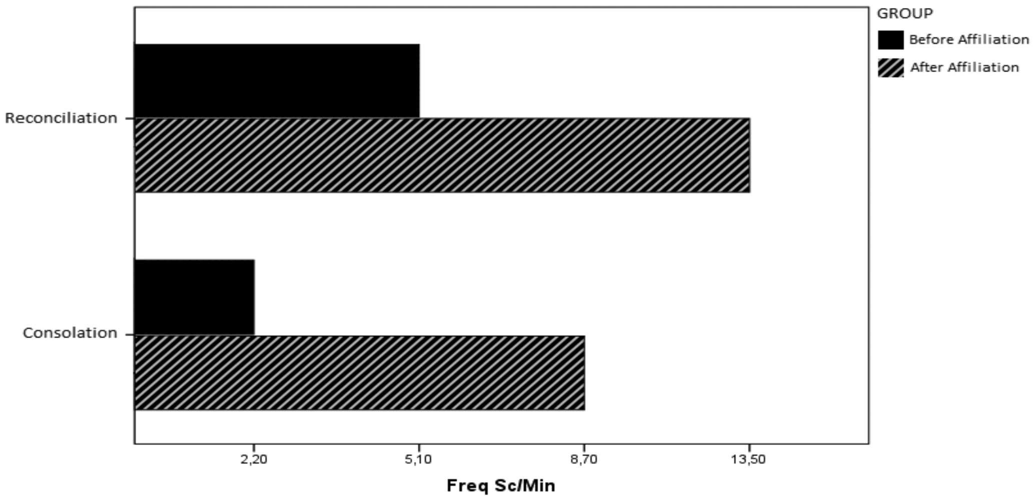

Fig 6a - Victim's post-conflict scratching rates before and after affiliations with aggressor (reconciliation) and bystander (consolation).

performed. Whenever dyadic affiliations were present (N=9), triadic affiliations took place 22,5% of the cases, in the absence of dyadic affiliations (N=31), triadic affiliations took place 77.5% of the cases (X^2=6.693, df=1, P=0.011). A significant correlation exists supporting the prediction that indeed triadic affiliations serve as part of a substitute for reconciliation in the first minutes of the PC. However, data shows that most triadic affiliations occurred earlier in the PC than dyadic affiliations (77.3% vs. 58.5%, respectively). This can actually mean the inverse: because there is an affiliation of/with the bystander, the perceived necessity for both opponents to reconcile decreases (Fig.9).

Prediction 3a) Stress reduction effects of PC affiliations. Self directed behaviors showed a tendency to be higher during the PCs when compared to baseline levels of the MCs suggesting that aggressive interactions elevated the stress levels in the PC that would continue high if no dyadic or triadic[10] affiliation was given, this is corroborated by the rates of self directed behaviors in the "no affiliation" category which were markedly higher than the other two. Additional events comprising dyadic+triadic affiliations (events where both occurred in the same PC) were removed due to their potentially confounding effects on self directed behaviors. Self-scratching rates per minute were calculated in the Wilcoxon Signed Rank Test for dyadic affiliations (Z=-2.014, N=28, P=0,044), for triadic affiliations (Z=-1.371, N=31, P=0.171) and for no affiliations in the PC (Z=-3.788, N=30, P<0.001). Likewise, self-grooming rates per minute were calculated in the Wilcoxon Signed Rank Test for dyadic affiliations (Z=-0.541, N=28, P=0.589), triadic affiliations (Z=-0.843, N=31, P=0.399), and for no affiliations in the PC (Z=-3.173, N=30, P=0.002). All tests were two-tailed (asymp. sig.), results shown in Fig7a&b. Afterwards, self-scratching rates during the PC were analyzed divided in two groups: before affiliation and after affiliation; both in reconciliation and consolation interactions (Fig6a). These were also calculated using Wilcoxon Signet Rank Test for reconciliation (Z=-2-980, N=28, P=0.003) and for consolation (Z=-2.324, N=19, P=0.02). The results show both a significant tendency for self-scratching behaviors to increase after affiliations and not to decrease as

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[10] With the only exception being the self-grooming rates in triadic affiliations shown in Fig6b which have higher MC rates than any other MC rates compared. This tendency may be due to the small sample size.

hypothesized. However, following Palagi and Norscia (2013) methodology, comparing consolation events directly with no affiliation events along with a baseline control, a Friedman's Test was made yielding significant results (X^2=8.899, df=2, N=19, P=0.02) to which a post-hoc Dunnett's test was made between variables. Consolation vs. No Affiliation (q= 0.2596, P=0.021), Consolation vs. MC (q=-0.1431, P= 0.205), and No Affiliation vs MC (q=(q=0,4027, P<0.001). These results suggest, indirectly, that unsolicited triadic affiliations do console (see Fig. 6b).

Prediction 2b) Grooming exploitation from the bystander. In the entire conflict data only two events were observed where the grooming given by the victim was greater than the grooming received by the victim (measured in seconds). These comprised the same dyad (SA_TA) which are better explained due to kin relation rather than coercion attempts.

Prediction 3b) More consolation offered after dyadic affiliations because of decrease in redirection. Just as prediction 2a) this one was not found in the A-Chimp group, first because no redirection of aggression was ever observed in the PC and second because most consolations (N=20) took place in the first minute well before most dyadic affiliations (solicited and unsolicited events of reconciliation) (N=10). The number of dyadic affiliation events occurring before consolation (unsolicited triadic affiliation) was N=3 versus consolation taking place before dyadic affiliation which was N=5.

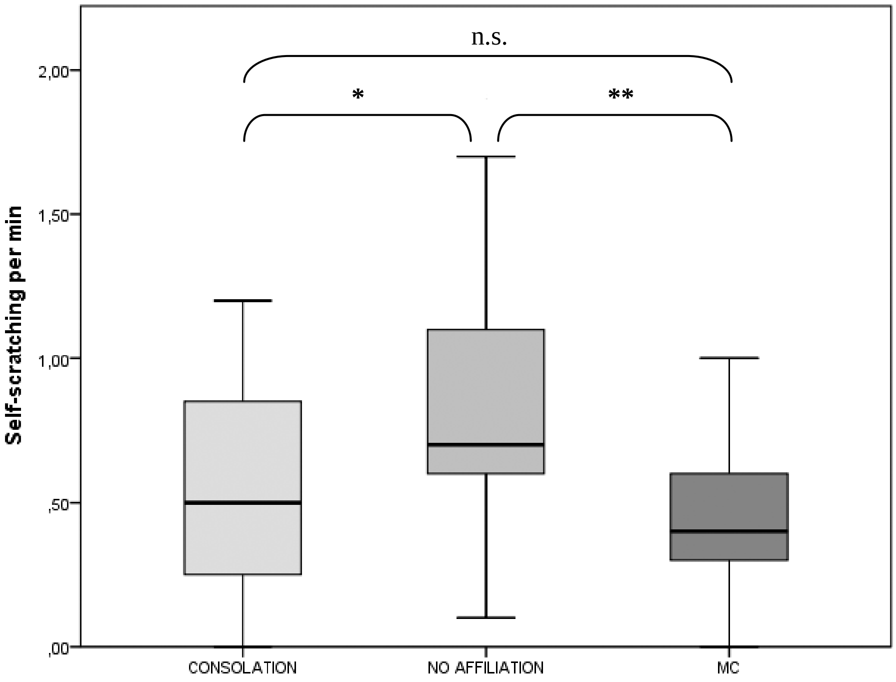

Fig 6b- Victim's post-conflict scratching rates in occurrence of consolation, where no affiliation occurred and in matched-control. *P=0.021; **P<0.001; n.s. (non-significant).

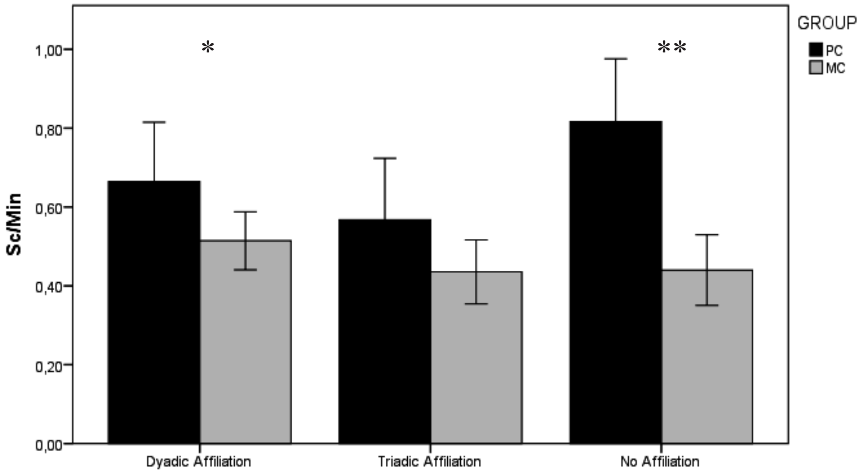

Fig. 7a. Rates of self-scratching per min. *P<0.05; **P=0.001.

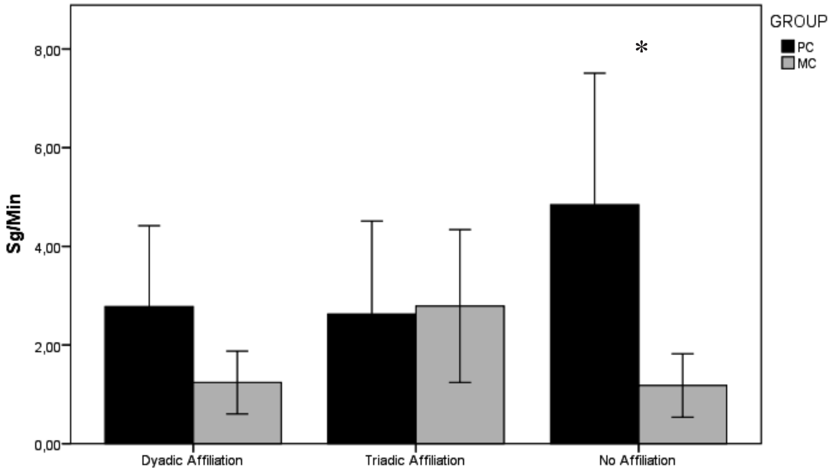

Fig. 7b. Rates of self-grooming per min. *P=0.002.

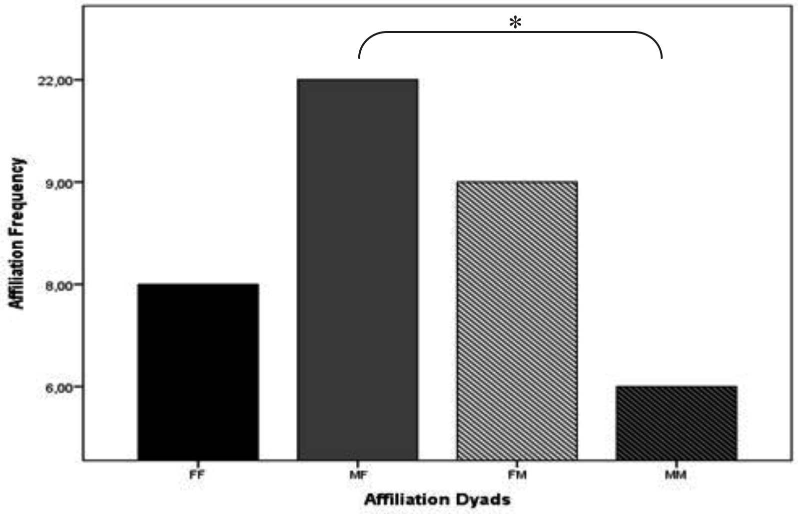

Fig. 8. Affiliation frequency among the difference sex classes. *P=0.002.

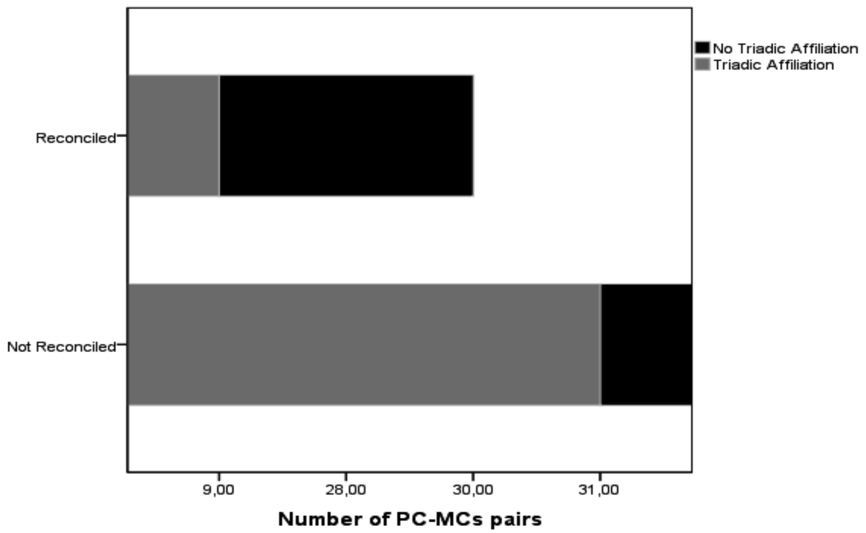

Fig. 9. The occurrence of triadic affiliations in the presence and absence of dyadic affiliations. P=0.01.

3.3. Discussion

This research has reinforced the existing evidence for dyadic affilliation (solicited and unsolicited affiliation between opponents) and triadic affiliation (solicited and unsolicited affiliation between victim and bystander) as emerging post-conflict behavioural patterns. The A-chimp group showed a similar configuration to observations made in the Arnhem chimpanzee group by Frans de Waal (1982) in that there were three adult males competing for the alpha position. A great amount of the conflict involved bluff displays or counter displays either directed to other males or to the females, from FR (the current alpha), RO (the oldest male and previous alpha) and LM (the youngest of the three) (31% of the conflicts). This group showed means of conciliatory tendencies within the known tendency among chimpanzees (CCT=22,3%; TCT=53,3%). To put these results in context, other studies showed CCTs of 15,5% (Kutsukake & Castles, 2001: wild), 15,9% (Wittig & Boesch, 2005; wild), 16,3% (Webb et al., 2014: captive), 17,3% (Arnold & Whiten, 2001: wild), 20,6% (Fuentes *et al.,* 2002: captive), 21,6% (Koski et al., 2007: captive), 28,8% (Palagi *et al*., 2006: captive), 41,2%[11] (Preuschoft *et al*., 2002) and 47,5% (Fraser & Aureli, 2008); and TCTs of 12% (Koski & Sterck, 2007: captive), 29,4% (Fraser & Aureli, 2008: captive) and 49,5%/53% (Palagi *et al*., 2006: captive).

The function of both dyadic and triadic affiliations revealed that stress levels increased after a conflict when comparing PCs with MCs. First, when comparing levels of self-scratching and self-grooming in the victims, all but one[12] were higher than the baseline indicating a rising of stress levels after a conflict that is unseen in control situations. It is possible that self-grooming is not as good as a predictor of stress levels when compared to self-scratching. All tendencies were comparable to previous research except the aforementioned self-grooming during triadic affiliation which was higher in the MC than in the PC, this might be due to the smaller sample size of this study (PC-MC=102). Furthermore, there was the issue of the purpose of self-grooming

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[11] These numbers are even more perplexing when considering there was only one adult male in the Yerkes group, females showing a high CCT similar to the CCT levels observed in the female chimpanzees at Chester Zoo which contained five adult males (Fraser & Aureli, 2008), proving that there is high variability regarding post-conflict strategies in the same primate species.

[12] Self-grooming levels in triadic affiliation interactions (both solicited and unsolicited bystander affiliation).

events particularly in conflicts of high level intensity since these often left wounds in the victim (e.g. a bite in a hand or a foot would leave the victim grooming that spot throughout the whole PC observation): in other words, proximal pain rather than ultimate stress was modulating the victim's grooming behaviour. Such events, in which it was clear that the individual was grooming a wound, were not counted as self-grooming. Interestingly, while Fraser *et al.* (2008) pooled the data from self-scratching and self-grooming, recent papers on conflict resolution in bonobos (Clay & de Waal, 2013, 2014; Palagi & Norscia, 2013) have left out self-grooming altogether from their publications further suggesting the weak reliability of self-grooming observations on stress possibly due to such confounds. The results having shown that conflicts are indeed stressful, when time came to compare if affiliation from either aggressor or bystander would decrease the stress levels in the victim (specifically self-scratching), further results confirmed that stress levels increased significantly after both reconciliation and consolation. One possible reason is the resulting asymmetry in observation time before affiliation and after affiliation. It is a fact that most affiliations occurred in the first minutes of the PCs leaving little observation time for self directed behaviours to occur in the victims. For instance, a looking at Fig.5c shows that 20 events of consolation occurred in the first minute[13] (74,1%), this means that the first 10% (1 min.) of the PC are consigned to observing self-scratching in the victim before affiliation while the remaining 90% (9 min.) are consigned to observing self-scratching after said affiliation for quite more than half of all occurrences in consolation. In spite of this, when comparing all occurrences scratching levels during consolation with all occurrences of no affiliation plus matched-controls, the post-hoc Dunnett's tests did confirm that there is a significant decrease in stress levels, thus confirming that, at a general level, consolation does console (see Fig. 6b).

When testing the supposition that triadic affiliations might be acting as a substitute for dyadic affiliations, a significant result was found showing the opposite; because bystander affiliations tended to occur earlier in the PC they may act as a restraint towards affiliation between opponents, however the number of

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[13] These results however pool all of the data of unsolicited bystander affiliation N= 27 (both events where consolation occurred with reconciliation and events where only consolation occurred). Of those, N=19 where tested in Fig. 5 due to confounding results of assigning to consolation events where both might have occurred.

triadic+dyadic affiliation occurrences is low (triadic occurring earlier than dyadic: N=9) limiting any significant *a posteriori* hypothesis test. This is one prediction that would benefit if a larger number of observations was made to enlarge the sample in order to test it adequately. Koski and Sterck (2007) were able to verify the assumption of whether unsolicited triadic affiliation tended to facilitate reconciliations and were able to find that in the event of consolation proper occurring earlier than reconciliation there was in fact a higher latency of dyadic affiliations: opponents did not reconcile earlier in the PC after consolation but rather late (N=19).

The prediction that male dyads tended to engage more frequently in triadic affiliations after a conflict was made on the assumption that male chimpanzees are known form closer bonds with other males (see Box 1). The results were however the opposite, it was the females who tended to be the main bystander when a male was a victim in a conflict. In fact, same sex dyads had the lowest number of affiliations of all four combinations with males affiliating with males being the lowest. Fraser *et al.* (2008) did find that females tended to offer more consolation (unsolicited triadic affiliations) in general. There is also partial data by Romero & de Waal (2010) when sex differences were tested, showing that females tended to offer more consolation (unsolicited triadic affiliations) to victims in the post-conflict, the consolers were individuals of low and medium rank only. An *a posteriori* hypothesis test was made by separating triadic affiliation into unsolicited events (consolation proper) and solicited events but no significant results were found due again probably to the small sample size.

There is some research connecting consoling behaviour to empathy of which Romero and de Waal (2010) subscribe, although consolation involves a higher degree of cognition, empathy itself is believed to be an ancient biological phenomenon connected to caregiving (Preston & de Waal, 2002). Experimental studies done in mice showed that females were more likely to approach cagemates that were restrained and in pain when compared to a control (Langford *et al*., 2010). For ethical reasons, similar experiments have cease to be conducted on primates and the ones that were conducted took dominance into account but not sex, (Massermann *et al.,* 1964; Wechkin *et al.,* 1964). However in the chimpanzee's closest relative after the bonobo, *Homo sapiens*, females have been observed to engage in helping behaviours more than males (Eckel and Grossman, 2008), and while providing support for a troubled friend, females tend to experience higher degrees of emotional contagion when compared to males (Magen and Konasewich, 2011). We should however be careful in interpreting such results as a matter of inherent empathy alone when comparing to consolation behaviours. For instance, despite aforementioned references on female empathy it would be expected that affiliations started by females would have the highest frequencies, however mixed sex dyads were the ones having the higher frequencies. This raises the question: why females don't console females as much as they do males, especially considering that females were the most recurrent recipients of aggression and no redirection was ever observed?

As previously noted, chimpanzee females tend to be less gregarious than males[14], socio-ecological and reproductive models have come forth explaining these observed differences. Food competition among chimpanzees may cause dispersion, since females are physically weaker than males it may benefit them to scatter from larger groups and forage for food alone (Goodall, 1986; Wrangham, 2000). Also, there are costs associated with female migration, namely intrasexual aggression, therefore, association of immigrant females to the resident males may act as a strategy to avoid aggression from the resident females (Kahlenberg *et al.*, 2008). Additionaly, female chimps may associate themselves with males to ensure conception, paternity uncertainty, or establish themselves as group members (Wrangham, 2000).

In the case of Romero and de Waal (2010) because her sample is large (a total of 3003 conflicts gathered in 8 years) it would be interesting to know if the females who offered consolation towards other group members were themselves frequent victims

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[14] There was a trend found in the literature concerning female bonding; it was barely observed in East African sites (Kibale, Mahale, Gombe) but quite present in the form of grooming and coalition bonds in West African sites (Bossou and Täi) (reviewed in Wrangham, 2000). However, this assumption is being challenged since more recently, Wakefield (2013) reported that females in the Ngogo community in Kibale, spent most of their time in association with other females and formed bonds with them based on mutual affinity. Moreover, Newton-Fisher (2006) confirmed that in the Sonso community in Budongo (an East African site), the females, who tended to be more gregarious than other eastern chimpanzees, formed coalitions against the males. Such cases were also seen in captivity, for example in the Arnhem Zoo, females were observed forming coalitions against males (de Waal, 1982; 1984) or in the San Diego Zoo (Baker & Smuts, 1994). No intrasexual coalitions were ever observed during this research at the Leipzig Zoo. Only in one explicit case did two females joined against the male, however both had been recipients of his aggression occurring in the same bluff display and soon joined the alpha male against the aggressor.

of aggression. These results also showed a greater tendency to console victims of high and medium rank than lower ranks.

Another hypothesis, that is grooming exploitation, was first observed in Barbary macaques (McFarland & Majolo, 2012) were it was found that bystanders received more grooming time from the victims than they actually gave and moreover they tended to associate more with subordinate victims than dominant ones. In great apes this hypothesis had not been tested yet. For a long time now, allogrooming has been observed to be a prevalent behaviour among all primate species (Goosen, 1987) and understood to have not just a hygienic function, such as the removal of skin flakes and ectoparasites (Dunbar, 2010), but also serving a social function, namely to maintain bonds between group members (Dunbar, 1991). For example, Terry (1970), observing chimpanzees, rhesus monkeys, langurs among others, proposed that it had a tension reduction function as it calmed and relaxed the recipient of the grooming. Additional research have strengthened this model such as Boccia et al. (1989) where it was found that grooming decreased the heart rates of the recipient, also Keverne et al. (1989) found a correlation between grooming and the release of beta-endorphis (a brain opioid associated with pleasure). Grooming can also be seen as altruistic since it costs the groomer and benefits the recipient with some primate species devoting up to 20% of their daily time engaging in it (Dunbar, 2010). Other associated costs are a decrease in vigilance be it predator vigilance (Cords, 1995) or in harassment by group members (Maestripieri, 1993). Consequently, we see grooming as currency for interactions involving conflict, in alliance formation (Dunbar, 1980; Schino, 2007) and appeasement by decreasing the risk of aggression both in dyadic affiliations (McKenna, 1978; Aureli & van Schaik, 1991) and triadic affiliations (Call *et al.,* 2002; Koski *et al.,* 2007). Thus conflicts may be the perfect breeding ground for this sort of exploitation where the victim gains an increased motivation to engage in grooming possibly guided by a fear of retaliation from whom she approaches or is approached by.

In the present research only two events were grooming given by the victim was higher than grooming received from the bystander in the consolation dyads. These happened both when Sandra was the victim and her sister, Tai, was the consoler. Since they are both kin and closely associated as shown by high amounts of grooming frequency (see Fig. 2) it is not likely to be any grooming exploitation. Curiously, another study involving Barbary macaques (Shutt *et al*., 2008) showed that giving the grooming rather than receiving it was associated with a decrease in stress levels, measured by presence of feacal glucocorticoid. These results illustrate that the costs and benefits of grooming are still a matter of dispute.

CHAPTER 4

The Bonobo Group: Methods, Results and Discussion

4.1. Research Methodology

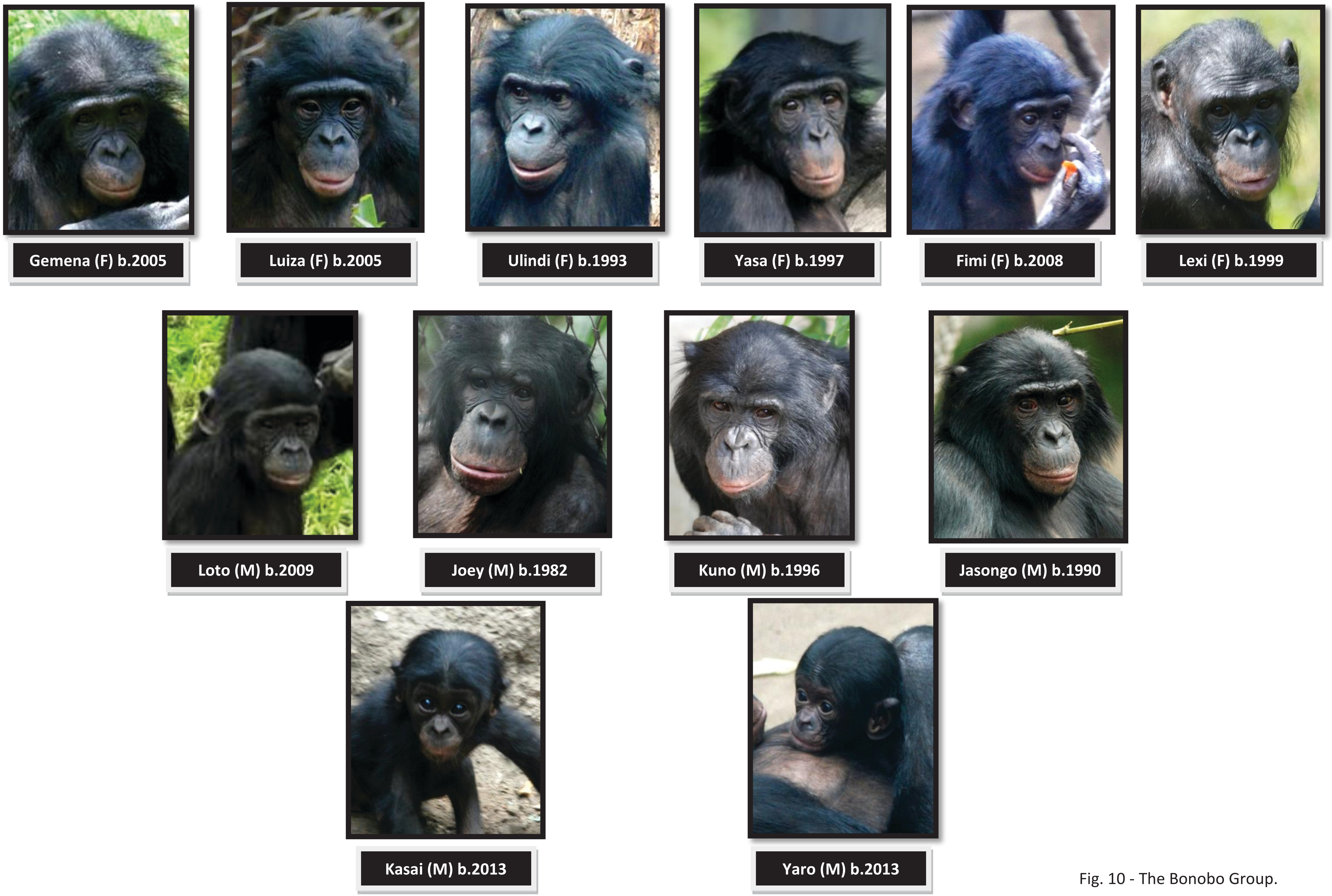
4.1.1. Study Subjects & Housing

This study was carried out on a group of bonobos (*Pan paniscus*) all born in captivity (see Fig10. for details). The bonobo group was comprised in total of 12 individuals (3 adult males, 3 adult females, 2 adolescent females and 1 juvenile female and 1 juvenile male plus 2 male infants). The group was housed at the Wolfgang Köhler Primate Research Center in the Leipzig Zoo, Germany since 2004. They had access to sleeping rooms (approx. 150m²), semi-natural indoor area (approx. 150m²), and outdoor enclosure (approx 4000 m²) both with many places for climbing (see Fig11a & Fig.11b). They were fed a variety of fruits and vegetables, occasionally supplemented by meat, eggs and yoghurt and had access to water *ad libitum*. Enclosures were equipped with environmental enrichment such as artificial termite mounds. Additional enrichment materials were provided for each subject every afternoon. The bonobo group underwent several changes throughout the study. From the start a new baby male had been born, then the alpha female and her son left the group, afterwards a new adolescent female was included and finally another male was born.

4.1.2. Observational Methods

Data was collected on both the bonobos and the A-Chimps, alternately, mornings and afternoons from March to September of 2013, in a combined total of 720 hours, 360h for the bonobos. All agonistic interactions between individuals were collected when visible by sampling all occurrences. Additional data on affilliative interactions (grooming, play, contact sitting) was gathered carried out at 5-min intervals (Altmann 1974).

Agonistic interactions were defined as any interaction involving aggressive behavioral patterns such as threat, charging display, brusque rush, chase, slap, pull, hit, trample or bite and involving submissive behavioral patterns and vocalizations such as bared teeth, whimper, screaming and urination (van Lawick-Goodall, 1968a; van Hoof, 1973). The identities of the opponents were recorded. A three stage scale of aggressive intensity was used borrowing elements from the three scale aggression of Palagi *et al.* (2004) and the five scale aggression of Clay and de Waal (2013).



Gemena (F) b.2005

Luiza (F) b.2005

Ulindi (F) b.1993

Yasa (F) b.1997

Fimi (F) b.2008

Lexi (F) b.1999

Loto (M) b.2009

Joey (M) b.1982

Kuno (M) b.1996

Jasongo (M) b.1990

Kasai (M) b.2013

Yaro (M) b.2013

Fig. 10 - The Bonobo Group.

Fig. 11a - The Bonobo Group Indoor Enclosure.

Fig. 11b - The Bonobo Group Outdoor Enclosure.

Stage 1 (low) involved threat, whistle bark and lunge without physical contact, stage 2 (medium) and involving physical contacts such as hit, slap or pull, along with display, charge and chase-fleeing, stage 3 (high) involved physical contacts such as severe or multiple hits, bites and stamping. All of these should be followed at least by bared teeth expressions whimpers, screams and urination by the victim respectively but not exclusively. If interactions displaying patterns from the stage 1 (no physical contacts) did not make the victim display any submissive behaviors they were not coded as an aggressive conflict.

Conflicts were also categorized based on directionality with unidirectional, meaning aggression from the aggressor to the victim and bidirectional, meaning aggression exchanged from between the two opponents. Whenever polyadic conflicts occurred (more individuals joined the conflict) the aggressor-victim dyad with the most intense aggressive patterns was chosen for the post-conflict observations.

The context of the conflicts was also categorized. For this study six categories of context were included: 1) Display, 2) Rough play, 3) Food, 4) Redirection, 5) Object competition and 6) Unknown. In order to differentiate whether opponents and bystanders tended to engage in affiliative interactions sooner after a conflict than in a control setting the Post-Conflict/Matched-Control method (PC/MC for short) introduced by de Waal and Yoshihara (1983) was used, where the focal animal was followed for 10 minutes and all self directed behaviors and interactions it had with other group members were recorded. If the conflict was resumed within 2 minutes the PC was cancelled starting only after the last aggressive pattern of the conflict event.

Self directed behaviors were recorded as a measure of anxiety in the Post-Conflict (Koski et al 2007; Fraser et al 2008) these were separated in duration of self-grooming and the frequency of self-scratching (a new scratching bout was assigned when scratching resumed after >5 seconds). All PC observations were conducted on both the victim and the aggressor with exception to situations in which, for technical reasons, the recording of both elements at the same time was not possible. In these cases, preference was given to the observation of the recipient of the aggression/victim.

Affiliative interactions occurring in the PC were defined as any interaction from or towards the victim involving affiliative behavioral patterns such as gentle touch, embrace, hold out hand invitations, kissing and contact sitting (de Waal, 1986; Goodall, 1986), other post-conflict affiliative behaviours described by de Waal for bonobos include mutual penis thrusting (in males); genito-genital rubbing (in females), ventro-ventral and ventro-dorsal mating between the sexes and manual genital massage (de Waal, 1987; 1993 *in* Mason & Mendonza, 1993). If the victim approached either the aggressor or the bystander in the PCs it was coded as a solicited affiliation, if the victim was approached by either aggressor or the bystander it was coded as an unsolicited affiliation.

The PC was matched with a control observation (MC) on the same individual at the same time of the previous conflict on the next possible day within 7 days in the absence of a previous conflict 10 minutes before the start of the control. The outdoor enclosure was divided into two sectors based on the activity and cohesion of the group, the indoor enclosure was counted as a third sector. Within these all individuals were visible and audible to each other with MC only starting when opponents were in the same sector. Only when these conditions met was the MC started.

4.1.3. Data Analysis

A total of 20 PC-MC pairs on adults, adolescents and juveniles were recorded (triadic affiliations N=6, dyadic affiliations N=5, both dyadic and triadic affiliations N=1, no affiliation N=8). For both reconciliation and triadic affiliation PC-MC pairs were labeled as "attracted" if the affiliation between opponents or between the victim and bystander occurred earlier in the PC than the MC, or just in the PC and labeled as "dispersed" if the affiliation occurred earlier in the MC than the PC, or just in the MC and labeled neutral if the affiliation occurred at the same time in both PC and MC or in neither. Any cases were reconciliation occurred together with triadic affiliation were coded separately in order to control for potentially confounding effects in cases were only reconciliation or triadic affiliation occurred. Agonistic supporters were considered as conflict participants and not as possible bystanders.

Relationship Quality. A weighted grooming network using UCINET 6 was made to visualize the grooming interactions (Fig. 3), relationship quality was assessed by the frequency grooming events among dyads, following Preutschof *et al.* (2002) as its study comprised a similar group size and grooming frequency. Two individuals were close when grooming events were >5 times, medium when dyads groomed 1-5 times and low if there were no grooming events. Conflict allies were also recorded when present, high supporters were individuals who aided another individual more than once, medium supporters aided once and low frequency supporters were never observed aiding in a conflict.

Post-Conflict Affiliations. The minimal number required of PC-MC pairs per focal animal was one. In order to evaluate reconciliation at the individual level the CCT method (corrected conciliatory tendency) was utilized (Veenema *et al.*, 1994) defined as "(Attracted Pairs minus Dispersed Pairs) divided by total pairs". For each individual the CCT was calculated, from which a mean CCT was obtained of the whole group. To test of triadic affiliations and its subset, consolation, the TCT method (triadic conciliatory tendency) introduced by Call *et al.* (2002) as a variation of the CCT method was used also defined as "(Attracted Pairs minus Dispersed Pairs) divided by total pairs" but substituting opponents for victim and bystander. Again, for each individual a TCT was calculated, from which a mean TCT was obtained for the whole group. Both individual CCTs and TCTs were compared via Wilcoxon Signed-Ranks test following the procedures suggested by Siegel and Castellan (1988) when N>15 an asymptotic test was used and when N_<15 an exact test was used.

To measure the stress levels in the PC-MC periods, rates of self-scratching (bouts per minute) and duration of self-grooming (seconds per minute) were recorded as in previous studies (Koski et al., 2007; Fraser et al., 2008). Individual means on the rates of self-scratching and durations of self-grooming per minute on PCs without dyadic or triadic affiliation were compared with individual mean levels of self-scratching and self-grooming during the entirety of the subsequent MC. A Wilcoxon Signed-Ranks test was used to compare the rates of self directed behaviors in the PC with their respective controls in the MC. No further tests were made due to the small sample size.

4.2. Results

Occurrence of Post-conflict Affiliations. The number of attracted, dispersed and neutral pairs were calculated for each of the 12 individuals. Regarding dyadic affiliations, The mean CCT for the whole group calculated from individual CCTs was 21,4% ± 17,4 SD. The mean TCT for the whole group also calculated from individual TCTs was 43,7% ± 12% SD. There were no significant results for consolation (unsolicited bystander affiliations with the victim. This result was confirmed by the time-rule method where most affiliations occurred in the first minutes of the PC: 58,5% of dyadic affiliations occurred in the first 3 minutes, 60% of triadic affiliations occurred in the first minute and of these triadic affiliations (see Fig. 13a & 13b).

Predition 2a) Triadic affiliations replace dyadic affiliations. Could not be significantly tested due to small sample size.

Prediction 3a) Stress reduction effects of PC affiliations. Though no significant results were found when testing for self-scratching before and after affiliation either in dyadic affiliations (Z=-1,289, P=0.37) and triadic affiliations (Z=-0.447, P=1). The same tendency found in the chimpanzees was also found in the bonobos, showing a higher rate of self-scratching after post-conflict affiliations and not before.

Prediction 3b) Grooming exploitation. No grooming asymmetries were observed during triadic affiliations.

Prediction 1c) More empathic bystander affiliation in bonobos. Circumstantial support against this prediction was found in that redirection of aggression was observed in the bonobos when no redirection was ever seen in the chimpanzees.

Prediction 2c) Lesser conflicts and more affiliation in the bonobos. A significant difference was found in the number of conflicts N=20 vs N=102. Conversely the chimpanzees showed a higher CCTs and TCTs when compared to the bonobos (however non significant).

Prediction 3c) Chimpanzees males are more aggressive than bonobo males. While proportions of the overall percentage of intensity levels of aggression coded for each conflict were comparable (see Fig. 15), male chimpanzees were involved in level 3 aggression frequently (N=21, 77.8% of all level 3 conflicts) while bonobo males did not reach that level (N=0).

Prediction 4c) Socio-sexual behaviours more prevalent in bonobo bystander affiliations. Only one such instance was observed in bonobos compared to two instances seen in the chimpanzees not counting matings.

Prediction 5c) Could not be tested due to significant small sample size.

Prediction 6c) Bonobo mothers engage actively in conflict prevention and bystander affiliation when a son is involved in comparison to chimpanzees. Only one mother met this criteria in the bonobo group, prediction could not be adequately tested.

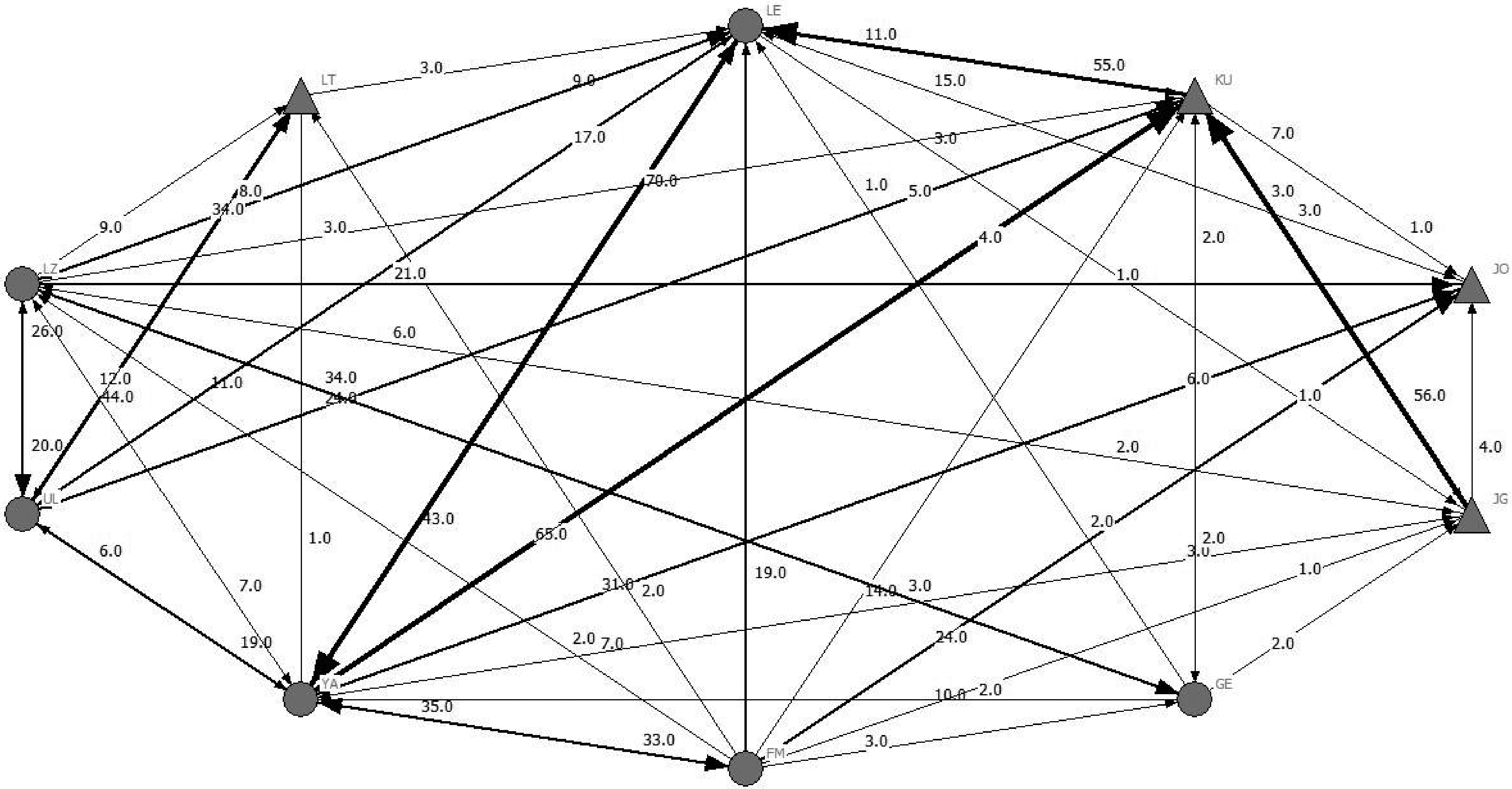


Fig. 12 - A weighted grooming network of the bonobos (triangles=males; circles=females).

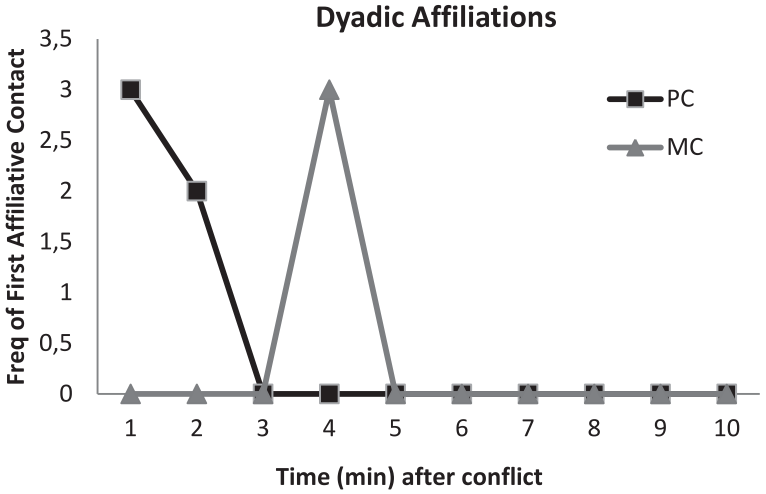


Fig. 13a - Distribution of the first affiliative contacts between opponents across time (pooled data from both solicited and unsolicited affiliations).

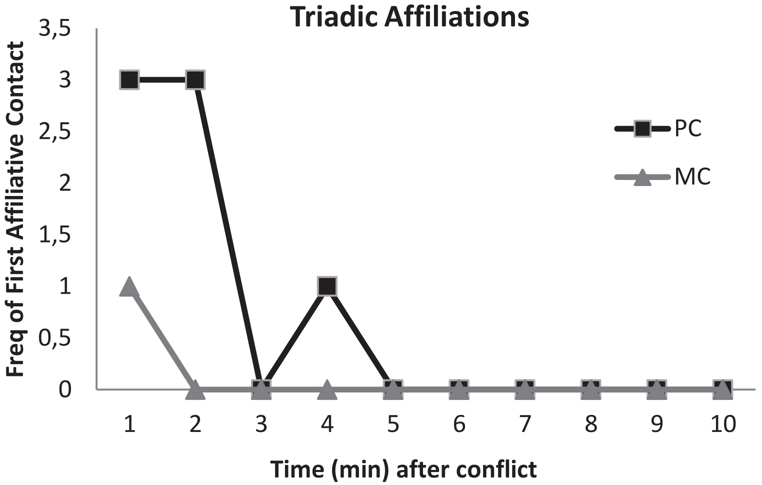


Fig. 13b - Distribution of the first affiliative contacts between opponents across time (pooled data from both solicited and unsolicited affiliations).

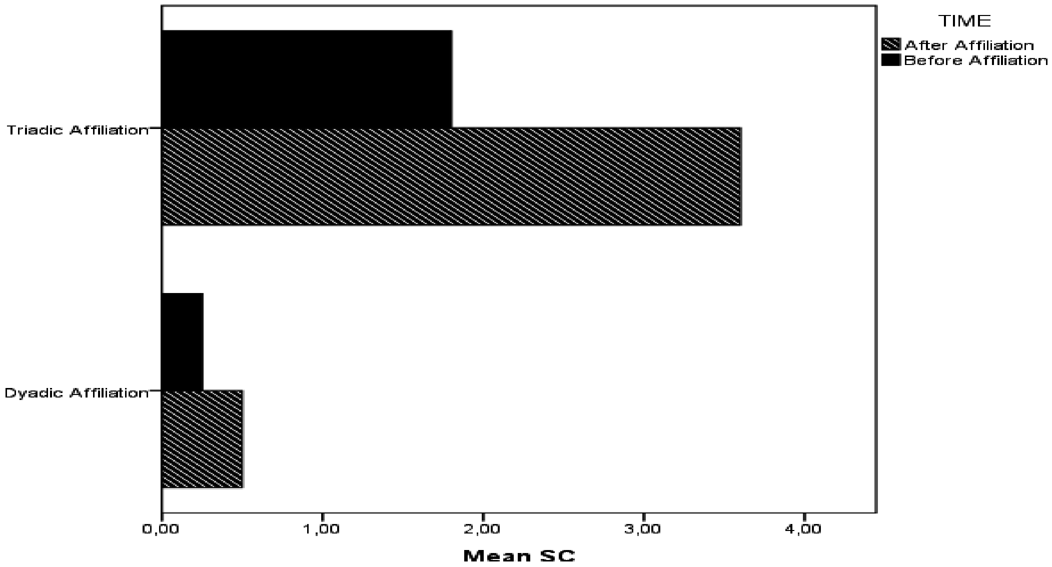


Fig. 14 - Victim's post-conflict scratching rates before and after affiliations with aggressor and bystander.

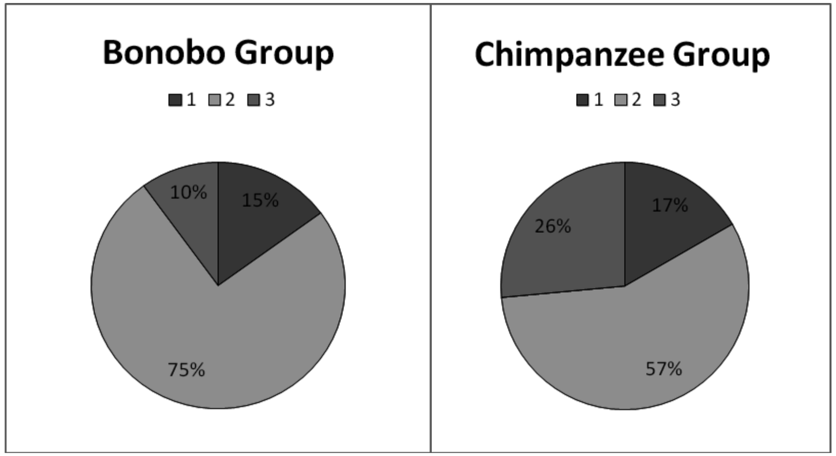


Fig. 15 - Percentages of the aggression levels occurring both in the Bonobo Group (1, N=3; 2, N=15; 3, N=2) and the Chimpanzee Group (1, N=17; 2, N=58, 3, N=27).

4.3. Discussion

The bonobo group showed a surprisingly low amount of conflicts during this research. For this reason this discussion will bear a more qualitative character than the previous one of the A-chimps which was more robustly supported by data analyses.
Only 20 PC-MC pairs in 360 hours of observation (group size N=8/10) not only when comparing it with the chimpanzees also in this study but with other studies on bonobo conflict, namely Palagi *et al.* (2004) with 167 PC-MC pairs in 968 hours of observation at the Appenheul Primate Park, Netherlands (group size N=11), or Clay and de Waal (2013) with 346 PC-MC pairs in 453 hours of observation at Lola Ya Bonobo, Congo (group size N=36). Reversing the underlying question: why do these studies show such a high number of conflicts in comparison to this one? One probable reason for this lies in methodology; for instance Palagi et al. (2004) coded aggressive conflicts at the lowest level starting with chase-fleeing without any submissive behaviour from the victim. This study in contrast only took aggressive interactions into account whenever the recipient of aggression displayed any such submissive behaviours (bared teeth, whimper or screaming); level 1 intensity level, according to Palagi et al. (2004) were not coded. These situations, however, were rare or even non-existent. Hence Palagi and colleagues greater number of conflicts is best explained by their coding of aggression where, in fact, the majority of the conflicts befell on the level 1 category (51%). Clay and de Waal (2013), at present, reported the greatest number of PC-MC in all of the bonobo conflict resolution research[15], they also boast the highest number of individuals in this type of study (group 1 = 21; group 2 = 15) which may account for a higher complexity and frequency of social interactions, aggression being one of them. They also emphasize a difference between orphan and mother-reared individuals where they found a significant difference in consolation (mother-reared individuals tended to engage more frequently in consolation than orphaned individuals). At one point the authors affirm that these individuals "*benefit from the support of their*

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[15] Not including Palagi and Norscia (2013) with a total PC-MC=555 which pool the data from 2000 July-October and 2002 April-July of the previous paper of 2004 with two new observation periods in September 2002 to June 2003 and 2009 August-October gathered in a total of 1674 hours of observation. Also, Surbeck et al. (2012), though not using the same PC-MC methodology, observed 577 aggressive encounters among bonobos gathered in a total of 420 hours of focal samples plus 2112 all occurrence samples at Lui Kotale, Congo.

mothers, which may consequently influence their temperament or willingness to approach others in distress". Conversely it can be argued that orphaned individuals become easier targets of aggression as they do not benefit from said support of their mothers during conflicts: it may be that the presence of mothers may act as a determent from hostility. Although, Clay and de Waal do not explicitly say if orphans are more at risk of aggression, they do show that adolescent males are the most frequent recipients of aggression. Considering that the study was made at Lola Ya Bonobo, the only sanctuary in the world responsible for the rescue of orphaned bonobos victims of the pet and bushmeat trade, it would benefit to see if there was a connection between individuals who frequently perform the aggression and who frequently receive it, with their rearing histories in mind.

But returning to the low numbers observed in this research: why are the bonobos so peaceful comparing to the other studies? Unlike the A-chimps, the bonobo group suffered from fluctuations in its composition all through this study, first the alpha female (Ulindi) left with her son (Loto), afterwards there was a birth (Yaro) and finally a new adolescent female (Gemena) joined the group. While the alpha female was present, two of males (Jasongo and Joey) were kept separated from her during the mornings and left to the sleeping quarters in the afternoon, while the alpha joined with the rest of the group. This was an arrangement the zookeepers made since the conflicts between them and the alpha had been characterized with a high rate of aggression, therefore for safety reasons these males were kept separated from her. Another reason might have been the design of the enclosures, unlike the A-chimp group where most of the individuals were visible t most of the time the bonobo indoor enclosure did not constantly allow for a full view of its individuals either in the tower or at ground level. Indeed some conflicts were indeed scratched for the reason that an individual would at times go out of sight. One additional cause may have had to do with the aim of the study where the bonobos were observed in alternation with the chimpanzees with the rarer conflicts among the bonobos emerging, at times, when observations were being done on the A-chimps. More attention could have been dedicated to the bonobos but it was precisely the point of the study to compare rates of conflict and post-conflict behaviour in the two species for the same amount of observational time.

Because the sample is so small with regards to conflicts, all related statistical analyses offer little power in terms of hypotheses testing. Even if significant results are to be found, because the size of the sample it is problematic to extrapolate the hypotheses for a whole population as true effects are difficult to detect. In spite of this, for the purposes of this thesis, they were still done in order to make a comparison, albeit superficial, to the chimpanzees also present in this study. In spite of this, there is support for the prediction that posited that chimpanzees would show more overall aggression in comparison to bonobos.

The prediction that bonobos would use more socio-sexual contacts in triadic affiliations did not find much support: only one case out of seven did an bystander and victim interacted in this sort (Loto consoling Kuno). Concerning the A-chimps, there was an individual, again Tai that would use a genital to mouth affiliative behaviour in two events, one consoling Sandra and another consoling Corrie. Also at one instance, not post-conflict related, it was observed Kara getting shocked from the wire while trying to reach for a food item and Tai went in and affiliated this way towards Kara thus reinforcing the stress reduction motivation underlying this behaviour. These instances were rare in part, probably, due to the semi-arboreal nature of the pose where Tai's hands would have to be clinging onto a branch. Curiously it was her mother, Riet that reconciled the most presenting her rear as to buffer aggression, but which also encouraged socio-sexual contacts. The fact that bonobos did not show a great deal of socio-sexual behaviours during triadic affiliations suggests that it may be a behaviour more prevalent in dyadic affiliations where there is a need to repair relationships or where it benefits both individuals to lower their stress levels than in triadic affiliations. There is significant evidence for this, Clay & de Waal (2014) did show that socio-sexual behaviours differed significantly from dyadic affiliations to unsolicited triadic affiliations (43.4% in reconciliation and 22% in consolation).

Another prediction, that bonobos would show more empathetic consolation behaviours did not find support. In fact, during conflicts two cases of redirection were observed, both Luiza venting her frustration on Jasongo (2 cases out of 6 conflicts were LZ was the aggressor). No redirection was ever observed in the chimpanzees.

The last prediction, that posited that bonobo mothers would intervene and console their sons a great deal more than chimpanzees. Conflict interventions were observed only once in the bonobos (Ulindi and Loto) and twice in the form of conflict alliance (Natasha and Frodo). However no mothers were observed consoling their kin in the A-chimps in contrast to the bonobos where one case was observed (Ulindi and Loto).

CHAPTER 5

General Discussion and Conclusion

5.1 General Discussion and Conclusion

A deliberate choice was made that the species investigated in this comparative research would be chimpanzees and bonobos due to their evolutionary closeness to each other and to humans. Comparative studies posit, in theory, clear advantages, for instance, the raw data of different species can be accessed, analyzed and discussed systematically in a single written work, sometimes with convincing null results that would not be publishable otherwise (Maclean *et al.,* 2012).

When measuring these results, particularly the chimpanzees and other research on chimpanzee conflict resolution, a complex picture emerges. A great deal of the reported variation cannot always be accounted for, though in some cases, suggestions have been made attributing these to group particularities. This too reveals the importance of replication of the research in the same species, 6-7 authors publishing 11-12 papers on chimpanzee conflict resolution is still few considering their variation, especially if a meta-analysis were to be done. It becomes challenging to test phylogenetic assumptions when it seems there are cultural conflict styles to be accounted for.

It is not merely the genus Pan, there are several examples in which primates in general show an immense behavioural adaptive potential. One notable fortuitous account is the Sapolsky and Share (2004), in which part of a troop of wild olive baboon males that was being followed by the authors started feeding on a nearby garbage dump. Subsequently, an outbreak of bovine tuberculosis spread from infected meat killed nearly half of the males of the troop between 1983 and 1986. These were also the most aggressive and dominant males in the troop leaving a faction of atypically unaggressive males. Nearly a decade later, observations done with this troop revealed that while none of the original surviving males were left, the new ones that had joined the group since had also adopted a relaxed social style, marked with low degrees of aggression and high degrees of affiliation towards the females. Another telling example is Hans Kummer's (1971) experimental field studies on the socialization of wild baboons where he would put two species of baboon interacting with one other, both with strikingly different social systems (olive baboon and hamadryas baboon).

Kummer would trap olive females and released them into hamadryas groups, conversely he would do the same with hamadryas females. The research showed that it took a surprisingly low amount of time for the females to acclimate to the new social environment. Cross species interactions did not stop there, de Waal and Johanowicz (1993) put two juvenile rhesus macaques (a typically despotic species where post-conflict affiliation is low) with a group of stump tailed macaques (a typically tolerant species with higher post-conflict affiliation rates) and over the course of a few months the rhesus macaques started exhibiting higher rates of reconciliation behaviours. It is also telling that neither of the two adopted the stump tailed macaques distinct gestures such as hold-out bottom or teeth chattering and instead increased their own conciliatory gestures. When put again in a rhesus group the two juveniles kept on with their affiliative behaviours.

The phrase that perhaps illustrate the richness of behaviour in the Pan genus is the late Toshisada Nishida's "*Chimpanzees are always new to me*" (in: de Waal, 2011). We have come to find in spite of phylogeny and social organization, that we are dealing with a species that displays a high degree of plasticity with long infancies where important learning takes place (Goodall, 1986) the same rationale applying to bonobos with recent comparisons revealing that they actually have a delayed development in comparison (Wobber *et al.,* 2010).

The results found in this research are still quite fragmentary to support an empathic integrated hypothesis versus an selfish integrated hypothesis separated by phylogeny alone. In fact, if such an investigation would most likely require a meta-analysis with information on several captive groups of both chimpanzees and bonobos in captivity and in the wild. Though conflict resolution has been now research in over 30 years it's methodologies keep improving on each other. This study has benefited from advances such has de Waal & Yoshihara (1983) PC/MC method, Aureli & van Shaik (1991) time rule method, Veenema et al.'s corrected conciliatory tendency method (Veneema *et al.,* 1994) and Call *et al.* (2002) triadic conciliatory tendency method. There are new finer grained methods both statistical and methodological that can be used in a further research. In the future it would be ideal to use the principal component analysis (PCA) on the three main components of relationship quality (value, security, compatibility) which have not yet been used in bonobo conflict research and scarcely on chimpanzees (Fraser *et al.*, 2008b) preferably in a larger bonobo group or at least equal in size with the chimpanzees. Also social network analysis which was only hinted at in this research should provide for powerful methods in the future such as the Elo-rating (Neumann *et al.*, 2011) which updates dominance ratings constantly following an aggressive interaction. By analyzing the factors involved in conflicts among non-human primates we can gain a wider understanding on the evolutionary pressures that guided the conflict resolution strategies in humans.

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