RECONCILIATION, CONSOLATION AND RELATIONSHIP QUALITY IN CHIMPANZEES

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CONTENTS

ABSTRACT

Conflicts of interest arise regularly in the lives of all group-living animals. The escalation from conflicts of interest to aggressive conflicts can be costly, and may damage the relationship between opponents, resulting in the loss of benefits afforded by the relationship and increased stress levels. These costs, however, may be mitigated through post-conflict interactions such as reconciliation (a post-conflict affiliative reunion between former opponents) and consolation (an affiliative post-conflict interaction directed from a third-party towards the recipient of aggression).

This study investigated post-conflict behaviour and relationship quality in 22 adult chimpanzees at Chester Zoo. The occurrence of reconciliation and consolation was demonstrated. Evidence for behavioural specificity (i.e. context-specific use of certain behaviours) was found for both reconciliation and consolation, which, along with high conciliatory tendencies, suggests an explicit style of post-conflict behaviour. Behavioural measures of stress were used to demonstrate that both reconciliation and consolation reduce post-conflict stress levels in recipients of aggression, providing the first evidence for the stress-alleviating function of consolation. Principal components analysis was employed to extract three key components of relationship quality from nine behavioural variables. Based on the loadings of the behavioural variables, the components were labelled Value, Compatibility and Security. The effects of multiple factors, including the

components of relationship quality, on the occurrence of reconciliation and consolation were analysed. Reconciliation occurred in the absence of consolation, and consolation occurred in the absence of reconciliation, indicating that consolation might function as an alternative to reconciliation. Recipients of aggression were more likely to receive consolation from individuals with whom they had a more valuable relationship, suggesting that chimpanzees are particularly responsive to the distress of valuable partners. Thus, chimpanzees may respond empathically to valuable partners by consoling recipients of aggression, thereby reducing their post-conflict stress levels, especially when reconciliation does not occur.

CHAPTER 1

General Introduction

1.1. Group Living

Conflict management is integral to the maintenance of group cohesion and the benefits associated with group living. Group living arises when the benefits of sociality outweigh the costs (Krause & Ruxton, 2002). As the resulting group size and composition varies considerably across taxa, it seems likely that the benefits and costs of group living also vary according to the species and habitat (Silk, 2007a).

One of the advantages of group living in primates may be predator avoidance (van Schaik, 1983). Large groups may be able to detect predators earlier and reduce the individual cost of vigilance (Stanford, 2002). Furthermore, the dilution effect of a large group lowers the individual risk of predation, and several members of a group may be able to defend themselves against a predator when an individual could not (Kappeler, 1997). Conversely, studies investigating the link between predation rate and group size in primates have reported mixed results, with some reporting a positive relationship (Anderson, 1986) and others reporting a negative relationship (Isbell, 1994). If group size is an effective anti-predator strategy, however, no relationship between group size and predation rate would be expected (Cheney &

Wrangham, 1987), but rather a positive relationship between group size and predation *risk* (Dunbar, 1988; Hill & Dunbar, 1998). If predator pressure were the primary contributor to the evolution of sociality, animals would be expected to form temporary parties when the risks of predation were highest, rather than forming permanent groups (Wrangham, 1979).

Defending resources from neighbouring groups is hypothesised to be another main benefit of group living in primates. In areas where food is clumped or monopolisable, groups have an advantage in defending such resources over solitary individuals (Dunbar, 1988). Female reproductive success is strongly linked to the quality and quantity of available food resources (e.g. Emery Thompson et al., 2007), thus females form groups when group living maximises access to food (Wrangham, 1979; Koenig, 2002). Males may then form part of such groups in order to defend reproductive access to females (Nunn & van Schaik, 2000). Other benefits of group living may include a reduced risk of infanticide (van Schaik, 1997), the opportunity for alloparental care (Ross & MacLarnon, 2000), cooperative hunting (Boesch et al., 2006a) and access to mates (Silk, 2007a).

1.2. Conflicts of Interest

Group living, however, also entails significant costs in terms of intra-group competition for access to limited resources. Conflicts of interest can arise between competitors when only one can gain possession of a critical resource such as food

(Koenig, 2002; Vogel et al., 2007) or females (Nunn & van Schaik, 2000). In addition to competing over the same resource, group members may also face difficulties when pursuing different objectives or have different motivations. Thus, conflicts of interest may arise between potential mating partners as a result of differing interests for males and females (Chapman et al., 2003; Chapman, 2006) or between parents and offspring, over weaning or scheduling of activities (Trivers, 1974; Maestripieri, 2002). Decisions may also be a source of conflict of interest, such as decisions over the direction of travel (Boinski, 2000), the change of group activity (Conradt & Roper, 2003), or the performance of behaviours requiring mutual consent such as grooming or playing (Bernstein, 2007).

Conflicts of interest frequently occur in all group-living animals, but their consequences have the potential to compromise the benefits associated with group living. If conflicts of interest are not managed, they may escalate into aggressive conflict, which may be costly for all participants through risk of injury, energetic costs, physiological costs such as increased stress levels and potential damage to the relationship between opponents, thus losing benefits afforded by the relationship (de Waal, 2000b; Aureli et al., 2002). The dissolution of a valuable relationship between partners may then impact on the cohesiveness of the group as a whole. Indeed, the removal of components necessary for conflict management within a group, such as disproportionately powerful group members who would normally intervene in aggressive conflicts between others, has been shown to increase levels of conflict and aggression, decrease socio-positive interactions and decrease the operation of repair mechanisms within the whole group (Flack et al., 2005). Thus, conflicts of interest between group members could impact negatively not only on the individuals involved but on the entire group. This result, however, is unlikely, as group living, and thus cooperation between group members, is such a valuable commodity that competition between partners is constrained to protect cooperative relationships (de Waal, 2000a). Moreover, conflict management strategies, including aggression avoidance and post-conflict mechanisms, may mitigate potential negative consequences of conflicts of interest by reducing the chances of aggressive escalation or repairing social damage caused by aggression if escalation does occur (Aureli & de Waal, 2000).

1.3. Aggressive Conflict

The Relational Model (de Waal, 1996; de Waal, 2000a) addresses the issue of resolving conflicts of interest whilst minimising costs of aggressive conflict. According to the model, when faced with conflicts of interest, potential opponents have a number of possible options, including tolerance, avoidance of confrontation, or aggressive conflict. The value of the source of the conflict of interest and the value of the relationship between competitors are paramount to the decision-making process, and thus whether aggressive escalation occurs. As the value of the resource or commodity in question increases, the benefits of aggressive conflict increase, but as the value of the relationship between competitors increases, the overall benefit of aggressive conflict decreases as relationship damage becomes more costly. However, if damage to the relationship can be repaired through post-conflict interactions, the benefits of aggressive conflict even between highly valuable partners may outweigh the costs if the value of the commodity is sufficiently high. Thus, the value of the commodity and the quality of the relationship between partners determine the likelihood of aggressive escalation, in addition to probability of relationship repair and the risk of injury (de Waal, 2000a). Wittig & Boesch (2003b) extended the Relational Model to take into account the relative fighting abilities of potential opponents, and thus the likelihood of winning a contest, in addition to the duration of the aggressive conflict, which would influence the energetic costs of aggression. In accordance with the extended Relational Model, wild chimpanzees (*Pan troglodytes*) were more likely to fight over resources that were most important to them, with females more likely to initiate aggressive conflict over food whereas males were more likely to engage in aggressive conflict in social contexts (Wittig & Boesch, 2003b). Furthermore, dominant individuals were initiators of longer, more aggressive conflicts as they could afford the additional energetic costs and the likelihood of winning was higher, although dominant individuals were more likely to fight non-cooperative partners to limit social damage. In contrast, subordinate partners limited the physical costs of aggression by initiating short conflicts with a lower intensity but risked higher social costs, which could be mitigated later though post-conflict interactions (Wittig & Boesch, 2003b).

1.4. Conflict Avoidance Strategies

The most effective strategy for reducing costs of aggressive conflict when faced with a conflict of interest is to prevent aggressive escalation. Indeed, to go one step further, the ideal strategy would be to reduce the likelihood of a conflict of interest arising in the first place. Grooming in primates has been shown to have a calming influence on the recipient, reducing behavioural and physiological correlates of stress (Schino et al., 1988; Aureli et al., 1999). Appeasing and submissive behaviours signal benign intent and/or submissive status (de Waal & Luttrell, 1985; Colmenares et al., 2000; Whitham & Maestripieri, 2003; Fraser & Plowman, *in press*). Thus, during periods of tension, when aggression may be more likely, appeasing, reassuring or submissive behaviour might prevent such conflicts from occurring (Judge, 2000). One situation in which conflict avoidance strategies can be studied is the period of tension prior to scheduled feeding times in provisioned groups. This situation requires individuals to anticipate an event known to elicit conflicts and to selectively increase behaviours that function to reduce tension and promote tolerance among partners to pre-emptively reduce the likelihood of conflict (Koyama, 2000). A number of primate species have been shown to accomplish this feat. Stump-tailed macaques (*Macaca arctoides*) were found to selectively increase time spent grooming alpha males, the most likely initiators of aggression, prior to feeding times, suggesting that the macaques were either appeasing likely opponents or strengthening coalitions with influential allies (Mayagoitia et al., 1993). Conversely, chimpanzees increased their rate of grooming towards kin and usual grooming partners, rather than dominant individuals (Koyama & Dunbar, 1996). As pre-feed association patterns were strongly correlated with spatial proximity during feeding times, the chimpanzees may have adopted a strategy to increase tolerance with those most likely to share food, and with those with whom conflicts of interest were most likely to arise. Furthermore, chimpanzees only increased affiliative behaviour prior to clumped feeding, when competition was higher and aggressive conflicts were more likely, and not prior to scatter feeds, when competition was lower and aggression less likely (Koyama & Dunbar, 1996). An increase in affiliative contacts such as kissing and embracing during 'celebrations' prior to feeding in chimpanzees has also been shown to reduce the occurrence of food-related aggression (de Waal, 1992) Bonobos (*Pan paniscus*) increase rates of social play in adults and juveniles prior to feeding times, seemingly to reduce tension and increase tolerance, as playing among adults is correlated with rates of co-feeding (Palagi et al., 2006b). During feeding, however, bonobos increase the rate of socio-sexual behaviours, possibly as a mechanism for reassurance and appeasement (de Waal, 1992; Palagi et al., 2006b).

Where food resources are patchily distributed, conflicts of interest can arise when groups reach a size where patches can be monopolised by a few individuals (Janson & Goldsmith, 1995). Thus, primates living in fission-fusion societies may reduce intra-group competition, and thus the likelihood of aggressive escalation, by fissioning into temporary subgroups according to local resource availability (Anderson et al., 2002). Fission may therefore function as a conflict management strategy. Conversely, fusion of subgroups may lead to aggressive conflict among subgroup members (Muller, 2002; Aureli & Schaffner, 2007). Under such circumstances, affiliative interactions between members of each subgroup may reduce tension and thus the likelihood of aggressive escalation. Spider monkeys (*Ateles geoffroyi*) embrace members of joining subgroups upon fusion, both in captivity (Schaffner & Aureli, 2005) and the wild (Aureli & Schaffner, 2007). Moreover, embraces at fusion have been shown to reduce the probability of aggression (Aureli & Schaffner, 2007). The risk of such a behaviour in exposing vulnerable body parts to potential aggressors increases the reliability of the signal of benign intent (Schaffner & Aureli, 2005). Chimpanzees also increase their rate of affiliative interactions after periods of separation, suggesting that these behaviours are linked to tension reduction and aggression avoidance strategies (Nishida et al., 1999; Okamoto et al., 2001).

High density conditions may be a source of tension and thus could potentially lead to an increase in aggressive conflict among group members. However, a number of studies have provided evidence for coping strategies in primate and non-primate species that may reduce the likelihood of severe aggression (reviewed in Judge, 2000). De Waal (1989) proposed a coping model in which primates increased rates of affiliative and submissive interactions during crowded conditions to reduce tension and the increased risk of aggression. While this model has been supported by some studies (e.g. Nieuwenhuijsen & de Waal, 1982; Sannen et al., 2004; Judge et al., 2006), others have found a decrease in affiliative, submissive and aggressive behaviours under crowded conditions (Aureli & de Waal, 1997; van Wolkenten et al., 2006), suggesting that rather than adopting a tension reduction strategy, these animals have adopted an inhibition strategy, reducing all social interactions in order to reduce the risk of aggressive conflict. Further studies have reported a decrease in social behaviour but an increase in mild aggressive and submissive behaviour (Judge & de Waal, 1993; Aureli et al., 1995), suggesting that the animals have adopted a conflict avoidance strategy, minimising the risks of severe aggression through warning threats and reaffirmation of dominance status. Strategies adopted, however, may vary according to duration of crowding (Judge, 2000). It is likely that the coping model, in which animals actively reduce the chances of aggressive escalation through increased affiliative and submissive behaviour, would take time to develop (de Waal, 1989), and thus inhibition and conflict avoidance strategies may be temporary responses to short-term crowding, before coping strategies have been developed. Accordingly studies of long-term crowding tend to conform to the coping model (Judge, 2000; Cordoni & Palagi, 2007), while studies investigating both short- and long-term crowding have found a change in strategy employed as the duration of crowding changes (Judge & de Waal, 1997; Videan & Fritz, 2007). However, the response to crowding does not always appear to be uniform across the group as individuals may be flexible in their response, selectively increasing rates of affiliation and decreasing rates of aggression towards their most likely opponents (Judge & de Waal, 1997; Caws & Aureli, 2003; Videan & Fritz, 2007).

Dominance-subordination relationships may also function as a mechanism of conflict avoidance. Traditional definitions of dominance were based primarily on the outcome of aggressive interactions or possession of resources (Drews, 1993), but dominance may also manifest itself in other ways. For example, if possession of resources were an absolute indicator of dominance status, taking food from another individual would unequivocally indicate that the taker of food was dominant over the previous possessor. However, a subordinate individual may be allowed to take food from a dominant partner, without any change to their dominance-subordination relationship, provided submissive signals are given (de Waal, 1986). Thus, inconsistencies in aggressive outcomes or possession of resources may not always be indicators of inconsistencies in dominance. Certain unidirectional signals, however, remain consistent in their direction regardless of the outcome of conflicts or possession of resources and can be recognised as formal indicators of dominance or submission (de Waal, 1986; Preuschoft, 1999; Preuschoft & van Schaik, 2000). Dominance-subordination relationships are long-term dyadic relationships characterised by an asymmetric distribution of power (Preuschoft & van Schaik, 2000). Such relationships depend on familiarity between members of a group and a shared history of interactions so that potential opponents have prior knowledge about each other's abilities. This saves time and energy that may otherwise be spent assessing the relative strength of unfamiliar opponents when conflicts of interest arise and saves the costly reoccurrence of the aggressive conflicts (Preuschoft & van Schaik, 2000). Where the outcome of a conflict is predictable, formal indicators of subordination or dominance may help to regulate the occurrence of aggression. Formal signals of subordination, such as pant-grunt greetings in chimpanzees (Noë et al., 1980; de Waal, 1982; Goodall, 1986) or silent bared-teeth in rhesus macaques, *Macaca mulatta*, (de Waal & Luttrell, 1985), which are always directed up the hierarchy, may allow subordinate individuals to signal their competitive inferiority and thus gain tolerance from dominant partners without risking attack (de Waal, 1986). Formal signals of dominance directed down the hierarchy, such as mock-bites in stump-tailed macaques (Maestripieri, 2005), may allow dominant individuals to arrest potentially disruptive conflicts with subordinate partners without wasting energy on aggressive conflict (Preuschoft & van Schaik, 2000). Thus, dominance may function as a conflict management strategy by conventionalising priority of access, therefore avoiding aggressive escalation over competitive resources (Preuschoft & van Schaik, 2000).

1.5. Post-Conflict Behaviour

1.5.1. Reconciliation

While conflict avoidance strategies may deal with a conflict of interest before it into escalates to aggression, aggressive conflicts are nonetheless a common occurrence in many gregarious species. Although aggressive escalation may be a last resort when other conflict management options have been explored (de Waal, 1996), post-conflict interactions may reduce some of the costs associated with aggression, thus minimising the risks of aggressive escalation (Aureli et al., 2002; de Waal, 2000b). Prior to the systematic study of post-conflict behaviour in primates, the traditional view was that aggression functioned to cause dispersal in all animals and thus a decreased probability of contact between opponents following aggressive conflict was predicted (the 'dispersal hypothesis'; reviewed in de Waal, 1993; de Waal, 2000a, 2000b). Although some conflicts might end in dispersal, this hypothesis was questioned when de Waal and van Roosmalen (1979) showed for the first time that chimpanzees sought out their former opponents after a conflict and were actually more likely to engage in affiliative behaviour immediately following the conflict than during subsequent interactions. The first post-conflict affiliative interaction between former opponents was labelled 'reconciliation' (de Waal & van Roosmalen, 1979). Although the term reconciliation implies a proven function of relationship repair, it was used as a heuristic term, from which predictions pertaining to relationship maintenance could be generated (de Waal, 1991; de Waal, 1993; de Waal, 2000a, 2000b). Thus, demonstrating the occurrence of reconciliation is not the same as demonstrating a relationship-repair function, although the latter is implied by the term reconciliation. Aureli et al., (2002) proposed a predictive framework within which the occurrence of reconciliation across species is determined according to the potential loss of benefits resulting from aggressive conflict and thus the need for relationship repair. Thus, reconciliation is possible in any species in which there are individualised relationships and intra-group aggression occurs, provided that aggression has the potential to disrupt relationships. If relationships are of sufficient value, the benefits of relationship repair should outweigh the risks of renewed attack, thus making reconciliation worthwhile (Aureli et al., 2002). Accordingly, since the first study on reconciliation in chimpanzees (de Waal & van Roosmalen, 1979), reconciliation has been demonstrated in all primate species in which the behaviour has been investigated with only a few exceptions, for which explanations have been provided (Aureli & de Waal, 2000; Arnold & Aureli, 2007).

Red-bellied tamarins (*Sanguinus labiatus*), are one of those exceptions, as their highly secure and cooperative relationships preclude disruption by conflict

(Schaffner et al., 2005). The tamarins are dependent upon each other for cooperation to such an extent that relationships cannot afford to be damaged, thus aggression is both rare and mild and does not appear to affect the relationship between partners (Schaffner & Caine, 2000). As relationships are not disturbed by aggressive conflict, there is no need for post-conflict relationship repair, and thus no need for reconciliation. Black lemurs (*Eulemur macaco*) present another exception to the occurrence of reconciliation (Roeder et al., 2002). In this case, relationships between adults are either so valuable that aggressive conflict is extremely rare, and if it does occur, might not disturb the relationship, or are so hostile that the relationship affords no benefits to either opponent. If the relationship is of such little value, no benefits are lost in aggressive conflict and there is nothing to repair, so reconciliation is not necessary in either case. There is some debate about the occurrence of reconciliation in ring-tail lemurs (*Lemur catta*), as original findings mirrored those for black lemurs (Kappeler, 1993), but evidence for reconciliation between valuable partners has since been found when the post-conflict period was extended to an hour (Rolland & Roeder, 2000). In a further study on two groups of ring-tail lemurs, reconciliation was demonstrated within the normal 10-minute post-conflict period in one group but not in the other (Palagi et al., 2005). The variation in the occurrence of reconciliation in the two groups, however, was attributed to seasonal differences in tolerance. Females may be more tolerant of males during the mating season, when relationships with males may be of higher value, and thus more likely to be worth repairing, than during the birthing season, when costs associated with the risks of reconciliation may have been too high for reconciliation to be worthwhile (Palagi et al., 2005). Another apparent exception to the occurrence of reconciliation in primate species is the case of Hanuman langurs, *Semnopithecus (Presbytis) entellus entellus*, (Sommer et al., 2002). Although the authors reported an overall absence of reconciliation in favour of post-conflict avoidance of former opponents, post-conflict affinity was observed between opponents within some age-sex classes, and thus reconciliation is likely to occur in Hanuman langurs among dyads for which the benefits of relationship repair outweigh the costs. Furthermore, their conclusion that majority of reports of reconciliation amongst primates are artificially inflated by captive conditions is unlikely to be valid. A thorough investigation into the sources of variation in reconciliation rates found no evidence that individuals in wild populations were less likely to reconcile than those in captive populations (Colmenares, 2006).

Reconciliation is not specific to primates, indeed the predictive framework proposed by Aureli et al. (2002) may be applicable to all gregarious animals. Although few studies have systematically investigated post-conflict behaviour in non-primate species, reconciliation has been demonstrated in spotted hyenas, *Crocuta crocuta,* (Hofer & East, 2000; Wahaj et al., 2001), dolphins, *Tursiops truncates,* (Weaver, 2003) and domestic goats, *Capra hircus,* (Schino, 1998). Interspecific reconciliation has also been observed between highly valuable partners such as cleaner wrasse *Labroides dimidiatus* and their client reef fish (Bshary & Würth, 2001). Further anecdotal evidence is available for reconciliation in feral sheep, *Ovis aries,* (Rowell & Rowell, 1993), dwarf mongooses, *Helegale undulata,* (Rasa, 1977), lions, *Panthera leo,* (Schaller, 1972) and mouflons, *Ovis ammon,* (Pfeffer, 1967) (reviewed in Schino, 2000).

The term reconciliation implies a relationship repair function, and this function has been demonstrated in all studies that have tested for it (see below). In fact, reconciliation may reduce the costs of aggressive conflict in a number of ways. Aggressive conflict may damage the relationship between opponents, thus reducing tolerance around resources and reducing the likelihood of agonistic support in future conflicts (Aureli et al., 2002). The original recipient of aggression is more likely to receive further aggression from both the original aggressor (Aureli & van Schaik, 1991; Cords, 1992; Watts, 1995a; Silk et al., 1996; Kutsukake & Castles, 2001; Wittig & Boesch, 2003a; Koski et al., 2007a) and from other group members following aggressive conflict (Kutsukake & Castles, 2001; Aureli et al., 1989; Wittig & Boesch, 2003a; Koski et al., 2007a). Following aggressive conflicts, recipients of aggression have also been shown to exhibit increased levels of self-directed behaviours (Aureli et al., 1989; Aureli, 1997; Castles & Whiten, 1998; Cooper et al., 2007; Koski et al., 2007b; Kutsukake & Castles, 2001; Majolo et al., 2005; Schino et al., 2007), a behavioural indicator stress of anxiety in primates (Maestripieri et al., 1992; Troisi, 2002). This effect may be due to the uncertainty about further aggression or about the status of relationships that may have been damaged by the preceding conflict (Aureli & van Schaik, 1991). Interestingly, some studies have also reported an increase in post-conflict levels of self-directed behaviours in aggressors (Aureli, 1997; Castles & Whiten, 1998; Das et al., 1998; Cooper et al., 2007; Schino et al., 2007), suggesting that the degeneration of a valuable relationship through aggressive conflict is detrimental to both opponents. Although reconciliation cannot reduce some costs of aggression, such as energy expenditure and injury, it has been shown reduce the likelihood of further aggression (Aureli & van Schaik, 1991; de Waal, 1993; Cords, 1992; Koyama, 2001; Kutsukake & Castles, 2001) and reduce levels of self-directed behaviour (Aureli & van Schaik, 1991; Castles & Whiten, 1998; Kutsukake & Castles, 2001; Fujisawa et al., 2005; Cooper et al., 2007), suggesting a stress-alleviating mechanism.

Reconciliation has also been shown to repair the relationship between former opponents in a number of ways. Cords (1992) used an experimental approach in which tolerance in long-tailed macaques (*Macaca fascicularis*) following reconciled conflicts between dominant and subordinate opponents was compared with tolerance following similar, but non-reconciled, conflicts. While non-reconciled conflicts resulted in reduced tolerance around a resource compared to baseline, tolerance after reconciled conflicts was restored to baseline levels. Cheney & Seyfarth (1997) conducted a series of playback experiments on female baboons (*Papio cyanocephalus ursinus*), who direct reconciliatory grunts towards their victims after aggressive conflicts (Cheney et al., 1995). Victims who heard their opponents' grunts played back to them after an aggressive conflict displayed an increased tendency to approach, and tolerate approaches from, their opponents compared to control conditions. Koyama (2001) investigated the longer-term effects of reconciliation on opponent relationships in wild Japanese macaques (*Macaca fuscata*) and found that grooming, proximity and approach rates between former opponents were significantly lower than baseline in the ten days following non-reconciled conflicts, but were restored to baseline levels but in the ten days following reconciliation. In wild chimpanzees, Wittig & Boesch (2005) showed that the post-reconciliation latency to affiliation between opponents was equal or shorter than baseline latency to affiliation, but opponents took significantly longer to affiliate when reconciliation did not take place. All of these studies show that reconciliation repairs the relationship between opponents and restores interactions and tolerance to baseline levels.

1.5.2. Consolation

Post-conflict interactions may also involve third-parties, i.e. group members other than the opponents or supporters during the conflict. Affiliative behaviour between the recipient of aggression and a third party was originally labelled 'consolation' (de Waal & van Roosmalen, 1979). Since then, however, a distinction has been made between affiliation initiated by the third party and affiliation initiated by the recipient of aggression (reviewed in Watts et al., 2000). The former has retained the label consolation while the latter is known as solicited consolation (Verbeek & de Waal, 1997). Although solicited consolation has been demonstrated in a variety of species (reviewed in Watts et al., 2000), consolation has only been demonstrated in great apes (de Waal & van Roosmalen, 1979; de Waal & Aureli, 1996; Wittig & Boesch, 2003a; Kutsukake & Castles, 2004; Palagi et al., 2004; Cordoni et al., 2006; Mallavarapu et al., 2006; Palagi et al., 2006a; Koski & Sterck, 2007; but see Call et al., 2002; Seed et al., 2007; see Chapter 6 for further details), and has thus received much less attention than reconciliation (Watts et al., 2000). The main function of consolation, as is implied by its name, is thought to be distress alleviation of the recipient of aggression (de Waal & van Roosmalen, 1979; de Waal & Aureli, 1997; Aureli, 1997), although this function has not been demonstrated yet. If consolation does reduce post-conflict stress, however, it may play a role in reducing the costs of aggressive conflict and thus form an important part of the decision-making process associated with aggressive escalation, possibly providing an alternative strategy to reconciliation (Wittig & Boesch, 2003b). The mechanism through which consolation occurs is likely to require some degree of empathy (de Waal & Aureli, 1996; Preston & de Waal, 2002; de Waal, 2008). As the quality of the relationship between partners is likely to modulate their empathic response (Anderson & Keltner, 2002; Aureli & Schaffner, 2002a; de Waal, 2008), valuable partners are predicted to be more likely to console recipients of aggression.

1.6. Behavioural Correlates of Stress in Primates

Displacement activities, usually self-directed behaviours in primates such as self-grooming, self-scratching, yawing or body-shaking, have been reported to occur at higher rates during periods of tension or uncertainty such as when making decisions over the direction of travel (Kummer, 1968) or whom to groom (Smuts, 1985), after aggressive conflicts (Aureli et al., 1989) or in proximity to dominant individuals (Castles et al., 1999). These behaviours are displayed without any apparent contextual significance and appear to be related to autonomic arousal (Maestripieri et al., 1992; Troisi, 2002). Direct evidence that these behaviours represent stress-related physiological changes in primates is lacking. There is, however, a growing body of circumstantial evidence that suggests that self-directed behaviours are reliable indicators of stress in primates.

Pharmacological studies have shown that rates of self-scratching in long-tailed macaques increased on administration of anxiogenic drugs, while anxiolytic drugs decreased rates of self-scratching (Schino et al., 1996), providing strong support for the link between self-directed behaviours and anxiety. Heart rates have been shown to increase following aggression (Boccia et al., 1989) and decrease when an individual receives grooming (Aureli et al., 1999). Rates of self-scratching also increased following aggression (Aureli et al., 1989) and decreased with grooming (Schino et al., 1988), suggesting that self-scratching rates correlate with heart rates under stressful conditions. Heart rates and scratching rates have also both been shown to increase with risk of aggression, such as when in proximity to a dominant or non-affiliative individual (Aureli et al., 1999; Castles et al., 1999; Kutsukake, 2003). Self-directed behaviours may be particularly useful in assessing stress levels in primates as they are sensitive to the degree of stress experienced by the individual. Using an experimental approach, rates of self-scratching by a chimpanzee were found to increase with the difficulty of a task and the number of incorrect responses given (Leavens et al., 2004). Recipients of aggression have been shown to display higher levels of self-directed behaviours following aggressive conflict with 'friends' or valuable partners, with whom aggression is more costly and thus more likely to be stressful (Aureli, 1997; Kutsukake & Castles, 2001; Cooper et al., 2007; Koski et al., 2007b). The increase in self-directed behaviours following aggression cannot be attributed to the need for increased self-maintenance as a result of dishevelment or injury during the conflict, as reconciliation reduces levels of self-directed behaviour to baseline (Aureli & van Schaik, 1991). Self-grooming and self-scratching have thus been used successfully in a number of studies across primate species to investigate the stress-inducing and stress-alleviating effects of aggressive conflict and post-conflict interactions and variations in stress levels therein (Aureli & van Schaik, 1991; Aureli, 1997; Castles & Whiten, 1998; Das et al., 1998; Kutsukake & Castles, 2001; Fujisawa et al., 2005; Cooper et al., 2007; Koski et al., 2007b; Schino et al., 2007). Levels of self-directed behaviour have also been used as an indicator of stress in primates to assess relationship security (Castles et al., 1999; Kutsukake, 2003), the effects of crowding (e.g. van Wolkenten et al., 2006; Cordoni & Palagi, 2007), and maternal style (Maestripieri, 1993).

1.7. Relationship Quality

Social relationships are built up through a history of past interactions between individuals, and can be characterised according to the nature of the interactions, such as mother-offspring relationships, consortships or alliances (Hinde, 1979). They function to solve the ecological problems such as predation avoidance and securing food resources, but also function to facilitate group living, solving problems such as coordination of group activities and intra-group competition (Cords, 1997). Social relationships can be viewed in a number of ways. Whereas Hinde (1979) described social relationships in terms of patterns of interactions between partners, from which future interactions could be predicted based on the characteristics of previous encounters, Kummer (1978) considered relationships to be investments that are beneficial to the individuals involved, suggesting that an individual will invest in a relationship to increase the benefits received from the partner over time. The two views are complementary and both aspects of social relationships should be considered. Relationships are not static, but dynamic, changing and developing with each interaction. As it is difficult, if not impossible, to measure the effect of each interaction between partners on overall fitness, little is known about how particular social relationships confer fitness advantages on individuals (Silk, 2007a). However, recent research suggests that the quality of social relationships may directly affect reproductive success in primates (Silk, 2007b). For example, in the Kanyawara community of chimpanzees, Uganda, agonistic support of the alpha male lead to increased mating opportunities for his supporters; thus, their relationship with the alpha male directly enhanced their reproductive success (Duffy et al., 2007). Male long-tailed macaques have been shown to groom females in 'payment' for sexual opportunities (Gumert, 2007). Female baboons (*Papio cynocephalus*) in Amboseli, Kenya, show increased reproductive success with increased social integration in the community, after controlling for possible confounding variables (Silk et al., 2003).

In spite of their immediate and long-term advantages, social relationships are relatively fragile. Aggressive conflicts have been shown to disrupt relationships, leading to an immediate loss of benefits they afforded (e.g. Cords, 1992; Koyama, 2001). As partners with highly valuable, cooperative relationships stand to lose more from disruption to their relationship than partners with less valuable relationships, reconciliation would be more likely to occur between valuable partners in order to repair their relationships and thus reinstate any benefits that might otherwise have been lost (de Waal & Aureli, 1997; Cords & Aureli, 2000; Aureli & Schaffner, 2006; Watts, 2006; see Chapter 5 for further details). Understanding the quality of the relationships between opponents is therefore key to understanding the patterns and determinants of reconciliation (van Schaik & Aureli, 2000). Although some aspects of relationship quality have been incorporated into studies of post-conflict behaviour, there has been no systematic study into relationship quality itself, in order to identify its individual components or to understand the sources of variation within the quality of relationships (see Chapter 4).

1.8. Chimpanzees

Chimpanzees were the subjects of the first study of reconciliation and consolation (de Waal & van Roosmalen, 1979), and thus have played a pivotal role in the development of post-conflict research. Furthermore, the tolerant and highly cooperative nature of their society (Brosnan et al., 2005; de Waal, 1982; Watts, 2002; Goodall, 1986; Mitani et al., 2000; Muller & Mitani, 2005) and high levels of competition over resources such as food or females (Duffy et al., 2007; Boesch et al., 2006b; Muller, 2007; Wittig & Boesch, 2003c; Williams et al., 2002) provide ample opportunity for frequent conflicts of interest and the development of valuable relationships, and thus make chimpanzees ideal subjects for this type of study. Their advanced cognitive skills (e.g. Hare et al., 2006) and their phylogenetic proximity to humans (Lockwood et al., 2004) further increase our interest in them.

1.8.1. Cognition

Research on chimpanzee cognition spans almost a century since the pioneering work of Köhler and Yerkes and covers a great many areas from tool use to social learning and from spatial understanding to communication and social strategies (Tomasello & Call, 1997). I will focus here on the aspects of cognition relevant to understanding post-conflict behaviour.

In 1978, Premack & Woodruff questioned whether chimpanzees were capable of mental state attribution, that is, to recognise others as having beliefs, goals, intentions and perspectives that differ from your own, known as 'theory of mind' (Premack & Woodruff, 1978). Since their original research, the cognitive abilities of chimpanzees, in particular their self-awareness and awareness of others, have been the subject of an ever-expanding field of research. However, understanding what chimpanzees know about themselves and others is not an easy task. We know that chimpanzees can recognise themselves in a mirror (Gallup, 1970; Povinelli et al., 1997), whereas monkeys cannot, suggesting that chimpanzees, but not monkeys, are self-aware (de Waal et al., 2005; reviewed in Gallup et al., 2000). Furthermore, chimpanzees may be aware of what other individuals know and adjust their behaviour accordingly, such as avoiding food visible to a dominant partner in preference of food hidden from the dominant partner's view or hiding from competitors (Hare et al., 2001; Hare et al., 2006). Chimpanzees may also be able to recognise emotional responses in others (Parr, 2001). Hence, the next logical step is to assume that they may be capable of empathic perspective-taking, i.e., emotional arousal through an understanding of another's situation or needs (de Waal, 2008). It is this degree of empathy that is thought to be the primary motivation behind altruistic behaviour in response to distress, pain or need in others (de Waal, 2008). However, despite anecdotal evidence of targeted helping (help or care based on a cognitive appreciation of the other's specific need or situation; de Waal, 2008) in their spontaneous social behaviour (de Waal, 1982, 2007), until recently, experimental studies failed to find evidence for any other-regarding preferences in apes (Jensen et al., 2006; Silk et al., 2005). New research, however, suggests that chimpanzees may behave altruistically (Warneken et al., 2007), helping both humans and conspecifics to complete tasks, thus showing that chimpanzees understand the needs of others and are motivated to assist them. Nevertheless, the debate about the degree to which primates and other animals are capable of understanding others' need and emotions and recognising them as different from their own continues (Preston & de Waal, 2002; Tomasello et al., 2003; Penn & Povinelli, 2007; de Waal, 2008). Consolation may play a part in this debate as it is one of the only naturally occurring behaviours on which systematic data has been collected that may involve representation of another's state (i.e., understanding that the recipient of aggression is distressed) and attempts to ameliorate that state (i.e., alleviating their distress) (de Waal & Aureli, 1996).

The advanced cognitive skills associated with understanding the needs of others may have evolved to deal with a social environment of increasing complexity (Dunbar, 1998; Dunbar & Schultz, 2007). It has been hypothesised that the complexity of human societies is such that humans have evolved specialised socio-cognitive skills for the transmission of knowledge and communication superior to that of non-human primates ('cultural intelligence hypothesis': Herrmann et al., 2007). Chimpanzees too, though, show transmission of knowledge through social learning and cultural variation across groups, both in captivity and the wild (Wrangham et al., 1994; Whiten et al., 1999; McGrew, 2004). The demonstration of both cultural conformity (Whiten et al., 2005) and the spread of arbitrary conventions (Bonnie et al., 2007) in chimpanzees, both previously thought to be uniquely human traits, further blurs the line between human and chimpanzee cognition. The differences in the levels of cultural cognition between humans and chimpanzees has been attributed to the human ability to share a common goal, or have shared intentionality (Tomasello et al., 2005). However, some of the cultural behaviours exhibited by chimpanzees suggest evidence for shared motivation and collaboration, including mediated reconciliation and consolation (Horner et al., 2005). There is evidence for cultural transmission of reconciliation in juvenile rhesus macaques, who greatly increased their rate of reconciliation after exposure to much more conciliatory stump-tailed macaques (de Waal & Johanowicz, 1993). However, not all traits exhibited by the stump-tailed macaques were exhibited by the rhesus macaques, suggesting that some behavioural elements are more susceptible to cultural transmission than others. It is possible, therefore, that some of the variation in patterns of post-conflict behaviour observed within species may be the result of cultural variation, although little is known about which aspects these might be.

1.8.2. Socioecology

There are four subspecies of chimpanzee: *Pan troglodytes verus*, found in equatorial West Africa, *P. t. vellerosus*, in Nigeria and Northern Cameroon, *P.t.troglodytes*, in Central Africa and *P.t. schweinfurthii*, in East Africa (Stumpf, 2007). Chimpanzees live in multi-male, multi-female communities, which may vary from 15 to 150 individuals (Stumpf, 2007). The nature of their fission-fusion society means that party size is subject to continuous fluctuation according the number of oestrous females, food abundance and group composition (Goodall, 1986; Boesch & Boesch-Achermann, 2000; Mitani & Amsler, 2003; Reynolds, 2005; reviewed in Stumpf, 2007). Male chimpanzees are philopatric, remaining permanently in their natal group, whereas females tend to transfer to a new group upon reaching sexual maturity when they are about 10 years old (Stumpf, 2007), although only half of all females have been reported to transfer in one community (Pusey et al., 1997) and none at all in another (Sugiyama, 1999). Chimpanzee females mate promiscuously (Watts, 2007), although recent research has shown that selectivity increases when conception is most likely (Stumpf & Boesch, 2005). Males compete for access to reproductive females, using coercion (Muller et al., 2007), mate-guarding (Watts, 1998) and consortships (Tutin, 1979; Manson, 1997) to try to counter female promiscuity and ensure paternity.

1.8.3. Social Relationships

Chimpanzee social relationships in all wild study populations are characterised by strong male-male bonds with strict, linear, dominance hierarchies (Goodall, 1986; Nishida et al., 1999; Boesch & Boesch-Achermann, 2000; Mitani et al., 2000; Watts, 2000b; Arnold & Whiten, 2003; Muller & Wrangham, 2004; Newton-Fisher, 2004). Similar relationships among males have also been documented in captive populations of chimpanzees (de Waal, 1982, 1986). These male bonds are manifested through frequent cooperation in coalitionary mate guarding (Watts, 1998), hunting (Boesch, 1994; Goodall, 1986), inter-group aggression (Muller, 2002; Wilson & Wrangham, 2003), and a higher tendency to associate with and groom each other than with females (Newton-Fisher, 1999; Mitani et al., 2000; Watts, 2000a). However, male-male competition is strong, especially for dominance status within the group as higher ranking males have higher reproductive success (Constable et al., 2001) . Thus males form coalitions to enhance their competitive abilities necessary to maintain or increase dominance status (de Waal, 1982; Nishida & Hosaka, 1996). Agonistic support is therefore frequent and valuable, and may form part of an exchange of beneficial commodities such as grooming (Watts, 2002; Koyama et al., 2006) or mating opportunities (Duffy et al., 2007). As the necessity for strong male-male bonds arises from fierce inter- and intra-group competition, populations in which competition is of a lesser degree may exhibit weaker bonds among males (Sugiyama, 1988; Muroyama & Sugiyama, 1994).

Female-female relationships in chimpanzees tend to be more fluid and transitory, although there appears to be considerable diversity across both wild and captive study sites (Baker & Smuts, 1994; Muroyama & Sugiyama, 1994; Stumpf, 2007). While females in Gombe, for instance, are relatively solitary and show little social interaction with other females (Goodall, 1986), female chimpanzees of the Taï Forest display a higher level of affiliation and tolerance (Boesch & Boesch-Achermann, 2000) and females in the Budongo Forest have been reported to form coalitions (Newton-Fisher, 2006). The degree of female gregariousness within chimpanzee populations is likely to be related to the distribution and quality of food resources, although female chimpanzees may face a compromise over habitat quality, scramble competition and threat from neighbouring communities in their choice of ranging areas (Emery Thompson et al., 2007). Within each population, female ranging areas are determined by dominance rank, with high ranking females having smaller core areas, while subordinate individuals may have to travel further and change their use of space over time in order to fulfil their needs (Murray et al., *in press*). Moreover, the quality of a female's core area may have a highly significant effect on her reproductive success (Emery Thompson et al., 2007). In Gombe, female rank was also correlated with reproductive success (Pusey et al., 1997), thus dominance is clearly important in female chimpanzees and yet female dominance interactions are rarely observed (de Waal, 1982; Goodall, 1986; Nishida et al., 1999; Arnold & Whiten, 2001). To date, a linear dominance hierarchy amongst females has only been found for chimpanzees of the Taï Forest, a possible adaptation to higher contest competition and predation rates compared to other field sites, leading to higher degree of gregariousness (Wittig & Boesch, 2003c). It seems likely, therefore, that social strategies adopted by female chimpanzees are dependent for the most part on local ecological variables. In captivity, variation in female social relationships among groups has been attributed to the stability of dominance relationships within the group. For example, females in the newly established group of chimpanzees at Detroit Zoo with unstable relationships exhibited high proportions of conflicts (assumed to be) in a dominance context and high rates of reconciliation compared to the females from the well established group of chimpanzees at Arnhem Zoo (Baker & Smuts, 1994).

1.9. Aims of the Study

Despite nearly three decades of research into post-conflict behaviour, there are still large gaps in our knowledge about its functions and underlying mechanisms. While reconciliation has been extensively studied, there is great variation in its patterns across and within species that has yet to be fully explained. Although a number of studies have investigated and demonstrated functions of reconciliation, no study has as yet demonstrated the stress-alleviating function of reconciliation in the species in which reconciliation was first described, chimpanzees. In light of the variation in the form and patterns of reconciliation across species, conclusions drawn from studies on a particular species can not necessarily be generalised to all species, and thus is it particularly important to investigate all aspects of reconciliation in every study species. Although there is considerable evidence that the occurrence of reconciliation is affected by quality of the relationship between former opponents (Arnold & Aureli, 2007; Cords & Aureli, 2000; Watts, 2006), there is little conformity in the way relationship quality is measured, and often no evidence to support assumptions made about the quality of particular dyadic relationships, such as those based on broad categories of age and/or sex combinations or those based on single behavioural variables. While the quality of the relationship between opponents and third parties is likely to affect triadic post-conflict interactions, no study has investigated this matter. Furthermore, the proposed function of consolation, stress alleviation, has not been demonstrated in any species.

The aims of this study were to investigate the occurrence, function and determinants of reconciliation and consolation in chimpanzees, and in particular to assess the influence of relationship quality on the occurrence of these post-conflict behaviours. Although other studies have investigated post-conflict behaviour in chimpanzees, the large degree of variation in methodology employed and results obtained makes it difficult to generalise. Furthermore, the variation in the general pattern of social relationships (Baker & Smuts, 1994; de Waal, 1994) and environmental variables (Colmenares, 2006) among study groups reinforce the need for studies on new groups of chimpanzees. This study, therefore, aimed to contribute data on the occurrence of reconciliation and consolation in chimpanzees at Chester Zoo in order to improve our knowledge of post-conflict behaviour in chimpanzees as a whole (Chapter 3). Furthermore, the interdependency of reconciliation and consolation was examined, testing predictions about the relative importance of the two post-conflict interactions based on their presumed functions. This study also aimed to test the original suggestion (de Waal & van Roosmalen, 1979) that behaviours rarely seen outside a post-conflict context, such as kiss and embrace, are used specifically for reconciliation and consolation respectively, and that the use of context-specific behaviours implies an explicit form of post-conflict behaviour in chimpanzees (Chapter 3).

I investigated relationship quality in Chapter 4, aiming to identify separate components of the relationship between individuals that comprise relationship quality as a whole. The components were derived from a number of behavioural variables, using novel, non-subjective methods to assess the relative importance of each variable and their categorisation within the components. The theoretical predictions of Cords & Aureli (2000), that the quality of a relationship comprises value, compatibility and security were evaluated as candidates for the derived components. Finally, factors such as kinship, sex-combination, age difference and relationship tenure were investigated as sources of variation within each of the components.

The aims of Chapter 5 were firstly to test the function of reconciliation as a stress-alleviating mechanism, a function never demonstrated in chimpanzees, using levels of self-directed behaviours as behavioural indicators of stress (Maestripieri et al., 1992; Troisi, 2002). Secondly the components of relationship quality obtained in Chapter 4, in addition to other relationship, conflict and post-conflict characteristics, were investigated as determinants of reconciliation. Although previous studies have investigated factors influencing the occurrence of reconciliation in chimpanzees, this study offers significant methodological improvements in the use of non-subjective composite measures of relationship quality and the use of (generalised) linear mixed models to analyse the data, improving the power of the analyses and validity of the results.

Finally, I tested the stress-alleviating function of consolation as implied by its name in Chapter 6, a function never before demonstrated. Evidence for such a function in chimpanzees would provide support for consolation being a critical behavior in the debate about the degree of empathic tendencies in great apes (de Waal, 2008). I further aimed to identify the determinants of consolation among opponents' relationships, conflict and post-conflict characteristics. Finally, as empathic responses are likely to be influenced by the quality of the relationship between partners (Anderson & Keltner, 2002), I investigated the influence of relationship quality between consolers and initial recipients of aggression on the probability of consolation.

CHAPTER 2

General Methods

2.1. Study Subjects

The subjects of this study were the adult chimpanzees housed at Chester Zoo, UK. The group was initially established in 1956 and during the study period the group size varied from 26 to 32, with 17 adult females, 5 adult males and 4-10 juveniles and infants (Table 2.1). All adults were present throughout the study and constituted the study subjects. In the thirty years prior to the study, three adult females were introduced from the Welsh Mountain Zoo, two in 1984 and one in 1990. One adult female was introduced from a private collection in 1985, one juvenile male was introduced to the group from Edinburgh Zoo in 1990 and 3 females and a juvenile were transferred to Dublin Zoo in 2002. Kinship for all analyses, was based on maternal lineages and kin included dyads with a coefficient of maternal relatedness of $r>0.125$. Following this definition, 16 dyads within the study subjects were classed as kin while 215 dyads were classed as non-kin.

The chimpanzees had access to a $2000m^2$ grassy outdoor island enclosure and a $143m^2$ indoor enclosure during the day. The outdoor enclosure contained bushes, shrubs, a large climbing structure, nets and ropes.

Table 2.1. Details of the chimpanzees housed at Chester Zoo during the study period.

Name	Code	Sex	Date of Birth	Place of Birth	Mother	Status
Boris	BO	M	1966	Wild	?	A
Wilson	WI	M	20/02/1968	Chester Zoo	Meg	A
Nicky	NI	M	21/01/1969	Chester Zoo	Jane	A
Friday	FR	M	06/02/1976	Chester Zoo	Jane	A
Dylan*	DY	M	09/04/1987	Chester Zoo	Farthing	A
Kate	KT	F	23/12/1970	Chester Zoo	Jane	A
Cleo	CL	F	1971	Wild	?	A
Heidi	HE	F	30/06/1972	Chester Zoo	Judy	A
Rosie	RO	F	29/01/1973	Chester Zoo	Jeanie	A
Halfpenny	HP	F	20/05/1975	Welsh Mountain Zoo	Penny	A
Farthing	FA	F	19/09/1975	Welsh Mountain Zoo	Marble	A
Mandy	MA	F	19/09/1977	Chester Zoo	Meg	A
Kan Kan	KN	F	14/11/1983	Chester Zoo	Kate	A
Sarah	SR	F	16/10/1986	Chester Zoo	Halfpenny	A
Sally	SL	F	04/06/1988	Chester Zoo	Rosie	A
Layla	LA	F	02/11/1990	Chester Zoo	Farthing	A
Alice	AL	F	06/11/1991	Chester Zoo	Florin	A

Whitney	WH	F	30/05/1993	Chester Zoo	Kan Kan	A
Zee Zee	ZZ	F	15/02/1994	Chester Zoo	Mandy	A
Lizzie	LZ	F	22/03/1995	Chester Zoo	Rosie	A
Holly	HO	F	12/12/1995	Chester Zoo	Sarah	A
Chrissie	CH	F	11/03/1996	Chester Zoo	Florin	A
Kiki[†]	KK	F	10/02/1996	Chester Zoo	Halfpenny	J
Patti	PT	F	24/07/1997	Chester Zoo	Kan Kan	J
Jethro	JT	M	08/02/2000	Chester Zoo	Sarah	J
Eric	ER	M	24/06/2003	Chester Zoo	Kan kan	I
Rhiannon	RH	F	21/10/2004	Chester Zoo	Heidi	I
Frankie	FK	F	25/12/2004	Chester Zoo	Alice	I
Dido	DD	F	29/12/2004	Chester Zoo	Zee Zee	I
Carlos	CA	M	06/03/2005	Chester Zoo	Whitney	I
Donna	DN	F	10/05/2005	Chester Zoo	Lizzie	I
Dusty[‡]	DU	F	26/05/2006	Chester Zoo	Chrissie	I

Dominant male [†]Mentally disabled. Died 18/09/2006 [‡] Died 30/09/2006

A=Adult, J=Juvenile, I=infant. Study subjects were all of the adults.

2.2. Housing and Husbandry

The indoor enclosure contained a large climbing frame with platforms, nets and ropes and the chimpanzees were supplied regularly with enrichment items. The chimpanzees had access to both the indoor and outdoor enclosure between 10am and 4pm every day for the majority of the study period. Between 4pm and 10am, the chimpanzees had access to a large indoor off-show enclosure in addition to the main indoor enclosure (except between 8am and 10am when the main indoor enclosure was cleaned). Between April and October, the chimpanzees also had access to the outside enclosure at night. The chimpanzees were fed two to three times a day at varying times on a mixture of fruit, vegetables, seeds and monkey pellets and had *ad libitum* access to water from indoor and outdoor moats.

2.3. Data Collection

Data were collected from January 2005 to October 2005 and January 2006 to October 2006 from 10am to 4pm on most weekdays, totalling 1748 observation hours.

Data were collected on each of the subjects using focal animal sampling (Altmann, 1974). At least 106 15-minute focal samples were conducted on each of the adult chimpanzees (mean =111, range 106 to 116). In order to ensure that focal samples were spread evenly throughout the day for each individual, samples were categorised into three time periods, 10:00 -12:00, 12:00-14:00 and 14:00 to 16:00. Focal individuals were chosen at random. The identities of all other adults within the same sector of the enclosure as the focal animal were recorded at the beginning and five minutes from the start of the focal observation. During focal observations, all approaches to within arm's reach of another adult were recorded. For each approach, the response was also recorded as follows: a positive response was scored when the approachee initiated an affiliative interaction with the approacher within 5s of the approach; a negative response was scored when the approachee moved away, screamed, or initiated any aggressive or submissive interaction with the approacher; all other responses to approaches were scored as neutral (see Table 2.2 for behavioural categories and definitions). Every minute during focal observations the identities of all adults within an arm's reach of the focal animal were recorded, specifying whether they were in gross body contact with, grooming, being groomed by or mutually grooming with the focal animal (Table 2.3)

Instantaneous scans of the entire group were carried out throughout the day with a minimum of 15-minute intervals between scans. In each scan, the identities of all visible adults were recorded followed by the identities of all adults grooming, or mutually grooming with, another adult and the direction of grooming. A total of 2128 group scans were collected during the study period.

All instances of begging were recorded and scored as successful if the beggar was given food or was allowed to take food from the possessor's hands or mouth. All instances of aggressive conflict between adults were recorded when visible and took priority over all other data collection. Aggressive conflict was defined as any interaction involving a bite, hit, brusque rush, trample, chase or threat in addition to screaming (van Hooff, 1974). The identities of the initial recipient of aggression

Table 2.3. Definitions of behavioural categories recorded during focal observations, PCs and MCs.

Self-directed behaviour	**Format: Actor Behaviour**
Self-grooming	Directed touching, licking, or intense visual inspection of own skin or hair.
Self-scratching	Individual repeatedly and rapidly rakes fingers through hair or skin.
Social Behaviour	**Format: Focal behaviour partner**
Affiliative	
Grooming	Directed touching, licking, or intense visual inspection of another's skin or hair.
Mutual Grooming	Two individuals groom each other simultaneously.
Kiss	Animal presses its lips against another individual's body.
Embrace	Individual places one or both arms around partner's body while in a lateral position or facing the partner.
Play	Two individuals chase, tickle or wrestle accompanied by play face.
Gentle Touch	Individual reaches out and gently touches another animal.
Finger in Mouth	An individual puts a finger in another animal's mouth.
Mount	One individual mounts another.

Offer Hand	Animal stretches hand out towards another individual (not in possession of food).
Aggressive/ Submissive	
Threaten	Individual shows threatening behaviour such as shaking wrist or slapping ground whilst staring at target.
Chase	One individual chases another around the enclosure.
Bite	Individual uses teeth to bite another.
Hit	Animal slaps or thumps another.
Brusque Rush	One animal charges at another at full speed with hair erect.
Trample	One animal jumps on top of another and stamps on its back.
Submissive Greeting	One individual crouches in front of a partner while pant-grunting.
Bluff Display	Charging behaviour with piloerection and pant-hoot vocalisations, not charging directly at another individual.
Other	
Beg	One animal holds hand out to another animal in possession of food.
Approach	One animal approaches another to within arm's reach.
Vocal	**Format: Actor Behaviour**
Scream	High pitched vocalisation accompanied by an open mouth and bared teeth

and the aggressor were recorded along with the intensity, directionality, outcome and whether the conflict started with a bluff display. The intensity was recorded as low if the conflict involved a threat and/or hit, as medium if it included chase or brusque rush and as high if it involved trample or bite. Directionality was scored as bi-directional if both participants engaged in aggressive behaviour and unidirectional if all aggressive behaviour was directed towards the initial recipient. As chimpanzees frequently engage in bi-directional aggression, both partners can become ‘victims’ of aggression, and thus I conducted my analyses on the initial recipient of aggression (heretofore referred to as the recipient). The outcome of the conflict was recorded as decided if there was a clear victor and undecided if neither participant of a bi-directional conflict showed signs of submission (e.g. pant-grunt greeting, fleeing or screaming). In polyadic conflicts, the aggressor-recipient dyad with the highest intensity of aggression was chosen for post-conflict observations.

Following de Waal & Yoshihara (1983), post-conflict observations (PCs) were conducted on an opponent for ten minutes immediately after the end of an aggressive conflict. The initial recipient of aggression was preferentially chosen for PCs, however, if a focal observation was being conducted on the aggressor when the conflict began, or the recipient was not clearly visible, the aggressor was chosen instead. During PCs all self-directed behaviours and social interactions were recorded. Self-directed behaviours were recorded as the duration of self-grooming and frequency of self-scratching, where a new scratching bout was recorded if scratching resumed after an interval of at least 5 seconds. Social interactions included affiliative, submissive and aggressive behaviours (see Table 2.2). If the conflict was renewed within two minutes of the start of the PC, the PC was abandoned and restarted once the conflict ceased.

Table 2.2. Definitions of behavioural categories recorded during one minute scans within focal observations.

BEHAVIOUR	Format: Actor behaviour
Proximity	Focal is within arm's length of partner
Contact sit	Focal is sitting in contact with partner
Grooming	Focal is grooming, or being groomed by, partner
Mutual Grooming	Both individuals are grooming each other simultaneously

Matched-control observations (MCs) were conducted on the same individual following the same procedure at the same time on the next possible day after the corresponding PC. If the focal individual was involved in an aggressive conflict within 10 minutes prior to the planned MC, the MC was postponed until at least 10 minutes after the end of the conflict, up to a maximum of one hour after the time of the corresponding PC. The outdoor enclosure was visually mapped into six sectors following the patterns of vegetation on the island and the indoor enclosure was counted as a seventh sector. Within each sector, all individuals were visible and audible to each other. MCs were only conducted when the recipient was within the same sector of the enclosure as the aggressor and was clearly visible to the observer. If these conditions were not met the MC was postponed until the next day for a maximum of one week.

2.4. Data Analysis

2.4.1. Mixed Models

Linear mixed models (LMMs) and generalised linear mixed models (GLMMs) were used throughout this study. Traditional analyses such as repeated measures ANOVAs, which are simple general linear models, have certain limitations such as not allowing unbalanced data sets (i.e., unequal numbers of observations in each condition), only allowing one covariate measurement per individual and requiring the dependent variable to be continuous. All of these limitations can be overcome using LMMs and GLMMs. LMMs are an extension of general linear models that allow both fixed and random variables to be fitted to a model. Fixed variables are the variables of interest in the study, the independent variables. Random variables (such as subject identity) are assumed to be values that are drawn from a larger population of values, and thus represent a random sample of all possible values of that variable. Unlike fixed variables, differences between levels of a random factor are of no interest (Tabachnick & Fidell, 2007). When working with repeated measures data, individuals are often not all represented equally in all conditions. In this study more than one PC observation was recorded for each subject, so PCs involving the same individual were not independent. Furthermore, not all individuals were involved in the same number of PCs, and PCs on each focal individual were not distributed equally across opponents, i.e., covariate measurements for PC observations differed within each individual. LMMs enable residual correlations due to the repeated observations of the same individual to be modelled, and thus control for variation within random factors and allow dyadic variability to be detected (Goldstein, 1999). Whereas traditional analyses require subjects to be represented under each condition for inclusion in the analysis, LMMs use all available data and thus increase the power of the analysis and the accuracy of the results. Moreover, ecological fallacy associated with pooling data is avoided. GLMMs are further extensions of LMMs in which greater flexibility in error distributions are permitted. In this study, GLMMs were used for models with binomial dependent variables and LMMs were used for models with continuous dependent variables, thus GLMMs were modelled with binomial error structures and log-link functions (Brown & Prescott, 1999). Both continuous and binomial independent variables were used in both LMMs and GLMMs. Random variables are by definition nominal. Maximum likelihood estimation was used for all models (Tabachnick & Fidell, 2007).

2.4.2. Model Selection

For all LMM and GLMM analyses, a set of candidate models was chosen using a step-up strategy whereby fixed variables were added to the model sequentially. The best model was selected based on Akaike's information criterion (AIC), which compares the adequacy of several models and identifies the most parsimonious model that best explains the variance of the dependent variable, while penalising for the number of variables in the model. The best model, which has the lowest AIC value, is the best model to predict values of the dependent variable in a new data set (Tabachnick & Fidell, 2007). Random variables were excluded from the best model when the variance component was estimated to be 0.

The assumptions of GLMM and LMM analyses (normal distribution, independence and homogeneity of residual variance) of the presented models were checked by visual inspection of the residuals and of predicted random variables. GLMMs did not show overdispersion. As the data set for the LMM analyses investigating the occurrence of consolation using the consolation index and TCT (see Chapter 7) had a skewed distribution, the best model for these analyses were rerun using bootstrap standard errors, which are robust against deviations from the assumptions of normal distribution, using STATA 9.1 (StataCorp, 2005). All other mixed model analyses were run in R version 2.4.1 using the lmer function (Bates & Sarkar, 2007; R Development Core Team, 2006).

2.4.3. Interpretation of Results

The estimate coefficient β is an indicator of the strength of the effect that an independent variable has on the dependent variable after controlling for all other independent variables. Values of β further away from 0 have a stronger effect on the dependent variable. For binomial independent variables in LMMs, β represents the difference between the effects of the two levels (e.g., kin and non-kin). For GLMMs, the e^{β} represents the odds ratio: an odds ratio of 1 indicates that the outcome under study (e.g., the occurrence of reconciliation or consolation) is equally likely in both conditions (e.g. kin and non-kin) if the independent variable is a binomial variable. An odds ratio greater than 1 indicates that the condition or event is e^{β} more likely in the first group (e.g. kin). For continuous independent variables (e.g. age), an odds ratio greater than 1 indicates that the outcome is e^{β} more likely with each unit increase (e.g. the older the subject is).

The variance for the random variables represents the correlation within subjects. Thus, where variance was close to zero, behavioural responses were relatively independent from the identity of the subjects.

2.4.4. Methodological Improvements for the Study of Post-Conflict Behaviour

Multivariate analyses were first introduced to the field of post-conflict behaviour in 1998 when log-linear analysis was used to investigate the variation in intra-group conciliatory tendencies (Schino et al., 1998; Kutsukake & Castles, 2001). The first multivariate approach to investigating reconciliation patterns at the level of the conflict was taken by Call et al. (1999), who used a logistic regression analysis, which allows a binomial dependent variable, i.e. the presence or absence of reconciliation. These studies offered significant improvements over univariate approaches in that the effects of single variables could be examined while the effects of other variables had been statistically removed. Thus, the reported effects were not confounded by correlations between variables and the relative importance of each variable could be assessed. However, being unable to control for individual variability, all significant effects had to be confirmed using univariate analyses at the individual level. In order to remove the need for confirmatory univariate analyses, later studies expanded on the logistic regression methods used by Call et al. (1999), by including the identity of the subjects as an independent variable in the analyses (Koski et al., 2007a; Wittig & Boesch, 2003a). Provided that significant effects of independent variables remained significant after the addition of subject identity as an extra independent variable, it could be concluded that repeated measurements of the same individual did not influence the results. This method, however, would not be valid if repeated measurements had significantly influenced the results. Alternative methods, such as matrix associations (Cooper et al., 2005) control for individual variation without losing information by reducing continuous variables to categorical variables, but do not offer the multivariate advantages of logistic regression and log-linear analyses.

(Generalised) linear mixed models offer an ideal solution for the study of post-conflict behaviour because they 1) control for individual variation in contribution to the data set, 2) permit unbalanced designs, 3) control for the potentially confounding effects of other variables, and 4) control for the identities of the subjects and partners using random factors. Mixed models have been successfully applied to studies investigating sources of variation within many aspects of animal behaviour such as age of dispersal in Siberian jays, *Perisoreus infaustus* (Ekman et al., 2002), sexual swelling size in chimpanzees (Deschner et al., 2004), stress levels in chacma baboons (*Papio hamadryas ursinus*) (Engh et al., 2006) and mate choice in brown bears (*Ursos arctos*) (Bellemain et al., 2006). Until now, however, studies of post-conflict behaviour have not taken advantage of the benefits provided by mixed models, with the notable exception of one recent study on conflict management following aggression in meerkats (*Suricata suricatta*) (Kutsukake & Clutton-Brock, *in press*).

CHAPTER 3

Reconciliation, Consolation and Post-Conflict Behavioural Specificity

3.1. Introduction

Aggressive conflict forms an integral part of the behavioural repertoire of all group-living animals. However, aggressive conflict can be very costly, not only in terms of the risk of injury and energetic costs, but also because damage to the relationship between opponents can lead to the loss of benefits afforded by that relationship (de Waal, 2000b; Aureli et al., 2002). Conflict avoidance strategies, such as using submissive or appeasing behaviours, can minimise the likelihood of escalation of a conflict of interest to aggressive conflict (de Waal, 1996; Preuschoft & van Schaik, 2000). If aggressive conflict does occur, however, peaceful post-conflict interactions can mitigate the costs (de Waal et al., 2000).

The primary mechanism for repairing damage caused by aggressive conflict is reconciliation, i.e. the peaceful post-conflict reunion of former opponents. Since it was first documented in chimpanzees (*Pan troglodytes*) (de Waal & van Roosmalen, 1979), reconciliation has been demonstrated in many species of primates, in addition to a few non-primate species (de Waal et al., 2000; de Waal, 2000b; Schino, 2000; Aureli et al., 2002; Silk, 2002a; Arnold & Aureli, 2007).

Reconciliation has been shown to repair the relationship between former opponents (Cords, 1992; Koyama, 2001), reduce post-conflict stress (Aureli & van Schaik, 1991; Cooper et al., 2007), and reduce the chances of renewed aggression (Watts, 1995a; Silk et al., 1996). Whereas reconciliation has been demonstrated in a number of studies on chimpanzees both in the wild and in captivity, there is a considerable amount of variation in the rates and patterns of reconciliation observed (de Waal & van Roosmalen, 1979; de Waal, 1986; Baker & Smuts, 1994; Arnold & Whiten, 2001; Fuentes et al., 2002; Preuschoft et al., 2002; Kutsukake & Castles, 2004; Wittig & Boesch, 2005; Koski et al., 2007b). Differences in both the physical and social settings across studies, in addition to methodological differences, may account for this variation (Colmenares, 2006). Given the many potentially influential factors, too few studies, however, are available in order to draw conclusions about the sources of within-species variation.

In addition to reconciliation, de Waal & van Roosmalen (1979) demonstrated the occurrence of another peaceful post-conflict interaction. Consolation is an affiliative interaction directed from a third party towards the recipient of aggression (de Waal & van Roosmalen, 1979) and has been suggested to provide distress alleviation (de Waal & Aureli, 1996). Third-party post-conflict affiliation may also be directed from the recipient of aggression to the third party, but in this case is labelled solicited consolation (Verbeek & de Waal, 1997). In primates, consolation has thus far only been demonstrated convincingly in great apes, possibly because monkeys lack the appropriate degree of empathy in order to perceive and respond to distress in others (de Waal & Aureli, 1996; Castles, 2000; Preston & de Waal, 2002; de Waal, 2008). Even in chimpanzees, not all studies have been able to demonstrate the occurrence of consolation (see Arnold & Whiten, 2001; Fuentes et al., 2002 for negative evidence). Affiliative interactions initiated by a third party have been observed in stump-tailed macaques (*Macaca arctoides*) but the behavioural patterns used suggest that it is more likely to prevent aggression rather than to console (Call et al., 2002; c.f. Schino et al., 2004). Third party post-conflict affiliation has also been demonstrated between mating partners in rooks (*Corvus frugilegus*), although affiliation was initiated by both the opponent and the third party and the majority of behaviours were mutual rather than directed (Seed et al., 2007).

Although solicited consolation has been demonstrated in many primate species (Watts et al., 2000), a number of studies on apes have not found an increased tendency for the recipient of aggression to affiliate with a third party when compared to control periods, even when consolation has been demonstrated (Wittig & Boesch, 2003a; Kutsukake & Castles, 2004; Koski & Sterck, 2007; but see Palagi et al., 2004; Cordoni et al., 2006; Mallavarapu et al., 2006; Palagi et al., 2006a). The inconsistencies in the results obtained from previous studies thus emphasise the need for further research in this area.

Species with relatively tolerant social systems, in which post-conflict behaviour is characterised by high rates of reconciliation, may be more likely to employ 'explicit' forms of reconciliation, using behaviours rarely used outside a conciliatory context (de Waal & Ren, 1988; Thierry, 2000; Thierry et al., in press). In these species, behavioural specificity, i.e., using behaviours that are relatively specific to a particular context such as reconciliation, might be necessary in order to make the actor's intentions explicit. The use of such context-specific explicit gestures may also be important for reaffirming dominance-subordination relationships after aggressive conflict (de Waal, 1993; Arnold & Barton, 2001a). In species with more despotic social systems, however, reconciliation is infrequent and routine friendly behaviour between former opponents may be enough to indicate reconciliation, and thus reconciliation is 'implicit'. Support for the differentiation of implicit (e.g. *Macaca fuscata*: Aureli et al., 1993; *Macaca mulatta* de Waal & Ren, 1988) and explicit (e.g. *Trachypithecus obscurus*: Arnold & Barton, 2001a; *Macaca arctoides*: de Waal & Ren, 1988) reconciliation has been provided in a number of species. Studies on chimpanzees, however, have reported mixed results. De Waal & van Roosmalen (1979) found that reconciliation in chimpanzees was likely to occur with a kiss, and consolation most likely to be expressed with an embrace. No other study, however, has been able to replicate this result or find any evidence for behavioural specificity for reconciliation in chimpanzees (Arnold & Whiten, 2001; Fuentes et al., 2002; Kutsukake & Castles, 2004; but see de Waal & Aureli, 1996 for consolation). Furthermore, no study has yet analysed the distribution of behaviours used for the first affiliative contact during post-conflict observations and during baseline conditions, controlling for individual variation.

The aims of this study were therefore, primarily to report on the post-conflict behaviour of chimpanzees at Chester Zoo, investigating the occurrence of reconciliation, consolation and solicited consolation for purposes of comparison with data from other studies. As reconciliation and consolation might both reduce post-conflict stress levels, but only reconciliation repairs the relationship between opponents, we would expect reconciliation to have the first priority for former opponents. Therefore, my second aim was to examine the interdependence of consolation and reconciliation, specifically testing the following predictions: 1. Consolation would not occur after reconciliation had occurred, as it would no longer be necessary; 2. Reconciliation would still occur after consolation in order to repair the relationship between opponents. The third aim was to investigate behavioural specificity for reconciliation and consolation in the study chimpanzees, comparing the relative occurrence of kiss and embrace during post-conflict interactions and during control periods.

3.2. Methods

3.2.1. Data Collection

Data were collected on all visible aggressive conflicts between adult subjects. The Post-Conflict (PC)-Matched-Control (MC) method was used to collect data on post-conflict behaviour on either the aggressor or recipient of aggression (see Chapter 2 for details).

3.2.2. Data Analysis

Data analysis was conducted on 256 PC-MC pairs, of which 234 were on recipients of aggression.

3.2.2.1. Reconciliation

Each PC-MC pair was labelled attracted if the first affiliative interaction between opponents occurred earlier in the PC than the MC. PC-MC pairs were labelled neutral if there was no affiliative interaction between the opponents in either observation or if it occurred at the same time in both the PC and the MC. PC-MC pairs were labelled dispersed if the first affiliative interaction between former opponents occurred earlier in the MC. In order to demonstrate the occurrence of reconciliation in the study group, the difference in the number of attracted and dispersed pairs for each individual was analysed using a Wilcoxon signed-rank test. A Kaplein-Meier survival analysis with a Mantel-Cox test was also performed to compare the latency to first affiliative contact in the PC and MC periods, taking into account 'censored' data (i.e. PC and MC periods in which no affiliation occurred before the end of the observation). Given the temporal patterns, the frequency of first affiliative contact between former opponents in the first minute of the PC and the mean frequency of contact per minute of the MC were compared at the individual level using a Wilcoxon signed-rank test. Following Veneema et al. (1994), the corrected conciliatory tendency (CCT) for each individual was calculated as follows: 100*((attracted pairs – dispersed pairs)/total number of PC-MC pairs). Individual CCTs were used to calculate the group mean. Mann-Whitney

U tests were used to compare CCT values for male-male, female-female and mixed-sex dyads.

3.2.2.2. Third-Party Affiliation

The following analyses were conducted only on PC-MC pairs in which the focal individual was the initial recipient of aggression (N=234). PC-MC pairs were labelled attracted if the first affiliative interaction between the recipient of aggression and third party (initiated by either individual) occurred earlier or only in the PC, dispersed if it occurred earlier or only in the MC and neutral if there was no affiliative interaction in either the PC or the MC, or it occurred at the same time in both. Wilcoxon signed-rank tests were used to compare the frequency of attracted and dispersed pairs. Latency to first affiliative contact between the recipient and third party in PC and MC observations was compared using survival analysis (see above for details). All third-party affiliation analyses were then repeated, this time differentiating between affiliative interactions initiated by the recipient of aggression (solicited consolation) and those initiated by a third-party (consolation). Affiliative interactions between the recipient and third party were classed as 'solicited' when the recipient approached or offered a hand towards the third party prior to the interaction or clearly initiated the interaction if both partners were already in proximity. Where the initiator of the interaction was unclear, such as when the interaction commenced prior to the start of the MC, or when partners in proximity to each other started mutual grooming, those PC-MC pairs were removed from these analyses (N=62). Mean individual triadic contact tendencies (TCTs) were calculated separately for consolation and solicited consolation as follows: 100*((attracted pairs – dispersed pairs)/total number of PC-MC pairs) (Call et al., 2002). TCTs of male-male, female-female and mixed-sex dyads were compared using Mann-Whitney U Tests.

3.2.2.3. Interdependency of Reconciliation and Consolation

For the purposes of the following analyses, reconciliation was operationally defined as the first affiliative contact between the opponents during the ten minutes following the conflict. Consolation was operationally defined as the first affiliative interaction initiated by a third party and directed towards the initial recipient of aggression during the ten minutes following the conflict. Only PC-MC pairs in which the focal individual was the recipient of aggression and in which, if applicable, the initiator of the first affiliative interaction between the third party and the recipient was clearly identifiable were included in the analysis (N=171). The probability of reconciliation occurring after and without consolation, and the probably of consolation occurring after and without reconciliation were compared using χ^2 tests.

3.2.2.4. Post-Conflict Behavioural Specificity

General linear mixed models (GLMMs) were used to investigate the relative frequencies of behaviours used for reconciliation, consolation and during MCs. As previous research has suggested that reconciliation tends to be characterised by kisses and consolation characterised by embraces (de Waal & van Roosmalen, 1979), I chose to focus on those two behaviours. In order to investigate the effects of reconciliation and consolation on the frequencies of kiss and embrace, each case of reconciliation and each case of consolation (defined as for the interdependency of reconciliation and consolation) during PCs and all cases of affiliation during MCs were entered as data points into the model. PCs in which both reconciliation and consolation occurred (N=33) were removed from the analysis so that the effects of reconciliation and consolation could be examined independently. The presence of kiss (or embrace) was entered as a dependent variable, with consolation and reconciliation entered as fixed explanatory variables. MCs were indicated by the absence of both reconciliation and consolation. The identity of the recipient of aggression was entered as a random variable.

In order to compare the relative frequency of kisses and embraces used for reconciliation with that for consolation, only PCs with either reconciliation or consolation were entered as data points, with kiss or embrace as a dependent variable, the identity of the recipient of aggression as a random factor and post-conflict interaction (reconciliation or consolation) as a fixed explanatory variable. A significance level of 0.05 was adopted throughout and all tests were two-tailed.

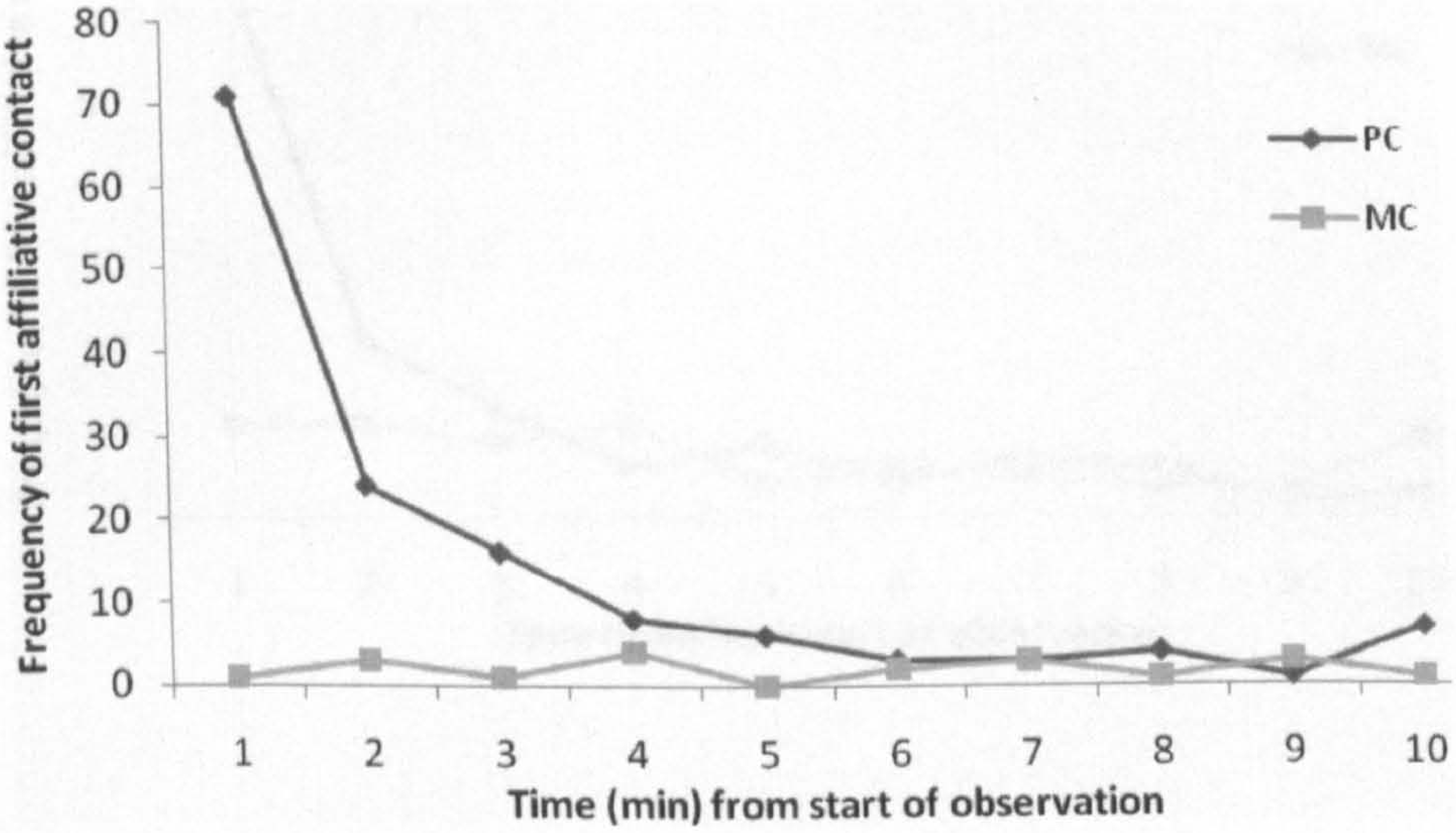
3.3. Results

3.3.1. Reconciliation

A significant difference was found between the proportions of attracted (mean ±SD=0.54±0.23) and dispersed (0.06±0.09) PC-MC pairs for each focal individual, demonstrating the occurrence of reconciliation (Wilcoxon signed-rank test: N=20, z=3.920, P<0.001). A survival analysis confirmed a significant tendency for the first affiliative contact to occur earlier in PC than in MC periods (Mantel-Cox: N=256 PC-MC pairs, χ^2=139.23, df=1, P<0.001). The temporal distribution of latency to first affiliative contact between opponents during PC and MC shows that the majority of first affiliative contacts between former opponents in the PC occurred in the first minute (Fig. 3.1). The frequency of contacts in the first minute of PCs was significantly higher than the mean frequency of contacts per minute in MCs when tested at the individual level (N=21, z=3.085, P<0.001).

Using Veneema et al's (1994) method for measuring the occurrence of reconciliation, the mean (±SD) corrected conciliatory tendency (CCT) per individual was found to be 47.5% (±24.6%). Mean individual CCT values for adult male recipients of aggression (34.1% ± 32.0%) were not found to be significantly different from mean individual CCT values for adult female recipients (51.5% ± 21.6%) (Mann-Whitney U test: n_1=5; n_2=17, U=31.0, P=0.390). CCT values for male-male dyads (23.81±30.22), however, were found to be significantly lower than those for female-female dyads (52.60±55.36) (n_1=8; n_2=67, U=156.5, P=0.023). No significant difference was found between CCT values for mixed-sex dyads (43.77±49.01) and male-male dyads (n_1=52; n_2=7, U=132.5, P=0.231) or for mixed-sex dyads and female-female dyads (n_1=52; n_2=67, U=1515.5, P=0.206).

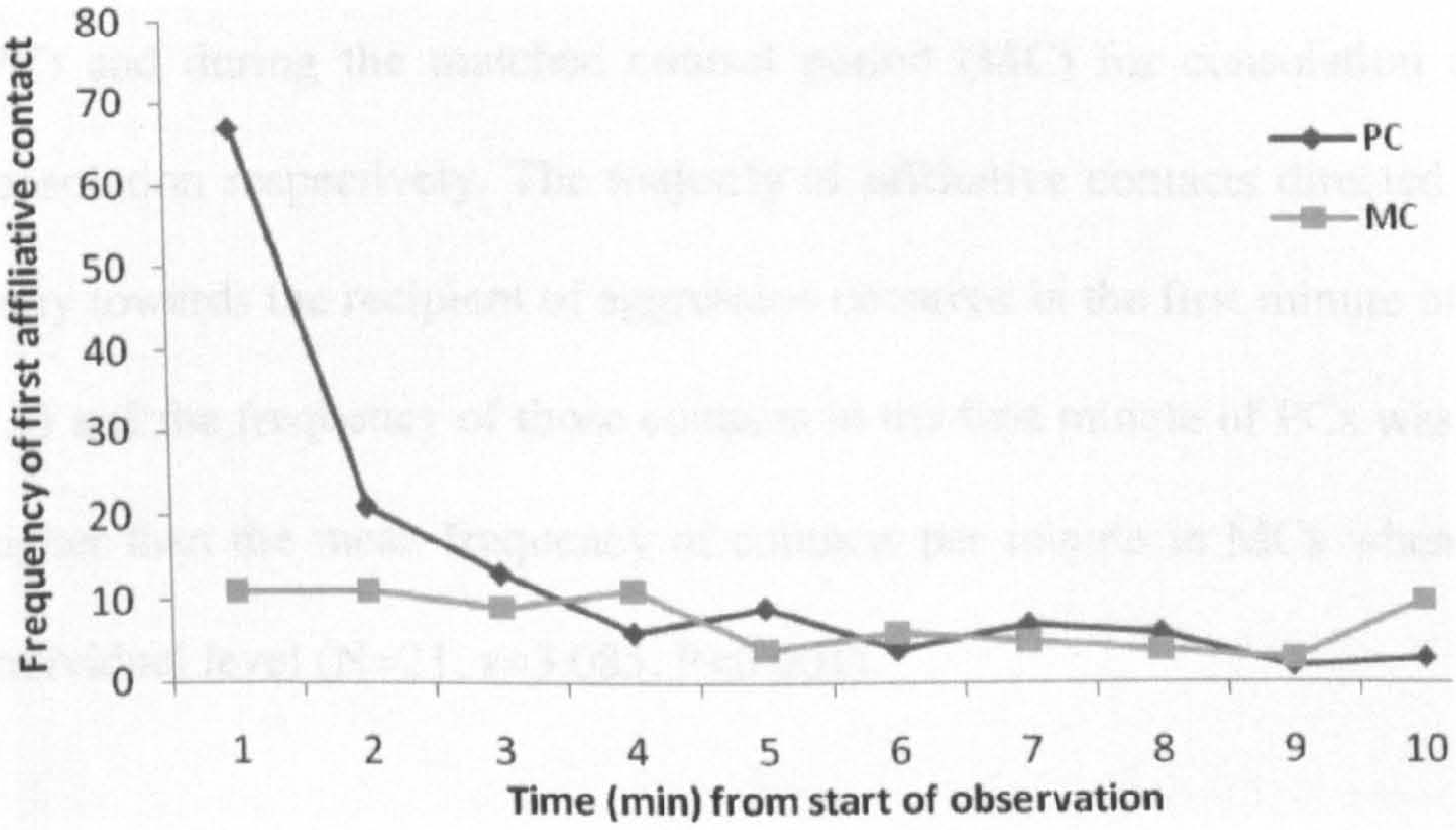
Fig. 3.1. Temporal distribution of latency to first affiliative contact between opponents in PCs and MCs.



3.3.2. Third-party affiliation

No significant difference was found between the proportion of attracted (mean ±SD=0.45±0.20) and dispersed (0.36±0.17) pairs when affiliation with a third-party (initiated by either individual) was examined (N=21, z=-1.234, P=0.217). The survival analysis indicated that there was no significant difference in the latency to third-party affiliative contact in PCs and MCs (N=234 PC-MC pairs, χ^2=0.444, df=1, P=0.505).

Fig. 3.2. Temporal distribution of latency to first affiliative contact between the recipient of aggression and a third party, regardless of initiative, in PCs and MCs.



3.3.3. Consolation and solicited consolation

The proportion of attracted PC-MC pairs (mean ± SD=0.41±0.26) was significantly higher than the proportion of dispersed PC-MC pairs (0.12±0.12) for consolation (N=19, z=3.382, P<0.001). However, for solicited consolation there was no significant difference found between the proportion of attracted (0.23±0.17) and dispersed (0.25±0.22) pairs (N=14, T=57.50, P=0.771), indicating that while consolation can be demonstrated as a post-conflict interaction, solicited consolation cannot. A survival analysis confirmed that affiliative interactions directed from the third party to the recipient of aggression were significantly more likely to occur earlier in PC than MC periods (N=171 PC-MC pairs, χ^2=24.267, df=1, P<0.001). Affiliative interactions directed from the recipient to a third party, however, were no more likely to occur earlier in the PC than the MC periods (N=171 PC-MC pairs, χ^2=0.217, df=1, P=0.642). Figures 3.3 and 3.4 show the temporal distribution of first affiliative contacts with a third party following an aggressive interaction (PC) and during the matched control period (MC) for consolation and solicited consolation respectively. The majority of affiliative contacts directed from a third party towards the recipient of aggression occurred in the first minute of the PC (Fig. 3.4) and the frequency of those contacts in the first minute of PCs was significantly higher than the mean frequency of contacts per minute in MCs when tested at the individual level (N=21, z=3.085, P<0.001).

Fig. 3.3. Temporal distribution of latency to first affiliative contact directed towards the recipient of aggression by a third party in PCs and MCs.

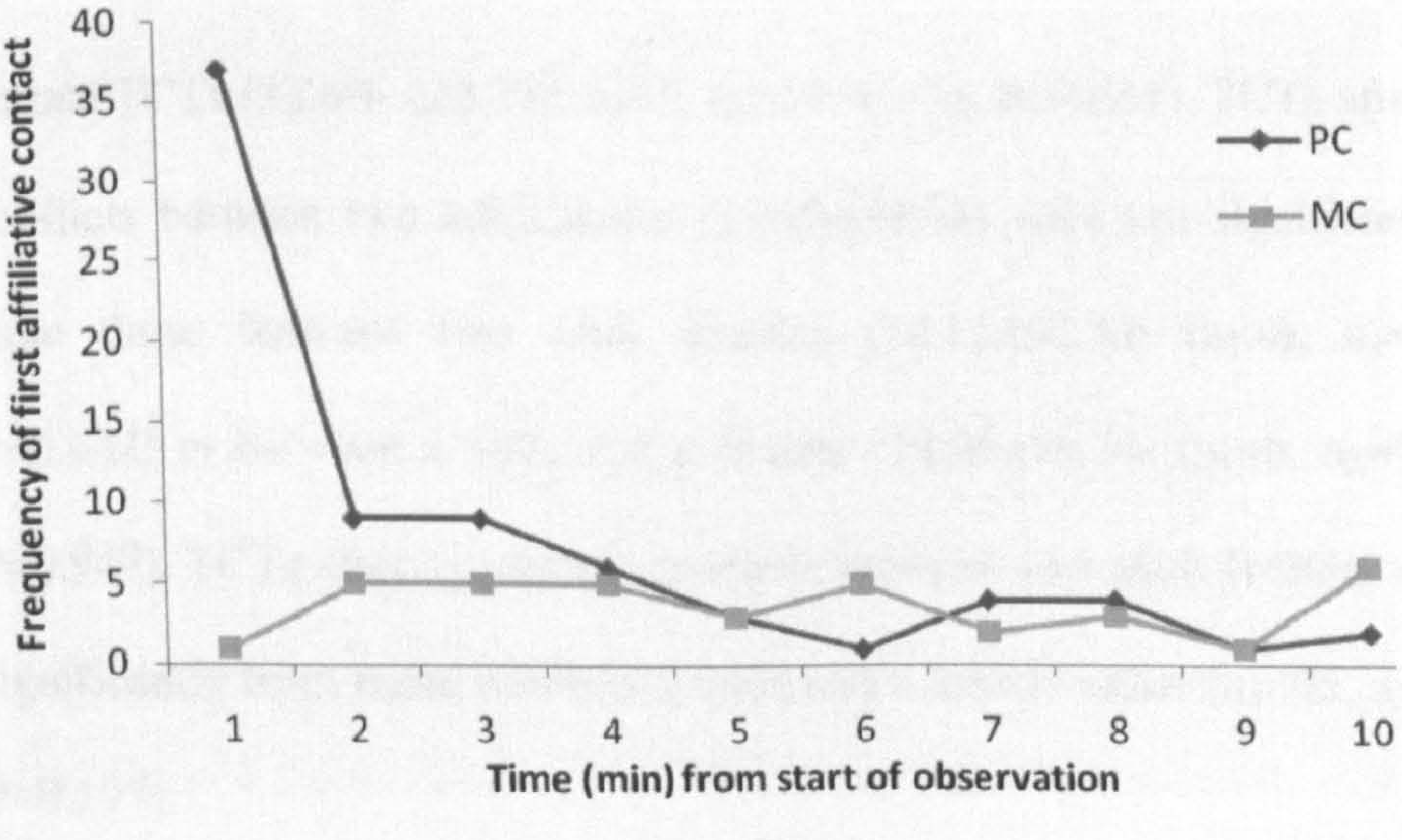
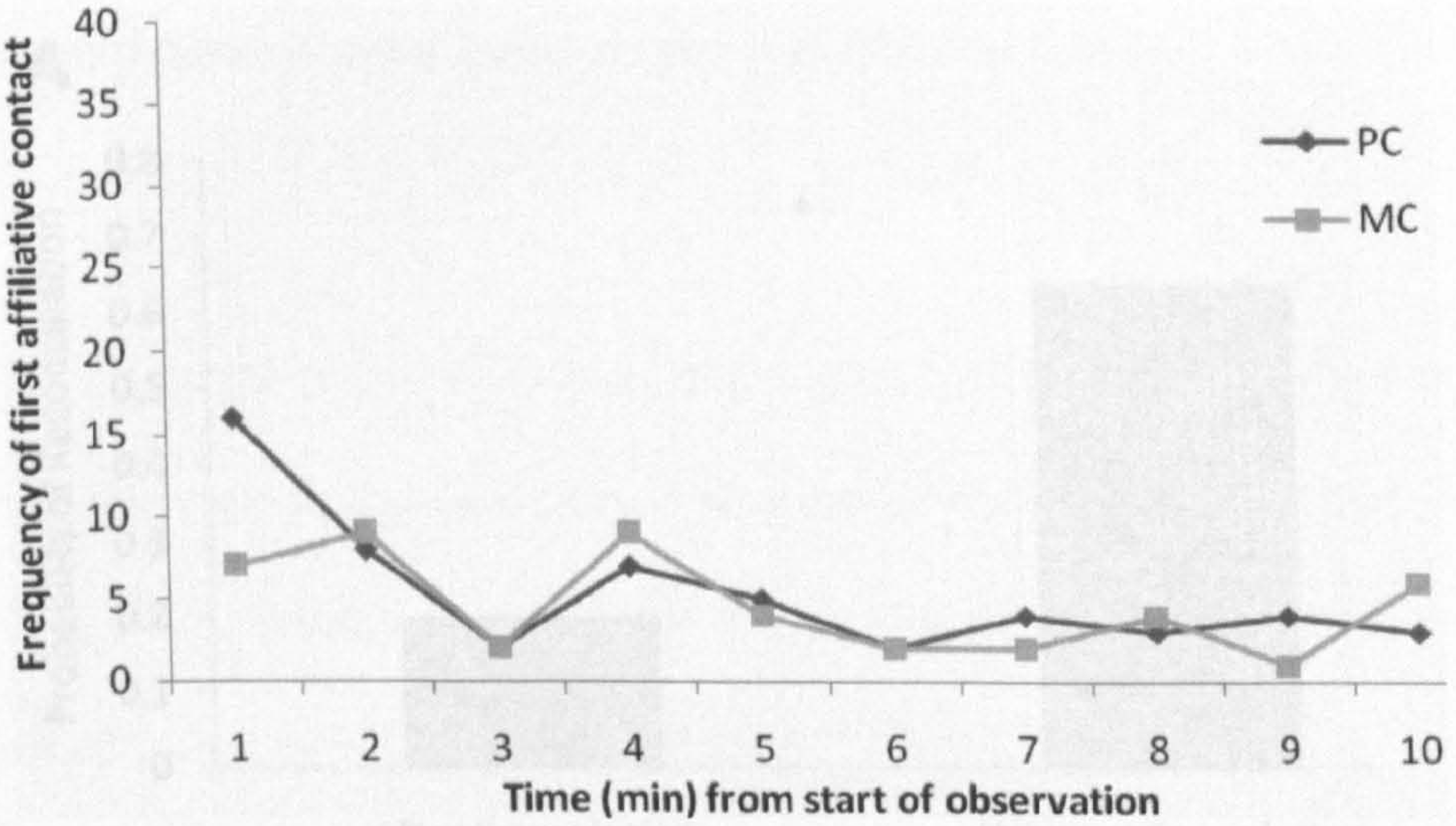
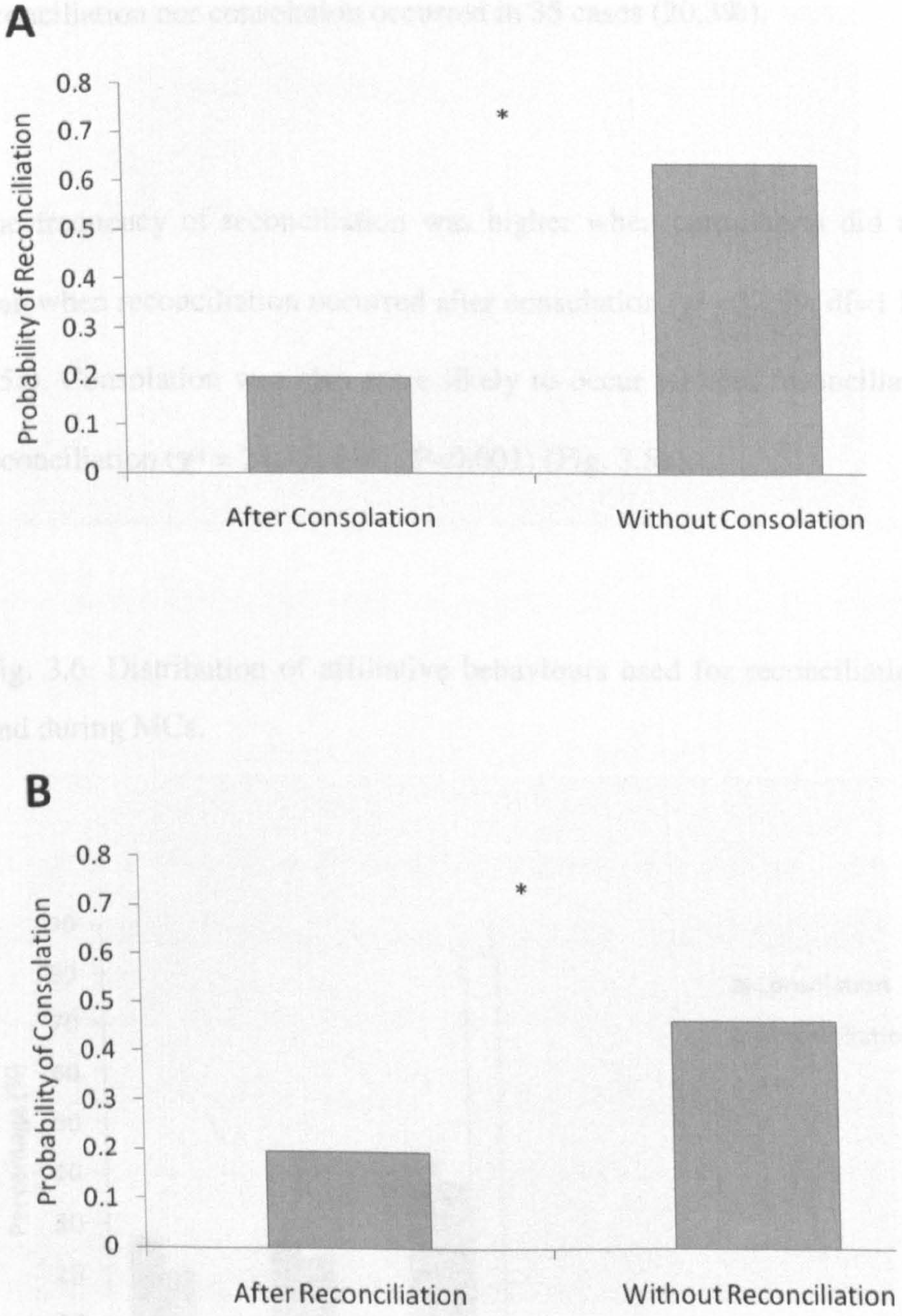


Fig. 3.4. Temporal distribution of latency to first affiliative contact directed from the recipient of aggression to a third party in PCs and MCs.



The mean individual TCT for consolation was 29.4%. Mean individual TCTs for male recipients of aggression (18.2% ±37.3%) were not significantly different from female TCTs (32.6% ±28.3%; n_1=5, n_2=17, U=36, P=0.634). TCTs after aggressive conflicts between two adult males (17.85±59.04) were not significantly different from those between two adult females (36.15±62.20) (n_1=6, n_2=45, U=109, P=0.442) or between a male and a female (18.06±56.26) (n_1=6, n_2=43, U=126.5, P=0.947). TCTs after aggressive conflicts between two adult females did not differ significantly from those between a male and a female either (n_1=45, n_2=43, U=814, P=0.177).

Fig. 3.5. a) Probability of reconciliation after consolation has taken place and in PCs without consolation. b) Probability of consolation occurring after reconciliation and in PCs without reconciliation.

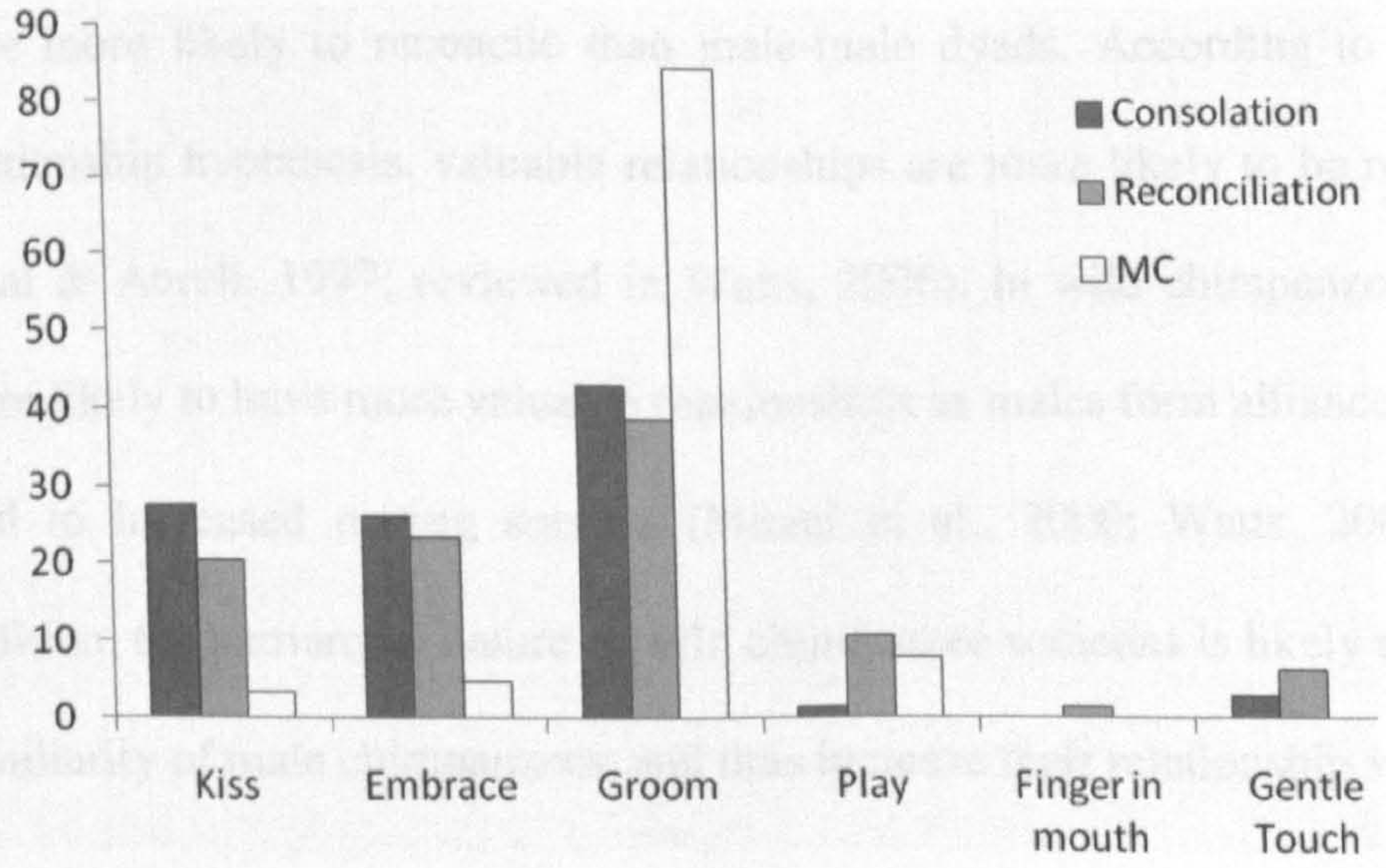


3.3.4. Interdependence of Reconciliation and Consolation.

Following my operational definitions (see Methods), reconciliation occurred 93 times (54.1%; N=171) and consolation occurred 77 times (44.8%). Reconciliation and consolation co-occurred 33 times (19.1%) in the same PC. Neither reconciliation nor consolation occurred in 35 cases (20.3%).

The frequency of reconciliation was higher when consolation did not take place than when reconciliation occurred after consolation ($\chi^2 = 32.99$, df=1 $P<0.001$) (Fig. 3.5a). Consolation was also more likely to occur without reconciliation than after reconciliation ($\chi^2 = 24.47$, df=1, $P<0.001$) (Fig. 3.5b).

Fig. 3.6. Distribution of affiliative behaviours used for reconciliation, consolation and during MCs.



3.3.5. Post-Conflict Behavioural Specificity

Figure 3.6 shows the distribution of all affiliative behaviours used for reconciliation, consolation and during MCs. Embrace and kiss were significantly more likely to be used for both reconciliation and consolation than during the control periods (see Table 3.1). Neither embrace nor kiss was more likely to be used for reconciliation than for consolation (see Table 3.2).

3.4. Discussion

This study confirmed the occurrence of reconciliation and consolation in captive chimpanzees. The overall conciliatory tendency (47.5%) is the highest reported for chimpanzees, although it is similar to the one found for other two captive chimpanzee groups (Baker & Smuts, 1994; Preuschoft et al., 2002).

Contrary to expectation based on chimpanzee socio-ecology, female-female dyads were more likely to reconcile than male-male dyads. According to the valuable relationship hypothesis, valuable relationships are more likely to be reconciled (de Waal & Aureli, 1997; reviewed in Watts, 2006). In wild chimpanzees, males are more likely to have more valuable relationships as males form alliances, which may lead to increased mating success (Mitani et al., 2000; Watts, 2002, 2006). In addition, the patriarchal nature of wild chimpanzee societies is likely to increase the familiarity of male chimpanzees, and thus increase their relationship value and

Table 3.1. GLMM comparing frequency of kiss and embrace used for reconciliation and consolation and during MCs.

Kiss	Fixed Effects	β	S.E.	z	P	Odds Ratio	95% CI
	Intercept	-2.54	0.39	-6.48	<0.01		
	Reconciliation	1.52	0.49	3.11	<0.01	4.57	1.72, 12.18
	Consolation	1.79	0.51	3.52	<0.01	5.99	2.16, 16.61
	Random Effects	Variance					
	Recipient	<0.01					
Embrace	Fixed Effects	B	S.E.	z	P	Odds Ratio	95% CI
	Intercept	-2.90	0.46	-6.32	<0.01		
	Reconciliation	1.71	0.55	3.12	<0.01	5.53	1.84, 16.61
	Consolation	1.80	0.58	3.13	<0.01	6.05	1.89. 19.30
	Random Effects	Variance					
	Recipient	<0.01					

Table 3.2. GLMM showing the frequency of kiss and embrace as behaviours used for different PC interactions (i.e. reconciliation and consolation).

Kiss	Fixed Effects	β	S.E.	z	P	Odds Ratio	95% CI
	Intercept	-0.76	0.32	-2.36	<0.01		
	PC Interaction	-0.25	0.44	-0.57	0.57	0.78	0.32, 1.88
	Random Effects	Variance					
	Recipient	<0.01					
Embrace	Fixed Effects	B	S.E.	z	P	Odds Ratio	95% CI
	Intercept	-1.10	0.35	-3.15	<0.01		
	PC Interaction	-0.09	0.46	-0.20	0.84	0.91	0.36, 2.29
	Random Effects	Variance					
	Recipient	<0.01					

tendency to reconcile, although recent research has shown that males are not necessarily more closely related than females (Mitani et al., 2000; Vigilant et al., 2001). In support of this, male-male dyads in wild chimpanzees have been reported to have higher conciliatory rates than female-female dyads (Arnold & Whiten, 2001). However, this finding was not supported by other studies on wild chimpanzees (Kutsukake & Castles, 2004; Wittig & Boesch, 2005). Furthermore, sex-combination has been shown to have no effect on relationship value among the subjects of this study, although female-female dyads were more compatible (i.e., tolerant) than mixed-sex or male-male dyads (Chapter 4), which may explain their higher conciliatory tendency in this study. While high conciliatory tendencies for female-female dyads have been reported in other captive groups of chimpanzees (Baker & Smuts, 1994; Fuentes et al., 2002; Preuschoft et al., 2002), male-male dyads at Arnhem Zoo displayed significantly higher tendencies to reconcile than female-female dyads (de Waal, 1986; Koski et al., 2007b), indicative of the plasticity of the nature of chimpanzee social relationships (Baker & Smuts, 1994; de Waal, 1994). Furthermore, when predictors of reconciliation in the current study group were analysed at the post-conflict interaction level, opponent sex-combination was not found to have a significant effect (Chapter 5). Thus sex-combination per se may not be a defining factor in determining variation in conciliatory tendencies within and between groups, but rather the relationship characteristics represented by certain sex-combinations, which may vary according to group history and socio-ecology.

The occurrence of consolation was confirmed as a post-conflict interaction as third parties were more likely to initiate affiliative contact with the recipient of aggression during post-conflict periods than during control periods. Recipients of aggression, however, were not more likely to initiate affiliation with bystanders after a conflict than during control periods, so solicited consolation could not be demonstrated as a post-conflict interaction. These findings support previous research on both captive and wild chimpanzees (Wittig & Boesch, 2003a; Kutsukake & Castles, 2004; Koski & Sterck, 2007), although consolation has not been demonstrated in some studies (Arnold & Whiten, 2001; Fuentes et al., 2002). Only one study has found evidence of both consolation and solicited consolation in chimpanzees (Palagi et al., 2006a), although both post-conflict interactions have been demonstrated in gorillas (Cordoni et al., 2006; Mallavarapu et al., 2006) and bonobos (Palagi et al., 2004). The mean individual triadic contact tendency for consolation found in this study fits within the range of the two other studies that have reported it in chimpanzees (Palagi et al., 2006a; Koski & Sterck, 2007). In further support of both studies, no effect of sex-combination on triadic contact tendencies was found.

Consolation was more likely to occur in the absence of reconciliation than after reconciliation, supporting my first prediction on the interdependence of reconciliation and consolation. Reconciliation, however, was not equally likely to occur after consolation as without consolation as we predicted. In fact, reconciliation was less likely to occur after consolation. These results were supported by similar findings using more powerful analyses (Chapter 5 and 6).

These findings could be interpreted as suggesting that reconciliation may be unnecessary after consolation, but this is unlikely as consolation is not expected to repair the relationship between former opponents. Alternatively, consolation may act as an alternative to reconciliation when reconciliation fails to occur (Wittig & Boesch, 2003a; Palagi et al., 2004; Palagi et al., 2006a). As reconciliation may carry risks of renewed aggression (Aureli et al., 2002), the benefits of reconciliation must outweigh the costs in order for it to occur. In cases where the relationship between opponents is of low value, and/or the risks of renewed aggression are high, consolation may function as an alternative to reconciliation, possibly reducing post-conflict stress levels in the victim of aggression (Chapter 6).

Kiss and embrace were used in a substantial proportion of cases of reconciliation and consolation, and both were found to be more likely to occur during PCs than MCs. This supports the view that chimpanzees exhibit 'explicit' reconciliation as opposed to 'implicit' reconciliation, as these two behaviours were rarely observed outside of a post-conflict context (c.f. de Waal & Ren, 1988). De Waal & Ren (1988) suggested that species with more tolerant social systems employ explicit gestures for reconciliation in order to reaffirm the relative status of the partners. In using conspicuous behaviours that are relatively rare outside a reconciliation or consolation context, it is possible that tolerant species, such as chimpanzees, require subordination to be made explicit before reconciliation is granted (de Waal, 1986). In support of this hypothesis, de Waal & Ren (1988) found that stump-tailed macaques displayed a rich repertoire of behavioural gestures during post-conflict reunions whereas the much more despotic rhesus macaques did not display any post-conflict behavioural specificity. Demaria & Thierry (2001) also found reconciliation to be less demonstrative in rhesus macaques than the more tolerant Tonkean macaques. The evidence for explicit reconciliation in chimpanzees, however, is mixed. In the first study on reconciliation and consolation, it was suggested that chimpanzees preferentially use kisses for reconciliation and embraces for consolation (de Waal & van Roosmalen, 1979). Since then, this finding has not been replicated (Arnold & Whiten, 2001; Fuentes et al., 2002; Kutsukake & Castles, 2004), although embraces were found to account for the majority of consolation contacts in the Yerkes chimpanzees (de Waal & Aureli, 1996). Wittig & Boesch (2005) claimed that reconciliation was explicit in their group of chimpanzees, but based this claim not on the type of behaviour used, but on the complexity of behavioural elements used for reconciliation.

The high levels of reconciliation found in this study are also consistent with an explicit style of reconciliation, as all species in which explicit reconciliation has been documented exhibit relatively high conciliatory tendencies (de Waal & Ren, 1988; Arnold & Barton, 2001a; Demaria & Thierry, 2001; Leca et al., 2002; Gruter, 2004; Thierry et al., in press). Moreover, Thierry et al. (in press) found that the relationship between high conciliatory tendencies and high rates of explicit conciliatory contacts across macaque species remained significant even after controlling for phylogeny, indicating that they are inter-related social traits. Furthermore, the relationship between these traits suggests that explicit contacts may facilitate the occurrence of reconciliation, pointing to a possible functional link between reconciliation and explicit contact (Thierry et al., in press). In chimpanzees, the high rates of reconciliation found in this and the original study showing an explicit style of reconciliation (de Waal & van Roosmalen, 1979), compared to the considerably lower rates of reconciliation in all studies that have shown an implicit style of reconciliation in chimpanzees (Arnold & Whiten, 2001; Fuentes et al., 2002; Kutsukake & Castles, 2004) may provide support for such a functional link. As Wittig & Boesch's (2005) suggestion that Taï chimpanzees employ explicit forms of reconciliation based on the complexity of their behavioural patterns is not supported by a high conciliatory tendency, it is possible that such complexity is not related to the use of context-specific conspicuous behaviours normally characteristic of explicit reconciliation.

While kissing was primarily used for reconciliation and embracing for consolation in the original study (de Waal & van Roosmalen, 1979), my findings show that kisses and embraces were equally likely to be used for either post-conflict interaction. In addition, kisses reported in this study were not the 'mouth-to-mouth kiss' described by de Waal and van Roosmalen (1979) but kisses placed on any part of a partner's body (mouth-to-mouth kisses were never observed). If behavioural specificity enables dominance-subordination relationships to be reaffirmed (de Waal, 1986; de Waal, 1993), it is unclear why kiss and embrace would be employed as those behaviours are unlikely to fulfil such a function as these behaviours are not signals of relative dominance status in chimpanzees (van Hooff, 1974; Goodall, 1986; de Waal, 1992). Moreover, if such 'explicit' contacts are a prerequisite for reconciliation, it might be considered surprising that these behaviours are only used for a proportion of all occurrences of reconciliation in species purportedly displaying an explicit conciliatory style. It could be that the reasons for differences in reconciliation style between species also apply to within-species differences. Just as species that generally display high levels of affiliation and tolerance may require a clearer signal for reconciliation than less tolerant species in which simple proximity is already meaningful (Arnold & Aureli, 2007), within a species, regular grooming partners may not perceive grooming to be as clear a signal of reconciliation as partners who rarely groom and thus might attribute a higher significance to the interaction. Stump-tailed macaque 'friends' (based on time spent contact sitting), however, were more likely to reconcile through allogrooming or contact sitting, both implicit behaviours, than 'non-friends' (Call et al., 1999), suggesting that clearer signals for reconciliation might not be necessary for close friends after all, at least for that species.

In order for reconciliation to take place, it is likely that the partners already have a valuable relationship (de Waal & Aureli, 1997; Watts, 2006). Within those valuable partners, however, variation in relationship compatibility and security might determine the type of behaviour used for reconciliation. The higher risks of renewed aggression for partners with less compatible and/or secure relationships may also result in a greater need for clarity of intentions, and thus an explicit style of reconciliation. Supporting the use of explicit behaviours where risks of renewed aggression are high, stump-tailed macaques were found to be more likely to engage in more explicit behaviours to reconcile when inter-opponent distance after a conflict was short, and thus reoccurrence of aggression was more likely (Call et al., 1999).

This study confirms the occurrence of post-conflict reconciliation and consolation, supporting the notion that consolation acts as a substitute for reconciliation when the latter fails to occur. In addition, this study provides evidence for behavioural specificity for both reconciliation and consolation, supporting an 'explicit' style of post-conflict affiliation in the study chimpanzees.

CHAPTER 4

Components of Relationship Quality

4.1. Introduction

A social relationship encompasses the host of social interactions that occur between two individuals over a period of time. It is the relative pattern and frequency of the interactions that determine the quality of the relationship between two individuals (Hinde, 1979). The quality of the relationship may then influence decisions over future interactions and predict partners' behaviour under different situations (van Schaik & Aureli, 2000; Aureli et al., 2002).

The variation in the quality of relationships between individuals and groups and species has been used to investigate the functions and patterns of many social interactions, such as mother-infant interactions (Schino et al., 1995; Maestripieri, 1998; Dwyer & Lawrence, 2000; Bardi et al., 2001; Maestripieri, 2001; Weaver & de Waal, 2002), cooperation and alliances (Mitani et al., 2000; de Villiers et al., 2003; Parsons et al., 2003; Lusseau, 2007), mating patterns (Manson, 1997; Soltis, 1999), post-conflict behaviour (Cords & Aureli, 2000; de Waal, 2000b; Wahaj et al., 2001; Aureli et al., 2002; Watts, 2006; Arnold & Aureli, 2007) and even vigilance behaviour (Kutsukake, 2006). In addition, the quality of social relationships has been used to investigate variation in reproductive success

(Armitage, 1986; Silk et al., 2006; reviewed in Silk, 2007a), infant survival rates (Silk et al., 2003) and leadership roles (Fischhoff et al., 2007). The sources of variation within social relationships, however, have received less attention.

Cords and Aureli (2000) proposed three main components of relationship quality: value, compatibility and security. The value of a relationship relates to the benefits afforded by that relationship, such as food sharing or agonistic support; the compatibility between two partners is a measure of tolerance and affiliation, based on a shared history of social exchanges; the security of a relationship is determined by the predictability and consistency of the behaviour of partners towards each other over time.

The study of primate conflict resolution provides a good example of how the effects of these components of relationship quality have been investigated. The quality of relationship between adult primates has long been thought to influence the occurrence of the post-conflict affiliative reunion between former opponents or reconciliation (Cords & Aureli, 2000; de Waal, 2000b; Watts, 2006; reviewed in Aureli et al., 2002). As reconciliation repairs the relationship between opponents, individuals with a more valuable relationship are expected to be more likely to reconcile in order to restore the benefits afforded by the relationship. Numerous studies have investigated the impact of relationship quality on reconciliation tendencies, and there is (mostly indirect) evidence showing that more valuable and compatible relationships are indeed reconciled more often than less valuable or compatible relationships (e.g. de Waal & Yoshihara, 1983; Aureli et al., 1989; Cords & Thurnheer, 1993; Aureli et al., 1997; de Waal, 2000b; Koyama, 2001; Kutsukake & Castles, 2001; Cooper et al., 2005; Majolo et al., 2005; Wittig & Boesch, 2005). There is, however, much variation and little consistency between studies in the way in which the value and compatibility of relationships were measured, and the difficulties in assessing the security of a relationship have meant that few studies have investigated all three components (Cords & Aureli, 2000; Watts, 2006; Arnold & Aureli, 2007).

One of the weaknesses of many studies involving relationship quality is the assumption that broad categories, such as kinship or age-sex combinations, represent different levels of relationship quality. As tolerance, affiliation or agonistic support between kin may all lead to inclusive fitness benefits (Anderson & Ricklefs, 1995; Silk, 2002b; Parsons et al., 2003), kinship is often used as an indirect indication of relationship value, especially in species that exhibit strong bonds between kin (e.g. de Waal & Yoshihara, 1983; Judge, 1991; Aureli, 1992; Aureli et al., 1997; Mitani et al., 2000; Chapais et al., 2001). Similarly, in some species particular sex-combinations are more likely to affiliate or form alliances than others. For example, in chimpanzees, male-male relationships are thought to have high value as males form alliances in intra-group disputes, which may lead to increased mating success (Nishida, 1997; Mitani et al., 2000; Watts, 2002, 2006). In addition, the importance of male alliances at the group level in intercommunity aggression also suggests a high relationship value between males (Wilson & Wrangham, 2003). Dyadic sex-combinations are thus often used as indirect indications of relationship value (de Waal & van Roosmalen, 1979; Watts, 1995a; Kutsukake & Castles, 2004; Manson et al., 2005; Koski et al., 2007a). Using such broad categories of relationship quality, however, may mask the effects of individual and dyadic variability within categories. Furthermore, no study has as yet tested the effects of sex-combination or kinship on components of relationship quality.

Another means used for assessing relationship quality is the relative frequency of social interactions linked to different aspects of relationship quality. Rates of agonistic support (Cooper et al., 2005), grooming (Majolo et al., 2005), time in proximity (Kutsukake & Castles, 2004), and food sharing (Wittig & Boesch, 2005) have all been used as measures of relationship value. Rates of grooming and proximity have also been used as measures of compatibility (Arnold & Whiten, 2001; Koski et al., 2007a). As self-directed behaviours such as self-scratching have been shown to be reliable indicators of uncertainty and anxiety in primates (Maestripieri et al., 1992; Troisi, 2002; pharmacological evidence: Schino et al., 1996), rates of self-scratching on the approach of other individuals have been used as a measure of security (Castles et al., 1999; Kutsukake, 2003). Whereas these measures can provide a valid assessment of relationship quality, choosing the best behaviour to represent each component of relationship quality can be difficult and runs the risk of interpreting relationship quality from the observer's perspective rather than from the animal's perspective. The use of a single behaviour may also limit the interpretability of the results (Silk, 2002c), and yet combining variables that represent a single component of relationship quality in a meaningful manner can be difficult.

One method of developing quantitative measures of relationship quality was pioneered in studies of mother-infant relationships in Old World monkeys. Several authors (Simpson & Howe, 1980; Tanaka, 1980; Fairbanks & Mcguire, 1987; Schino et al., 1995) used principal components analysis (PCA) to reduce the large number of independent variables to a few behavioural dimensions that describe mother-infant interactions in a less subjective manner. Each extracted component offered a more comprehensive and conceptually more coherent measure of each dimension of relationship quality. Using this method, the effects of a number of different variables, such as maternal experience, social and demographic influences and hormonal status, on mother-offspring relationships and maternal style have been investigated (Schino et al., 1995; Maestripieri, 1998; Dwyer & Lawrence, 2000; Bardi et al., 2001). This method has also been extrapolated to the study of mating patterns and consortships in primates (Manson, 1997; Soltis, 1999). Applying this method to the study of adult social relationships could provide comprehensive, composite measures of relationship quality specific to the particular study subjects.

The aims of this study were therefore firstly to determine the components of relationship quality in a large group of zoo chimpanzees based on a number of behavioural variables, and investigate whether they could be candidates for the components of value, compatibility and security hypothesised by Cords and Aureli (2000). Secondly, we aimed to investigate whether factors, such as kinship, sex-combination, age difference and relationship tenure, were responsible for variation in each of these components.

4.2. Methods

4.2.1. Data Collection

Focal animal sampling, group scan sampling and all occurrences methods were used to collect data on the quality of the relationships of the study subjects (see Chapter 2 for further details).

4.2.2. Data Analysis

4.2.3. Components of Relationship Quality

Composite measures of relationship quality were obtained using principal components analysis (PCA). PCA is a statistical technique that can be used to identify underlying factors, or principal components, that explain the pattern of correlations within sets of variables (Tabachnick & Fidell, 2007). The correlations between variables are thought to occur as a result of these variables sharing a component. Variables that are correlated with one another, which are also largely independent of other sets of variables, are combined into uncorrelated linear components. The first component is the combination of variables that accounts for the most variance within the sample. Successive components explain progressively smaller portions of the variance and are uncorrelated with other components. Component loadings are the coefficients of the correlation between the components and the variables. Coefficients of correlation greater than 0.5 or less than -0.5 were considered to be high loadings. A varimax rotation was used to simplify the interpretation of the components. Varimax rotation is an orthogonal rotation method that minimizes the number of variables that have high loadings on each component. Eigenvalues are the sum of the squares of the component loadings and reflect the total variance explained by each component. A minimum eigenvalue of 1.0 was used to determine the number of components extracted from the PCA (Tabachnick & Fidell, 2007). Because the components are not correlated with one another, the total variance explained is the sum of the variance explained by each component.

Nine behavioural variables for each dyad of individuals were entered into the PCA. For descriptions of each variable, see Table 4.1. Symmetry in grooming between individuals A and B was calculated using the following formula: A grooms B/(A grooms B + B grooms A). For each dyad, the lowest of the two values obtained reversing A's and B's roles was chosen to represent the degree of symmetry, so values ranged from 0 to 0.5, with higher values indicating more symmetrical exchanges. Consistency in affiliation was measured by the coefficient of variation in the proportion of scans in which two partners were grooming or in proximity with each other calculated over six blocks of three months each. An index of agonistic support was created by calculating the frequency of support as a function

Table 4.1. Descriptions of variables entered into the principal component analysis.

Variable Name	**Variable Description**
Grooming	Proportion of scans spent in mutual or uni-directional grooming.
Grooming symmetry	Symmetry in grooming within the dyad.
Consistency of affiliation	Variation in proximity and grooming over time within the dyad.
Proximity	Proportion of scans spent within arm's reach (including gross body contact), excluding grooming.
Tolerance to approaches	Proportion of approaches with a positive or neutral response.
Support	Index of agonistic support (frequency of support / opportunity to support).
Counter-intervention	Index of counter-intervention (frequency of intervention / opportunity to intervene).
Aggression	Frequency of aggressive conflict.
Successful begging	Frequency of successful begging attempts.

of the opportunity to support (i.e. the number of conflicts where A supported B or B supported A divided by the total number of conflicts involving A or B, excluding those in which A and B were opponents). A similar index was calculated for counter-intervention (agonistic intervention against a partner, c.f. de Waal &

Luttrell, 1988). As all occurrences of aggression and begging were recorded when visible without bias, the frequency of aggression and successful begging were used.

4.2.4. Factors Affecting Relationship Quality

The influence of characteristics of the dyad on the extracted components was assessed using multiple regression analysis. The independent variables entered into multiple regression models were kinship (kin or non-kin), sex-combination (dyads including males: male-male and male-female; or dyads including no males: female-female), age difference between partners (in years) and relationship tenure (in years). Kinship was based on maternal lineages, and kin included dyads with a coefficient of maternal relatedness of $r>0.125$. Relationship tenure was the time spent together in the group and was calculated using the age of the youngest partner or the number of years since introduction to the group for non-natal group members, whichever was least. The dependent variables used in the analysis were the scores obtained for each dyad for each of the components extracted from the PCA. In order to correct for skewness and kurtosis in the data, a negative inverse transformation was applied to the data, when necessary. An alpha level of 0.05 was adopted for all tests. All analyses were conducted in SPSS v. 14.0

4.3. Results

4.3.1. Components of Relationship Quality

Three components were extracted from the principal components analysis. Components 1, 2 and 3 explained 27.0%, 15.9%, and 13.9% of overall variance respectively, making up a total of 56.7%. Table 4.2 shows the loadings of the behavioural variables on each of the extracted components. The first component was characterised by behaviours that indicate the importance of the relationship in terms of its direct benefits (grooming, agonistic support, successful begging), and thus was labelled Value. Proximity also loaded highly on this component. Component 2 showed high positive loadings for counter-intervention and aggression and a strong negative loading for tolerance to approaches, suggesting that the component represented low tolerance and affiliation between partners. Whereas these characteristics suggest an incompatibility of the partners, the component was labelled Compatibility for ease of interpretation. In all later analyses involving the second component, the signs for the scores obtained for each dyad for that component were inversed so that they represented the degree of compatibility as opposed to the incompatibility of the dyad. The third component consisted of behaviours indicating a lack of stability or predictability in the relationship (consistency of affiliation) and a high degree of inequality (grooming symmetry), which approximated Security as defined by Cords and Aureli (2000), and was hence labelled as such.

Table 4.2. Varimax rotated component matrix. Values represent coefficients of correlation between each variable and each component. Values of >0.5 or <-0.5 were considered high loadings.

	Component		
	1	2	3
Grooming	.824	-.047	.138
Grooming symmetry	.029	-.134	.678
Consistency of affiliation	.131	-.011	.686
Proximity	.763	-.150	.052
Tolerance to Approaches	.085	-.666	-.388
Support	.808	-.016	-.127
Counter-Intervention	-.019	.660	-.292
Aggression	-.052	.711	-.122
Begging	.695	.021	.178

4.3.2. Factors Affecting Relationship Quality

Overall, the characteristics of the dyads we investigated adequately explained the variance in each of the relationship quality components (Value: $r = 0.497$, $r^2 = 0.247$, $F_{4,222} = 18.211$, $P<0.001$; Compatibility: $r= 0.359$, $r^2=0.151$, $F_{4,222}=9.876$, $P<0.001$; Security: $r=0.304$, $r^2=0.092$, $F_{4,222}=5.634$, $P<0.001$). Results of the multiple regression analysis are given in Table 4.3.

Significant positive correlations were found between Value and kinship and Value and relationship tenure, indicating that kin and individuals who have been together in the group for a long time had more valuable relationships. A negative relationship was found between age difference and Value, indicating that individuals of a similar age were more valuable. The sex combination of the dyad was found to have no effect on the Value of the relationship.

Table 4.3. Influence of relationship characteristics on components of relationship quality (standardised β coefficients, *F* values and *P* values).

		Kinship	Sex-combination	Age difference	Relationship tenure
Value	β	0.335	-0.019	-0.157	0.265
F		5.717	-0.295	-2.067	3.471
P		<0.001	0.769	0.040	0.001
Compatibility	β	0.150	-0.379	0.059	0.197
F		2.413	-5.497	0.749	2.426
P		0.017	0.000	0.454	0.016
Security	β	0.119	0.285	-0.207	-0.265
F		1.856	3.991	-2.560	-3.160
P		0.065	<0.001	0.011	0.002

Kinship and relationship tenure were also positively correlated with Compatibility, whereas no correlation was found between age difference and Compatibility. In addition, female-female dyads were found to be more compatible than dyads including males. Although the correlation between kinship and Security was not significant, an almost significant positive correlation suggests that kin tended to be more secure than non-kin. A negative correlation was found between sex combination and Security, indicating that dyads including males were more secure. A negative correlation between age difference and Security showed that individuals of a similar age were more secure, but a negative correlation between relationship tenure and Security revealed that individuals who had spent longer together in the group were less secure partners.

4.4. Discussion

This study identified three components of relationship quality in Chester Zoo chimpanzees. Based on the loadings of the behavioural variables, the components were labelled Value, Compatibility and Security, approximating those proposed by Cords and Aureli (2000). The findings of this study confirm, therefore, that there are at least three independent aspects of relationship quality. Studies of the quality of social relationships have thus far focussed mainly on relationships as a whole, often using rates of affiliative behaviour as an indication of the general tenor of the relationship (Cords, 1997; Cords & Aureli, 2000; Silk, 2002c). In finding three separate components of relationship quality, this study confirms theoretical predictions (Cords & Aureli, 2000) and emphasises the need to investigate social relationships in more detail. In particular, such results provide an opportunity to both examine sources of variation within each component (see below) and investigate the effects of each component on social interactions independently (Chapters 5 and 6). The use of PCA allowed the components to be identified in a non-subjective manner, reflecting more closely the animals' perspective and the complex patterning of their multiple social interactions. By providing composite, quantitative measures for each component, this method represents a significant improvement for the study of adult-adult social relationships.

A number of factors appear to affect the three components of relationship quality in the study group. Kin were found to have more valuable relationships than non-kin. The inclusive fitness benefits associated with relationships between genetically related individuals (Silk, 2002b) make this result unsurprising, although recent studies have suggested that kinship is not a required element for close social bonds or fitness-enhancing alliances between wild male chimpanzees (Mitani et al., 2000; Vigilant et al., 2001; Langergraber et al., 2007). The high degree of compatibility between kin found in this study mirrors reports of close associations and tolerance between kin across taxa (Belisle & Chapais, 2001; Silk, 2002b; Mckinnon et al., 2006; Möller et al., 2006; Bashaw et al., 2007). The high level of familiarity between kin makes it likely that their interactions are rather predictable over time. This is supported by my finding that kin are likely to have more secure relationships than non-kin, although this trend did not quite reach significance.

Contrary to expectations based on data on wild chimpanzees, sex combination did not affect the value of relationships. Male chimpanzees usually form alliances with each other that influence dominance ranks, and thus reproductive success, whereas cooperation between male-female dyads and female-female dyads is less likely to affect their fitness (Mitani et al., 2000; Watts, 2006). Thus, male-male dyads are often classified as highly valuable. Mixed-sex dyads, however, have been suggested to have equally valuable relationships as male-male dyads because females represent potential mating partners for males (Wittig & Boesch, 2003a) whereas males may play a valuable role in protecting females and buffering female-female competition (Pusey et al., 1997). In a captive situation females are often more closely related than in the wild and are more likely to remain in their natal group leading to a higher degree of familiarity between females and are therefore more likely to exchange valuable services such as grooming, agonistic support and food sharing (de Waal, 1994).

The male subjects in this study appeared to be characterised by particularly low levels of competition over females and hierarchal positions, and male-male agonistic support was relatively rare. It is possible that the low levels of competition and support in males in addition to high levels of affiliation among females counteracted the expected differentiation in relationship value between dyads with and without males. This result highlights the need to determine relationship quality based on information derived from the particular study group, and reveals the possible danger of generalising across groups the effects of broad categories, such as sex combinations, even within the same species.

The high degree of compatibility between females in this study is in direct contrast with data on patterns of association in wild chimpanzees (Goodall, 1986; Arnold & Whiten, 2001; Stumpf, 2007; but see Boesch & Boesch-Achermann, 2000), but supports data from some captive studies (Preuschoft et al., 2002) and shows the plasticity of the nature of female chimpanzee relationships (Baker & Smuts, 1994; Pusey et al., 1997). It is worth noting here that the measure of compatibility used in this study reflected low levels of aggression and counter-intervention and a high proportion of positive or neutral responses to approaches. Other studies have measured compatibility in terms of the amount of time spent grooming (Arnold & Whiten, 2001; Preuschoft et al., 2002; Koski et al., 2007b), a behaviour that had high loading on the relationship value component in the PCA conducted in my study. Thus, my measure of compatibility better represents tolerance and the overall tenor of interactions (c.f. Cords & Aureli, 2000) within the dyad, as opposed to affiliation based on services provided (such as grooming).

While female-female dyads may be more compatible, dyads including males were found to have more secure relationships, an unexpected result based on typical opportunistic changes in male-male relationships (de Waal, 1982; Goodall, 1986). In the study group, male-male dyads could be more secure as a result of the stability of their positions within the dominance hierarchy. As the other four males were considerably older than the dominant male, who was in his prime, there was little competition over dominance positions and so their relationships were unlikely to change over time. The females' relationships, however, were more likely to be fluid, changing over time as younger females, who did not leave the group, age and bear offspring, of which several were born during the study period.

Individuals of a similar age were found to have a more valuable relationship. This finding supports de Waal and Luttrell's (1986) 'similarity principle', which states that as members of the same age cohort share similar needs, access to resources and power, these individuals are likely to be in the best position to provide and exchange fitness benefits, and thus are more likely to have valuable relationships. It is possible that age may also be used as a proxy for paternal relatedness, given that high-ranking males monopolise access to females and thus agemates are likely to be half-siblings (Silk, 2002b). Individuals of a similar age were also found to have a more secure relationship in this study, in agreement with findings in other species in which preferential associations between individuals of a similar age remain consistent over time (Widdig et al., 2001).

Partners with longer relationship tenure had a more valuable and more compatible, but less secure relationship than those who had spent less time together. Kummer (1978) proposed that social relationships are investments that maximise the long-term gain for both partners from their relationship with each other. It is likely, therefore, that individuals who have interacted over longer periods would display a more valuable and compatible relationship than those who have spent less time together. Why those relationships would be less secure, however, is unclear, as a long history of social interactions is likely to make a relationship less susceptible to damage (Brosnan et al., 2005), and thus would be expected to be more secure. It is possible that the results were confounded by the ambiguous nature of the measure we used for relationship tenure. Relationship tenure was based on the age of the youngest partner in most dyads and thus combined the differing effects of familiarity and social experience. While familiarity with partners increases with time spent together in the group for all dyads, the social experience is different depending on the age gap between partners. For example, an individual's social experience is dramatically different when growing up with an age-mate from that of spending the same amount of time in the group with an individual that was already adult when the individual was born. The component labelled 'Security' may also not be truly representative of relationship security. Relationship security refers to the perceived probability the relationship will change over time, which relates to the consistency of the partner's behavioural response (Cords & Aureli, 2000). The component labelled Security in this study was based on positive loadings from two variables, consistency of affiliation and symmetry in grooming. Whereas the consistency of affiliation fits Cords & Aureli's (2000) definition of security, the symmetry of grooming refers to the variation between partners in grooming given during the whole study period rather than variation over time. In addition, the relationship factors (kinship, sex-combination, age difference and time spent together) explained a mere 9.2% of the variation within the component labelled security, which in turn explained just 13.9% of the overall variation in the behavioural variables used in the PCA. The results pertaining to relationship security must therefore be treated with caution.

The results of this study are based on dyadic data, and thus only one score per dyad for each relationship component was used. Although some of the behavioural variables used in the analyses are by nature symmetrical, such as time spent in proximity, it is likely that most interactions between individuals in the same dyad are not symmetrical. Thus the relationship between partners may be assessed differently from each partner's perspective. Reciprocity, however, has been suggested to play in important role in strong social bonds (de Waal & Luttrell, 1988; Cords, 1997; Silk, 2002c), and thus the quality of the relationship from each partner's perspective level is likely to be similar for partners with highly valuable, compatible and secure relationships. The size of the dataset precluded us from carrying out analyses at the individual level (i.e., a score for each partner in any dyad), but this is certainly an issue to be addressed in future studies.

The results of this study raise interesting issues about the factors that determine the quality of relationships in chimpanzees. Further studies on other captive and wild chimpanzees are needed in order to determine the consistency of these results across different populations and the sources of variation therein. Although some of the results were unexpected based on chimpanzee socio-ecology, they fit well overall with the history and social dynamics of the study group. The methods used in this study confer significant advantages in producing quantitative composite measures of each component of relationship quality. The findings of this study therefore promote the use of such measures in future studies on a variety of species requiring an assessment of the qualities of dyadic social relationships.

CHAPTER 5

Function and Determinants of Reconciliation

5.1. Introduction

Reconciliation, i.e. post-conflict affiliation between former opponents, plays a pivotal role in reducing the costs of aggressive conflict and maintaining group cohesion (de Waal & van Roosmalen, 1979; de Waal, 1986). Aggressive conflict can disrupt the relationship between opponents, leading to a loss of benefits afforded by the relationship, such as tolerance around resources or agonistic support (Kappeler & van Schaik, 1992; Aureli et al., 2002). Reconciliation may mitigate negative consequences of aggressive conflict by repairing the relationship between former opponents (Cords, 1992; Koyama, 2001; Wittig & Boesch, 2005), and reducing the likelihood of renewed aggression (Aureli & van Schaik, 1991; Watts, 1995b; Silk et al., 1996).

Approaching a former opponent soon after the end of an aggressive conflict also carries risks of renewed attack, however, and so attempting reconciliation may be costly (Aureli et al., 2002). Furthermore, the benefits of reconciliation may vary depending on how much opponents stand to lose as a result of damage to their relationship. Reconciliation, therefore, should only occur if the benefits outweigh the costs. The valuable relationship hypothesis (de Waal & Aureli, 1997; reviewed in Watts, 2006) predicts that reconciliation should be more likely to occur between partners with highly valuable relationships than between those with less valuable relationships, as the benefits of relationship repair would be higher for the former than the latter. As kin are likely to have more valuable relationships than non-kin, support has been found for this hypothesis in a number of species in which kin reconcile more than non-kin (de Waal & Ren, 1988; Watts, 1995b; Castles et al., 1996; Silk et al., 1996; Aureli et al., 1997; Leca et al., 2002; see Watts, 2006; and Arnold & Aureli, 2007 for reviews). Similarly, assumptions can be made about the likely value of partners within certain age or sex combinations, such as between male peers who may be more likely to form alliances in some species or between female partners who may share a longer history of familiarity in others. Reconciliation was more likely between partners in the age-sex combination that was expected to be more valuable (Schino et al., 1998; Arnold & Barton, 2001a; Palagi et al., 2004; Koski et al., 2007b). In other studies, high frequencies of certain types of interactions deemed to provide benefits to partners, such as agonistic support, food-sharing, grooming or even just time spent in proximity, have been used as proxy of relationship value when studying sources of variation within reconciliation rates (Wittig & Boesch, 2005; Cooper et al., 2005; Majolo et al., 2005).

The value, however, may not be the only aspect of the opponents' relationship to affect the occurrence of reconciliation. Cords & Aureli (2000) suggested that the quality of a relationship between two individuals comprised three independent components. In addition to relationship value, characterised by its associated benefits, there is the compatibility of the partners, which is based on the general tenor of social interactions between partners. Another component is security, which relates to the predictability of the relationship or the consistency of interactions over time. While valuable partners may be more likely to reconcile because of the high benefits in repairing their relationship, compatible partners may be more likely to reconcile because the risks of renewed aggression, and thus the costs of reconciliation, may be lower (Cords & Aureli, 2000). In support of this prediction, highly affiliative partners across a variety of species have been shown to reconcile more than those with less affiliative relationships (e.g. de Waal & Yoshihara, 1983; Aureli et al., 1989; Castles et al., 1996; Call et al., 1999; Arnold & Whiten, 2001; Preuschoft et al., 2002; Koski et al., 2007b). For partners with very secure relationships, however, reconciliation may not be necessary as their relationship may not be damaged by the previous conflict. This may be the case for immature long-tailed macaques (*Macaca fascicularis*), who were more likely to reconcile with non-kin than with kin, with whom they presumably had more secure relationships (Cords, 1988; Cords & Aureli, 1993). The highly secure nature of relationships in small family groups of tamarin (*Saguinus labiatus*) may explain why their relationships are not disrupted by aggression and thus why reconciliation has not been demonstrated in this species (Schaffner et al., 2005). Furthermore, juvenile brown capuchins (*Cebus apella*) who had secure relationships with their mothers were less likely to reconcile with other adults, and were less aroused following such conflicts, compared with juveniles who had insecure relationships with their mothers and whose conflicts with other adults resulted in higher arousal and a higher likelihood of reconciliation (Weaver & de Waal, 2003).

Chimpanzees provide an ideal model for studying the effects of relationship quality components on the occurrence of reconciliation as they boast one of the highest conciliatory tendencies of all primates (Arnold & Aureli, 2007; Chapter 3). Furthermore there their relationships are characterised by high intra-group variation in quality (de Waal, 1982; Goodall, 1986). While a number of studies, both in the wild and captivity, have investigated possible determinants of reconciliation in chimpanzees (de Waal & van Roosmalen, 1979; de Waal, 1986; Arnold & Whiten, 2001; Fuentes et al., 2002; Preuschoft et al., 2002; Wittig & Boesch, 2003a; Kutsukake & Castles, 2004; Koski et al., 2007a), no study has yet investigated the effects of all three components of relationship quality on the occurrence of reconciliation.

In addition to its function in relationship repair, reconciliation is also likely to reduce post-conflict stress levels, especially in the victim, or main recipient of aggression (Aureli & Smucny, 2000; Aureli & Schino, 2004). The post-conflict increase in stress levels may be due to the risks of renewed aggression and/or disruption of the opponents' relationship, leading to thus uncertainty of the social environment (Aureli & van Schaik, 1991; Aureli & Smucny, 2000). Levels of self-directed behaviour, such as self-scratching or self-grooming, have been shown to be correlated with stress levels in primates (Maestripieri et al., 1992; Troisi, 2002), a link further supported by pharmacological evidence (Schino et al., 1996). Levels of self-directed behaviours in a number of species have been shown to remain elevated above baseline when reconciliation does not occur, but to reduce to baseline levels following reconciliation, suggesting a stress-reduction function (Aureli & van Schaik, 1991; Castles & Whiten, 1998; Kutsukake & Castles, 2001; Cooper et al., 2007). This function, however, has never been demonstrated in apes, despite being investigated in both wild and captive chimpanzees (Arnold & Whiten, 2001; Koski et al., 2007b).

This study aimed therefore to test the stress-reduction function of reconciliation in a large zoo group of chimpanzees. Furthermore, conflict and post-conflict characteristics, such as the initiation of conflict with a bluff display, intensity and directionality of aggression, the outcome of the conflict and the occurrence of consolation, were investigated as determinants of reconciliation, in addition to the value, compatibility and security of the relationship and kinship and sex-combination.

5.2. Methods

5.2.1. Data collection

All occurrences of food-sharing and aggressive interactions were recorded. Post-conflict behaviour of the recipient of aggression or the aggressor was recorded using the post-conflict (PC) - matched control (MC) method (de Waal & Yoshihara 1983; see Chapter 2 for details).

5.2.2. Data Analysis

A total of 256 PC-MC pairs were collected, of which 22 were on aggressors and 234 were on the initial recipient of aggression. PC-MC pairs were collected for all 22 adult subjects (mean ±SD PC-MC pairs per subject = 11.6 ± 5.96, range=3-26). PC-MC pairs were collected for 149 aggressor-recipient dyads.

5.2.2.1. Function of Reconciliation

As the majority of post-conflict affiliative interactions occurred in the first minute of the PC (Chapter 3), PCs with reconciliation were operationally defined as those in which an affiliative interaction between the former opponents occurred in the first minute of the PC. PCs in which consolation (i.e., an affiliative interaction directed from a third party towards the recipient of aggression) occurred in the first minute were excluded from the analyses. PCs without reconciliation were those in which neither reconciliation nor consolation occurred in the whole ten minutes of the PC. PCs on aggressors were not considered for these analyses.

Post-conflict stress levels were assessed using self-directed behaviours (Maestripieri et al., 1992; Troisi, 2002). In particular, we used rates of self-scratching and the duration of self-grooming, both previously successfully used in post-conflict studies (Aureli & van Schaik, 1991). In order to determine whether aggressive conflict lead to increased post-conflict stress levels, individual mean rates of self-scratching and mean durations of self-grooming for each minute of PCs without reconciliation were compared to individual mean levels (and 95% confidence intervals) across the whole 10-minute MC. This allowed us to define a time window in which the PC values differed from the control values (cf. Aureli & van Schaik, 1991).

Given the operational definition of reconciliation (i.e., occurrence in the first PC minute), mean rates of self-scratching and mean time spent self-grooming during the time window in which PC values differed from MCs, but excluding the first minute, were used to determine the effects of reconciliation on self-directed behaviour. Such values for PCs with reconciliation and PCs without reconciliation were compared with each other and with mean MC levels for the whole 10 minutes. Linear mixed models (LMMs) were used for these comparisons. Levels of self-scratching or self-grooming were entered as continuous dependent variables and the identities of the focal individual and opponent were entered as random variables. In addition we included the random variable 'PC-MC pair' for which each PC and its corresponding MC were given a unique number. The occurrence of reconciliation (i.e. PC with reconciliation or PC without reconciliation) or type of observation (i.e. PC or MC) was entered as a fixed explanatory variable.

5.2.2.2. Determinants of Reconciliation

As the operational definition of reconciliation used for demonstrating its function would be too conservative leading to an excessive reduction in sample size for these analyses, a different definition was used. Following de Waal & Yoshihara's (1983) procedure, PC-MC pairs were labelled attracted if affiliative interaction occurred earlier in the PC than in the MC, or only in the PC. Neutral pairs had no affiliative interaction in either the PC or the MC, or at the same time in both. Pairs in which affiliative interaction occurred earlier, or only in MC, were labelled dispersed. For reconciliation, the first affiliative interaction was between the former opponents, and was directed from a third party to the initial recipient of aggression for consolation. PC-MC pairs in which it was unclear who had initiated the contact between consoler and recipient were not considered in order to ensure that consolation had not been solicited by the recipient of aggression (see Chapter 6). For these analyses, reconciliation was considered to have taken place when the PC-MC pair was attracted. A similar operational definition for consolation was used. Neutral or dispersed pairs indicated an absence of reconciliation or consolation.

Factors affecting the occurrence of reconciliation were investigated at the PC level using generalised linear mixed models (GLMMs) fitted with a binomial dependent variable, the presence or absence of reconciliation. Initially the analysis was run using factors traditionally used to determine those affecting the occurrence of reconciliation, entered as fixed variables (see Table 5.1 for descriptions). Characteristics of the relationship between the recipient and the aggressor were kinship, sex combination and benefit. Benefit was a measure of relationship value based on the occurrence of food-sharing and agonistic support that was previously used with success in a study of the determinants of reconciliation in wild chimpanzees (Wittig & Boesch, 2005). In addition we included conflict characteristics (directionality, outcome, intensity) as fixed variables and the identities of the focal individual and the opponent as random variables. We refer to this analysis as the 'traditional' analysis.

Next, we reran the analysis, this time targeting factors more specific to chimpanzee behaviour, namely initiation of aggression with a bluff display and consolation, to investigate their impact on the occurrence of reconciliation (see Table 5.1 for descriptions of variables). These factors form a substantial part of chimpanzee conflict and post-conflict behaviour and yet are not present in many other primate species. In the study group 19% of conflicts were initiated with a bluff display and consolation (as defined above) occurred in 45% of PCs. In this analysis, we also replaced the relationship characteristic variables used in the traditional analysis (kinship, sex combination and benefit) with measures of each of the components of relationship quality (value, compatibility and security) obtained using principle components analysis (Chapter 4). All the other variables remained the same. We refer to this analysis as the 'targeted' analysis. To assess the relative importance of the significant variables in the traditional and targeted analyses, variables from the traditional analysis that had a significant effect on the occurrence of reconciliation were added to the best model from targeted analysis to see whether their effect remained significant.

Table 5.1. Variables used in GLMM for the determinants of reconciliation.

Name	**Traditional Analysis**	**Targeted analysis**	**Type**
Response variable			
Reconciliation	X	X	Binomial (yes, no)
Fixed explanatory variables (relationship characteristics)			
Benefit	X		Ordinal (1= no food-sharing or agonistic support, 2= either food-sharing or support, 3= both)
Value		X	Continuous
Compatibility		X	Continuous
Security		X	Continuous
Sex combination	X		Binomial (1=including males, 0=no males)
Kinship	X		Binomial (yes, no)
Fixed explanatory variables (conflict characteristics)			
Outcome	X	X	Binomial (1=decided, 0=undecided)
Intensity	X	X	Ordinal (1=low, 2=medium, 3=high)
Directionality	X	X	Binomial (1=bi-directional, 0=unidirectional)

Bluff		X	Binomial (1=starts with bluff display, 0= no bluff display)
Post-conflict variables			
Consolation		X	Binomial (yes, no)
Random variables			
Recipient	X	X	Nominal
Aggressor	X	X	Nominal

See Chapter 2 for behavioural definitions

5.3. Results

5.3.1. Function of Reconciliation

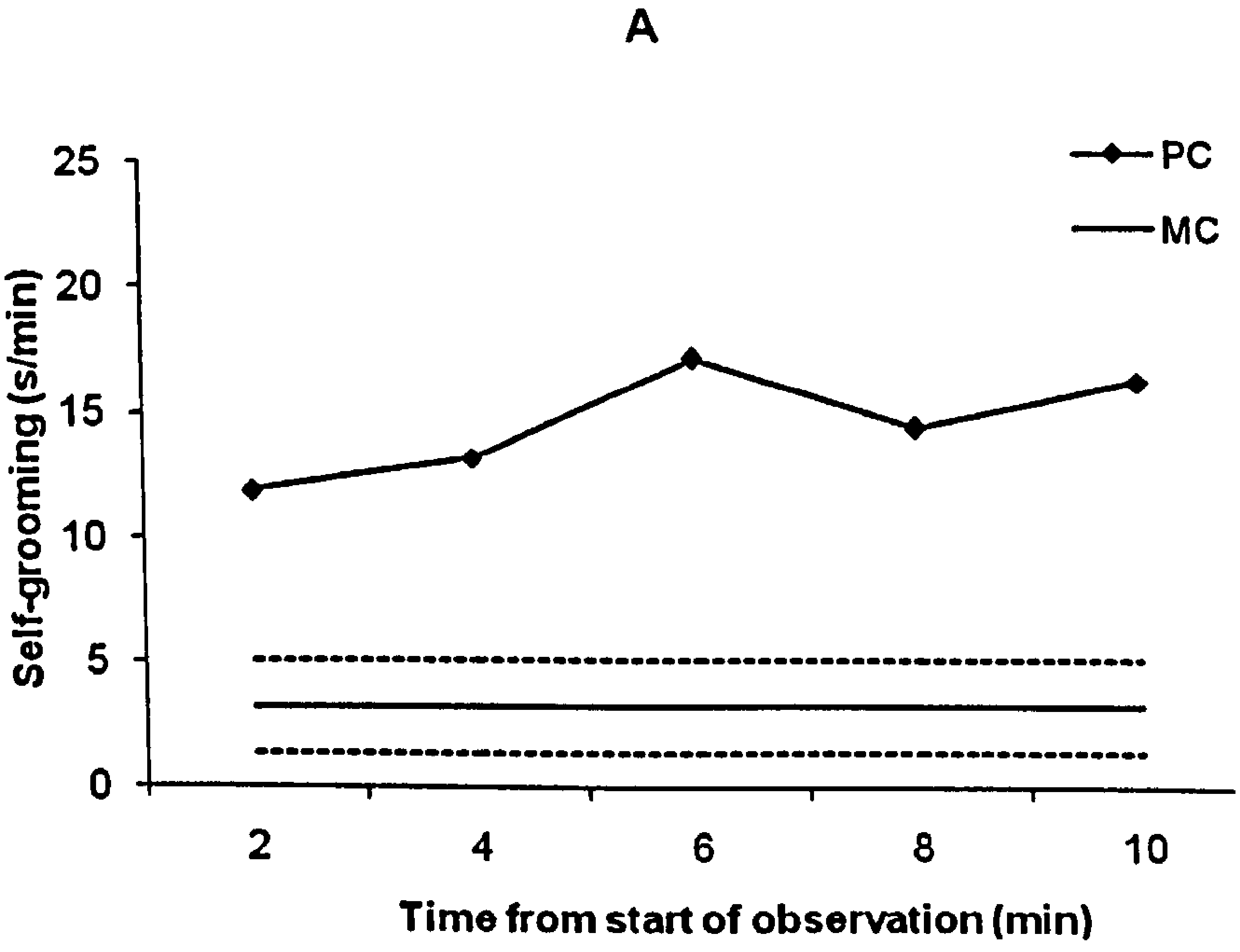
Levels of self-grooming and self-scratching were elevated above baseline for the entire 10 minutes of PCs without reconciliation or consolation (Fig. 5.1), suggesting that aggressive conflict raised stress levels and that they remained raised for the full PC if no reconciliation or consolation occurred. These results were confirmed when analyses were conducted while controlling for individual variation using linear mixed models (LMMs). As consolation and reconciliation occurred mostly in the first minute of the PCs (Chapter 3) the following analyses focused on minutes 2-10 (see Methods). The mean levels of self-grooming and self-scratching for PCs without reconciliation or consolation for minutes 2-10 were higher than the mean levels of MCs (self-grooming: β=11.37 s per min, 95%C.I.:5.79, 17.20, P=<0.001; self-scratching: β=0.11 bouts per min, 95%C.I.:0.02, 0.19, P=<0.014, Fig. 5.2; Table 5.2).

Table 5.2. Variables in the best LMMs showing the effects of observation type (PC with no consolation or reconciliation, or MC) on levels of self-scratching and self-grooming.

Self-scratching	Fixed Effects	β	95% C.I.	S.E.	t	P
	Intercept	0.126	0.06, 0.19	0.030	4.158	<0.001
	Observation type	0.107	0.02, 0.19	0.043	2.505	0.014
	Random Effects	Variance				
	PC-MC Pair	<0.001				
	Error	<0.001				
Self-grooming	Fixed Effects	β	95% C.I.	S.E.	t	P
	Intercept	3.795	-0.30, 7.80	2.037	1.863	0.066
	Observation type	11.370	5.79, 17.20	2.789	4.076	<0.001
	Random Effects	Variance				
	PC-MC pair	11.230				
	Error	167.292				

For binomial variables such as observation type (PC=1, MC=0), β represents the difference between the two levels, i.e. PC – MC.

Fig. 5.1 Mean self-grooming (A) and self-scratching (B) levels during post-conflict periods without reconciliation or consolation. For PC data, means for every second minute are used. Means for the whole 10 minutes are used for MC data, with 95% confidence intervals.



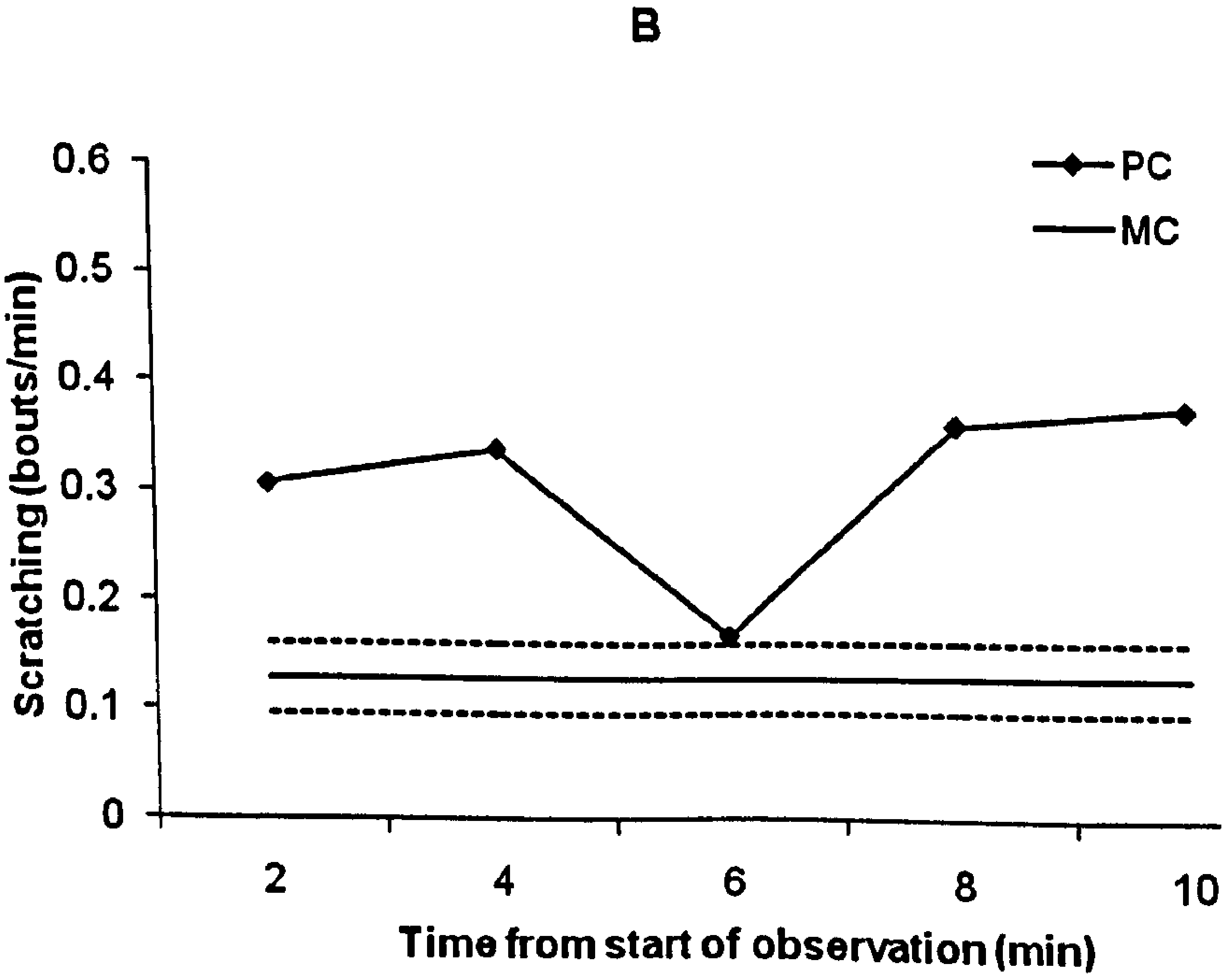


Fig. 5.2 Mean (+S.E.) time spent self-grooming (A) and mean (+S.E.) rate of self-scratching (B) during minutes 2-10 of PCs without consolation or reconciliation and PCs with reconciliation, and during MCs. *P<0.05

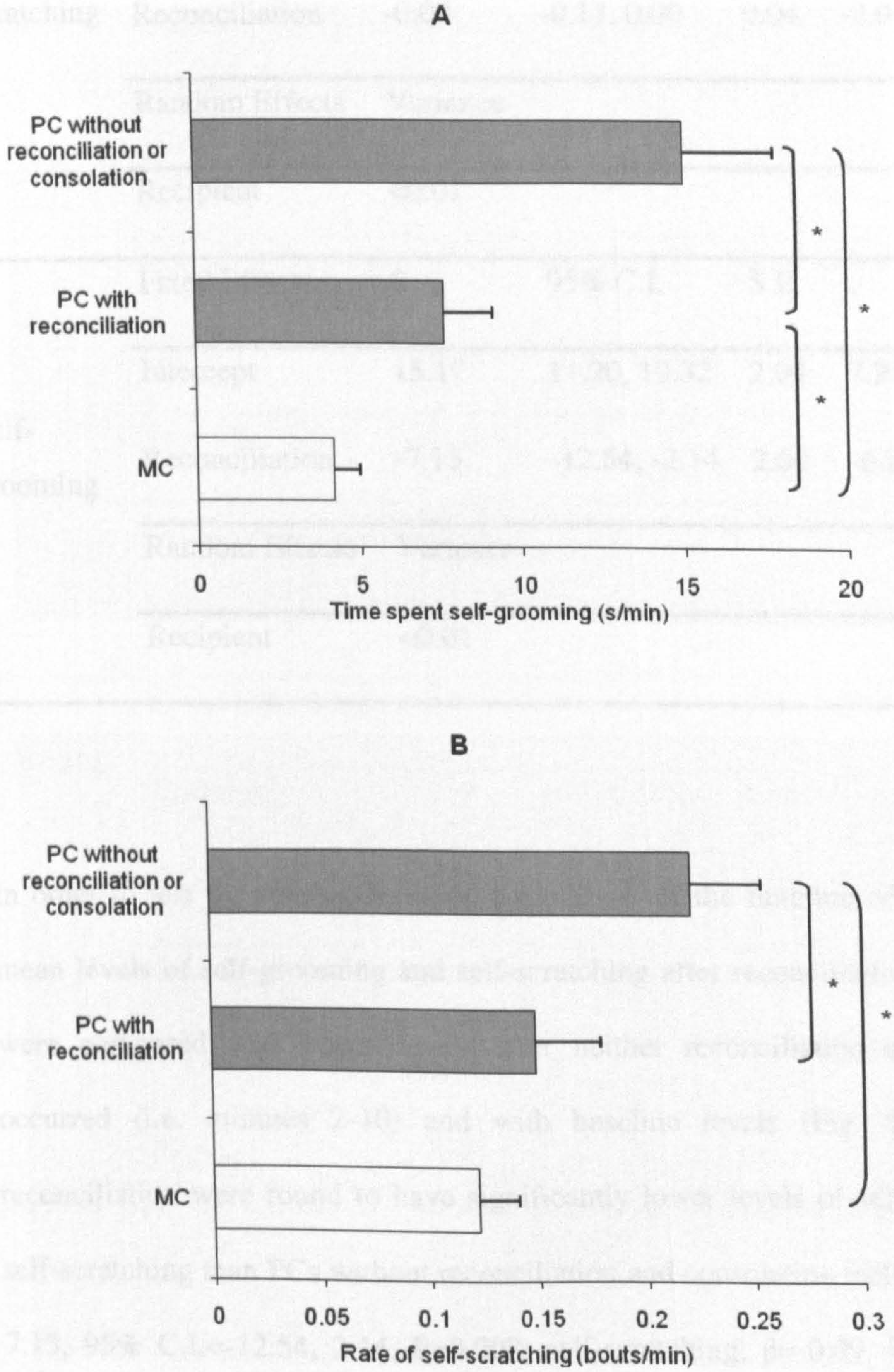


Table 5.3. Variables in the best LMM showing the effect of reconciliation on self-scratching and self-grooming levels in PCs with and without reconciliation.

	Fixed Effects	β	95% C.I.	S.E.	t	P
Scratching	Intercept	0.23	0.17, 0.30	0.03	7.11	<0.001
	Reconciliation	-0.09	-0.17, 0.00	0.04	-2.04	0.043
	Random Effects	Variance				
	Recipient	<0.01				
	Fixed Effects	β	95% C.I.	S.E.	t	P
Self-grooming	Intercept	15.17	11.20, 19.32	2.09	7.25	<0.001
	Reconciliation	-7.13	-12.54, -2.14	2.66	-6.29	0.008
	Random Effects	Variance				
	Recipient	<0.01				

In order to test the stress-alleviation hypothesis for the function of reconciliation, mean levels of self-grooming and self-scratching after reconciliation had occurred were compared with mean levels after neither reconciliation nor consolation occurred (i.e. minutes 2-10) and with baseline levels (Fig. 5.2). PCs after reconciliation were found to have significantly lower levels of self-grooming and self-scratching than PCs without reconciliation and consolation (self-grooming: β=-7.13, 95% C.I.=-12.54, 2.14, P=0.008; self-scratching: β=-0.09, 95% C.I.=-0.17, 0.00, P=0.043, Table 5.3), indicating that reconciliation reduces levels of self-directed behaviour. No significant difference was found between levels of scratching after reconciliation and during MCs (β=-0.01, 95% C.I. =-0.07, 0.5, P=0.787). Levels of self-grooming, however, were still higher after reconciliation than during MCs (β=3.93, 95% C.I. =0.57, 7.39, P=0.021, Table 5.4).

Table 5.4. Variables in the best LMM showing the effects of observation type (PC with reconciliation or MC) on levels of self-scratching and self-grooming.

Scratching	Fixed Effects	β	95% C.I.	S.E.	t	P
	Intercept	0.15	0.10, 0.20	0.03	5.84	<0.001
	PC/MC	-0.01	-0.08, 0.06	0.03	-0.24	0.809
	Random Effects	Variance				
	PC-MC pair	0.01				
	Error	0.03				
Self-grooming	Fixed Effects	β	95% C.I.	S.E.	t	P
	Intercept	2.379	0.03, 4.81	1.25	1.90	0.060
	PC/MC	5.213	1.73, 8.44	1.67	3.12	0.002
	Random Effects	Variance				
	Recipient	2.37				
	Error	74.20				

5.3.2. Determinants of Reconciliation

The traditional analysis revealed that partners with a more beneficial relationship were more likely to reconcile than those with a less beneficial relationship (β=0.446, Odds ratio=1.56, 95% C.I.= 1.01, 2.41, P=0.040). Female-female dyads were found to be more likely to reconcile than dyads including males (β=-0.64, Odds ratio=0.53, 95% C.I. = 0.30, 0.93, P=0.025). None of the other variables were included in the best model (Table 5.5).

Table 5.5. Variables in the best GLMM explaining the occurrence of reconciliation in the traditional analysis.

Fixed Effects	β	S.E.	z	P	Odds Ratio	95% CI
Intercept	-0.282	0.398	-0.708	0.479		
Sex combination	-0.635	0.284	-2.234	0.025	0.530	0.30, 0.93
Benefit	0.446	0.217	2.055	0.040	1.560	1.01, 2.41
Random Effects	**Variance**					
Recipient	0.247					

In the targeted analysis, the only significant predictors of reconciliation were consolation and initiation of aggression with bluff display. Conflicts were less likely to be reconciled if consolation occurred (β=0.80, Odds ratio=0.45, 95% C.I.

= 0.24, 0.85, P=0.012), or if the aggressive interaction started with a bluff display (β=-0.91, Odds ratio=0.40, 95% C.I. = 0.18, 0.88, P=0.021) (Table 5.6). When the targeted analysis was repeated including the significant variables from the traditional analysis, those variables (sex combination and benefit) no longer had a significant effect on reconciliation and were not included in the best model.

Table 5.6. Variables in the best GLMM explaining the occurrence of reconciliation in the targeted analysis.

Fixed Effects	β	S.E.	z	P	Odds Ratio	95% CI
Intercept	0.505	0.235	2.150	0.032		
Consolation	-0.804	0.320	-2.512	0.012	0.45	0.85, 0.24
Bluff	-0.907	0.392	-2.316	0.021	0.40	0.88, 0.18

Random Effects	Variance
Recipient	<0.001

5.4. Discussion

This study provides support for the stress reduction function of reconciliation in chimpanzees. Additionally, the findings suggest that relationship quality variables may not be the most important determinants of reconciliation in the study group, and that behaviours more specific to chimpanzees, i.e., the occurrence of consolation and initiation of aggression with a bluff display, may play a more decisive role.

Levels of self-directed behaviour in recipients of aggression were higher following a conflict without reconciliation and consolation than during control periods, confirming the stressful effect of aggressive conflict. Following reconciliation, however, levels of self-directed behaviour were significantly lower than cases in which reconciliation did not occur, suggesting that reconciliation reduces post-conflict stress levels in chimpanzee recipients of aggression. Although this function has been demonstrated in monkeys (Aureli & van Schaik, 1991; Aureli, 1997; Castles & Whiten, 1998; Kutsukake & Castles, 2001; Cooper et al., 2007), it has not been previously shown in any ape species. Arnold & Whiten (2001) were the first to investigate the link between post-conflict stress and reconciliation in chimpanzees. Although they found a reduction in scratching rates after reconciled conflicts compared to non-reconciled conflicts, scratching rates in post-conflict periods without reconciliation were actually lower than during control periods, so no conclusions could be made about the effect of reconciliation on post-conflict stress. Koski et al. (2007b) did find that post-conflict levels of scratching were elevated above baseline levels when reconciliation did not occur, mirroring the findings of my study. However, they did not find any difference in scratching rates before and after reconciliation or between reconciled and non-reconciled conflicts, and so could not demonstrate a stress-reduction function of reconciliation. This was in obvious contrast with studies on monkeys, where such a function was demonstrated any time it was investigated, provided that levels of self-directed behaviour were elevated following aggression.

Its effectiveness in reducing post-conflict stress is likely due to reconciliation removing the probable causes of stress, namely the risks of renewed aggression and the potential loss of benefits afforded by the relationship with the opponent. The stress-reduction function of reconciliation is thus complementary to the aggression reduction and relationship repair functions previously shown in chimpanzees (Wittig & Boesch, 2005). Moreover, the post-conflict emotional response may mediate the occurrence of reconciliation by motivating the opponents to exchange affiliative behaviour and repair their relationship (Aureli, 1997; Aureli & Smucny, 2000; Aureli & Schino, 2004) . Thus, valuable partners, for whom relationship disruption is most costly, may experience higher levels of post-conflict stress, which in turn functions as a proximate factor in facilitating reconciliation, resulting in the reported high conciliatory tendencies between those partners (the integrated hypothesis: Aureli, 1997). This hypothesis is supported by evidence in long-tailed macaques (Aureli, 1997), Japanese macaques (*Macaca fuscata*) (Kutsukake & Castles, 2001). Indirect evidence was found in bonnet macaques (*Macaca radiata*) (Cooper et al., 2007) and chimpanzees (Koski et al., 2007b). For example, rates of scratching after conflicts between adult males in chimpanzee were higher than after conflicts between adult females, and male-male conflicts were more likely to be reconciled than female-female conflicts (Koski et al., 2007b). In providing support for a stress reduction function of reconciliation, the study supports the complementarity of the stress-reduction, renewed aggression avoidance and relationship repair functions of reconciliation shown in other species (de Waal, 2000b; Aureli et al., 2002; Arnold & Aureli, 2007).

Examining the determinants of reconciliation using variables considered in many previous studies (the traditional analysis), I found that the sex-combination of the opponent dyad was one of two strongest predictors of reconciliation. Confirming the finding that female-female dyads had the highest conciliatory tendencies (Chapter 3), the results of the LMM revealed that female-female partners were most likely to reconcile. The multivariate approach used in this study had the advantage of controlling for the effects of other variables and enabled the analysis to be conducted at the dyadic level, thus avoiding problems of ecological fallacy associated with pooling data (Watts, 2006). Measures such as conciliatory tendencies (used in Chapter 3), however, control for potential differences in baseline levels of affiliation across dyads. Thus, the two analyses complement each other effectively, and the consistency of their results strengthens the conclusions.

Although many other studies have investigated the effect of sex combination on reconciliation in chimpanzees (de Waal, 1986; Arnold & Whiten, 2001; Fuentes et al., 2002; Preuschoft et al., 2002; Wittig & Boesch, 2003b; Kutsukake & Castles, 2004; Koski et al., 2007a, see Chapter 3 for a full discussion), only two of those used multivariate analyses to examine the differential effects of potential predictors of reconciliation. Both studies, like mine, found partner sex combinations to have a significant effect (Koski et al., 2007a; Wittig & Boesch, 2003a). Interestingly, however, one study found that male-male dyads were more likely to reconcile (Koski et al., 2007a), whereas the other found reconciliation to be most likely within mixed-sex dyads (Wittig & Boesch, 2003a). Both contrast with my finding that female-female dyads were most likely to reconcile. Thus, partner sex combination may not be a reliable predictor of reconciliation across groups of chimpanzees. Other aspects of the relationship between the opponents, which are reflected in different sex combinations in different studies, may be the critical factors affecting the occurrence of reconciliation (see Chapter 3).

The traditional analysis also revealed that the study chimpanzees were more likely to reconcile with partners with whom they had a valuable relationship. In concurrence with Wittig & Boesch (2003a), dyads with high relationship benefit were more likely to reconcile than those with a low relationship benefit, providing further support for the valuable relationship hypothesis in chimpanzees (Watts, 2006). The measure of relationship benefit used in these analyses, however, was fairly crude. Although it combined data from two presumably beneficial interactions, agonistic support and food-sharing, the measure did not take into account the frequency of either of these behaviours. It simply reflected for each dyad the absence of both interactions, the occurrence of only one of the interactions or both over the entire observation period. A single occurrence of both interactions between two partners was thus sufficient to merit a high benefit classification of their relationship. Therefore, this measure may not give an accurate representation of the value of all relationships, and results should be treated with caution. Combining two separate variables such as food-sharing and agonistic support whilst retaining information about the relative frequency of their occurrence can be difficult. One option is to enter food-sharing and agonistic support into a principle components analysis along with other relationship variables to identify relevant composite factors (see Chapter 4). A composite factor based on valuable interactions, such as food-sharing and agonistic support, could therefore provide a conceptually more coherent measure of relationship value, which could be used to determine the effect of relationship value on the occurrence of reconciliation (see below).

There has been considerable variation in rates of reconciliation and in the factors shown to affect the occurrence of reconciliation across chimpanzee studies (reviewed in Colmenares, 2006; Watts, 2006; Arnold & Aureli, 2007). Furthermore, there has been little consistency in the variables tested across studies, and little justification for the variables used. Relationship value has, for example, been assessed using proximity (Kutsukake & Castles, 2004), agonistic support (Preuschoft et al., 2002; Watts, 2006), grooming (Watts, 2006), a combination of food-sharing and agonistic support (Wittig & Boesch, 2005) and partner sex combination (Koski et al., 2007b; Arnold & Whiten, 2001; de Waal, 1986). It is unsurprising, therefore, that the results from these studies differ as much as the methods employed. Moreover, in the handful of studies on reconciliation in chimpanzees, there is considerable variation in group composition and settings (Colmenares, 2006). Whereas it can be useful for purposes of comparison to run analyses on determinants of reconciliation using variables applicable to most primate and non-primate species, such as those used in the 'traditional analysis', in order to fully understand the factors affecting reconciliation, behaviours specific to the group under study should also be included. Thus, the 'targeted analysis' included measures of relationship quality specific to the study group, obtained in a non-subjective manner (Chapter 4), and also included two variables characteristic of chimpanzee behaviour that had not previously been considered, the initiation of aggression with a bluff display and the occurrence of consolation.

Despite suggestions from the results of the traditional analysis that relationship value and sex combination predicted the occurrence of reconciliation, no characteristics of the relationship between opponents proved to have a significant effect in the targeted analysis. Reconciliation was, however, less likely to occur if the conflict was initiated with a bluff display. Bluff displays often involve hitting individuals in passing, in a similar manner to which the display performer might hit nearby objects while charging (Goodall, 1986). Aggression starting with a bluff display, therefore, does not appear to be aimed towards a particular individual, but rather towards anyone who happens to be nearby. Thus, aggression may not be perceived as a 'personal' attack and may not damage the relationship between the opponents. If this is correct, reconciliation may not be necessary after a conflict initiated with a bluff display.

Although this study has shown the benefits of reconciliation in terms of stress alleviation, many conflicts are never reconciled. Non-reconciled conflicts may lead to prolonged elevated stress levels in recipients of aggression (Aureli & van Schaik, 1991; Castles & Whiten, 1998; Kutsukake & Castles, 2001; Cooper et al., 2007), which may have detrimental consequences for their health and well-being (Sapolsky, 2004). For apes, one option for the alleviation of stress levels after non-reconciled conflicts is consolation (Chapter 6). The targeted analysis revealed that reconciliation was less likely to occur when consolation took place. These findings together support the hypothesis that consolation acts as an alternative to reconciliation, alleviating stress levels in the recipient of aggression when reconciliation fails to occur (Wittig & Boesch, 2003a; Palagi et al., 2006a; see Chapter 6). While an argument could be made that reconciliation does not occur after consolation because stress alleviation has already taken place, this would seem an unlikely scenario as reconciliation offers additional benefits in terms of relationship repair.

This study has highlighted a number of methodological improvements for the study of post-conflict behaviour. Using LMMs to investigate the effect of reconciliation on self-directed behaviours allowed the possible differential contribution of individuals to the data set to be controlled for. In addition, LMMs are better equipped to deal with missing values than traditional analyses, thus enabling a larger data set to be used, resulting in a more powerful analysis. The mixed model approach to investigating the effects of relationship and conflict characteristics on the occurrence of reconciliation allowed the effects of each independent variable to be examined separately, while controlling for the effects of other variables including differential contribution of individuals to the data set. Furthermore, we used composite measures of relationship quality, specific to the study group, based on a number of different behaviours obtained in a non-subjective manner (Chapter 4). The three emerging components allowed a comprehensive evaluation of the influence of relationship quality on the occurrence of reconciliation. Although none of the relationship quality variables were significant predictors of reconciliation in the target analysis, their importance in determining the occurrence of reconciliation may have been masked by the stronger effects of consolation and the initiation of aggression with a bluff display. The difference in results obtained using the traditional and targeted analyses highlights the importance of choosing variables carefully and considering variables relevant to the species and the population studied. Further studies on other chimpanzee populations using similar variables are required in order to understand the nature of the variation in patterns of reconciliation in different groups of chimpanzees.

CHAPTER 6

Function and Determinants of Consolation

6.1. Introduction

Conflicts of interest may arise frequently in group-living species over access to resources, positions in the dominance hierarchy, or decisions about courses of action. The escalation of a conflict of interest into an aggressive conflict can be very costly, including risk of injury, increased stress levels and damage to the relationship between opponents, thus undermining any benefits afforded by that relationship (de Waal, 2000b). We should, therefore, expect forms of conflict management to mitigate the negative consequences of aggressive escalation. Reconciliation, i.e., a post-conflict affiliative reunion between former opponents (de Waal & van Roosmalen, 1979), has been demonstrated in many primate species and some non-primate species (de Waal, 2000b; Schino, 2000; Silk, 2002a; Judge, 2003; Arnold & Aureli, 2007). A body of evidence exists showing that reconciliation repairs the relationship between former opponents disturbed by the previous conflict and reduces post-conflict stress levels (Aureli & van Schaik, 1991; Cords, 1992; de Waal, 2000b; Koyama, 2001; Aureli et al., 2002). A separate category of post-conflict interactions is affiliation directed from a third party towards the recipient of aggression, known as consolation (de Waal & van Roosmalen, 1979), which has recently begun to receive attention as it may relate to empathic and cognitive differences between Hominoids and monkeys (de Waal & Aureli, 1996; Castles, 2000).

Consolation has been demonstrated convincingly only in the great apes (*Pan troglodytes*: de Waal & van Roosmalen, 1979; de Waal & Aureli, 1996; Wittig & Boesch, 2003a; Kutsukake & Castles, 2004; Palagi et al., 2006a; Koski & Sterck, 2007; *Pan paniscus*: Palagi et al., 2004; *Gorilla gorilla*: Cordoni et al., 2006; Mallavarapu et al., 2006). De Waal & Aureli (1996) have speculated that consolation may reflect a level of empathy unique to humans and apes. Following Preston & de Waal's (2002) discussion of the mechanisms and levels of empathy, consolation may represent an intermediate level that corresponds with 'sympathetic concern' in developmental psychology (de Waal, 2008). Monkeys seem to lack this particular level (Watts et al., 2000; Schino et al., 2004) but intriguingly there is suggestive evidence for it in large-brained birds (Seed et al., 2007).

The present study, however, is not about the mechanisms of consolation, but about its effect and possible function, which as its name suggests is post-conflict stress alleviation in recent recipients of aggression (de Waal & van Roosmalen, 1979; Aureli, 1997; de Waal & Aureli, 1997). Only one study has thus far tested this hypothesis but was unable to provide support for a stress-alleviating effect (Koski & Sterck, 2007). If a stress-alleviating effect of consolation were found, it would suggest that chimpanzees may be capable of detecting distress experienced by conspecifics and thus would provide indirect support for the capacity for sympathetic concern, or an intermediate level of empathy, in chimpanzees.

Although reconciliation is beneficial in reducing post-conflict stress and repairing inter-opponent relationships, to approach a former opponent soon after a conflict carries the risk of renewed aggression (Aureli et al., 2002; Arnold & Aureli, 2007). In addition, in some cases one party may not be interested in reconciliation because the relationship might not be worth repairing (Cords & Aureli, 2000; Aureli et al., 2002). A further hypothesis, therefore, advocates that consolation may serve as a substitute for reconciliation when the latter fails to occur, presuming that consolation alleviates post-conflict stress (Watts et al., 2000; Wittig & Boesch, 2003a; Palagi et al., 2006a). The substitute for reconciliation hypothesis has received some indirect support, as consolation was more likely to occur in the absence of reconciliation in some studies (Wittig & Boesch, 2003a; Palagi et al., 2004; Palagi et al., 2006a), but not in others (Koski & Sterck, 2007). Thus, overall there is no empirical evidence that consolation serves to reduce stress, or that it serves this function especially in the absence of reconciliation. Because of this, some researchers prefer the more neutral label 'triadic post-conflict affiliation' (Koski & Sterck, 2007; Kutsukake & Castles, 2004). Here, as we specifically aimed to test the hypothesis that triadic post-conflict affiliation has a calming function, and as we only investigated affiliative interactions directed towards the initial recipient of aggression, we employed the term 'consolation'.

The quality of the relationship between former opponents, in addition to the characteristics of the preceding conflict, may affect the occurrence of consolation (Watts et al., 2000). Cords & Aureli (2000) suggested that the quality of a relationship between two individuals is comprised of three separate components: value, compatibility, and security. The value of the relationship refers to the advantages (or fitness benefits) afforded by the relationship. Compatibility is a measure of the tolerance and affiliation between the two partners. The security of the relationship indicates its predictability or consistency over time. The influence of relationship quality, and in particular relationship value, on the occurrence of reconciliation has long been investigated, although measures of relationship quality and interpretation of its effects have varied (de Waal, 2000b; Aureli et al., 2002; Judge, 2003; Watts, 2006; Arnold & Aureli, 2007). The effect of relationship quality on consolation, however, has received much less attention. Only two studies, both on chimpanzees, have examined the determinants of consolation, both investigating two of the relationship quality components, value and compatibility, in addition to conflict characteristics, but found conflicting results. Koski et al. (2007a) found no significant predictors of consolation, whereas Wittig & Boesch (2003a) found that chimpanzees were more likely to receive consolation after conflicts between same-sex partners, after conflicts between partners providing only limited benefits to each other and after conflicts where relatively few competitors were present. While both studies incorporated some aspect of relationship quality into their analyses both focused on the relationship between the former opponents, not the relationship with potential consolers. Although some effort has been made in recent studies of post-conflict behaviour to distinguish between the effects of each of the components of relationship quality (i.e., value, compatibility and security) on reconciliation (Cooper et al., 2005; Koski & Sterck, 2007; Watts, 2006), no study has as yet examined the impact of all three relationship components between former opponents and between the recipient of aggression and potential consolers on the occurrence of consolation.

In this study we aimed firstly to investigate the function of consolation in a large zoo group of chimpanzees, specifically testing the prediction that consolation reduces post-conflict stress. We used self-directed behaviours, in particular self-scratching and self-grooming as an index of stress as these behaviours are reliable indicators of stress in primates (Maestripieri et al., 1992; Troisi, 2002). Rates of self-directed behaviour have been shown to increase in primates under stressful conditions such as following aggression (reviewed in Aureli et al., 2002). The link between self-directed behaviours and stress levels is further supported by pharmacological evidence (Schino et al., 1996). Reconciliation has been shown to reduce post-conflict rates of self-directed behaviours to baseline levels (Aureli & van Schaik, 1991; Castles & Whiten, 1998; Kutsukake & Castles, 2001). If consolation has a stress-reducing function as well, rates of self-directed behaviours would also be expected to decrease following its occurrence.

Our second aim was to examine the social determinants of consolation, studying the effects of conflict characteristics, reconciliation and inter-opponent relationship quality on the occurrence of consolation. Lastly, we investigated the effect of relationship quality between the initial recipient of aggression and potential consolers on the rate of consolation using novel techniques to obtain separate, composite measures of value, compatibility and security.

6.2. Methods

6.2.1. Data Collection

All occurrences of aggression were recorded when visible. The post-conflict (PC) - matched-control (MC) method (de Waal & Yoshihara, 1983) was used to collect post-conflict data on the recipient of aggression (see Chapter 2 for details).

6.2.2. Data Analysis

A total of 234 PC-MC pairs were collected on 22 recipients of aggression involving 129 distinct aggressor-recipient dyads (mean ±SD PC-MC pairs per recipient = 10.6 ± 5.7, range=2-25).

6.2.2.1. Function of Consolation

As the majority of post-conflict affiliative interactions occurred in the first minute of the PC (Chapter 3), PCs with consolation were operationally defined as those in which an affiliative behaviour was initiated by a third party towards the recipient of aggression in the 1st minute. Initiators were the individuals starting the affiliative contact. If affiliative contact was preceded by offering a hand, the partner offering the hand was considered to be the initiator Third parties were defined as any adult subject not involved as an opponent of the recipient of aggression in the preceding conflict, including supporters of the original aggressor. PCs in which both reconciliation and consolation occurred in the first minute were not included in the analyses (N=6). In addition, PC-MC pairs in which the initiator of the first affiliative interaction between the recipient and a third party was unclear in either the PC or the MC were removed (N=62). PCs with no reconciliation or consolation were those in which neither post-conflict interaction occurred in the entire PC period.

Post-conflict stress levels were assessed using self-directed behaviours (Maestripieri et al., 1992; Troisi, 2002). In particular, I used rates of self-scratching (bouts per minute) and the duration of self-grooming (seconds per minute), both previously successfully used in post-conflict studies (Aureli & van Schaik, 1991).

Given the operational definition of consolation (i.e., occurrence in the first PC minute), mean rates of self-scratching and mean time spent self-grooming during the time window in which PC values differed from MCs, but excluding the first minute, (i.e. minutes 2-10, Chapter 5) were used to determine the effects of consolation on self-directed behaviour. Such values for PCs with consolation and PCs without consolation or reconciliation were compared with mean MC levels for the whole 10 minutes using linear mixed models (LMMs). Levels of self-scratching or self-grooming were entered as continuous dependent variables and the identity of the initial recipient of aggression was entered as a random variable in the initial model. In addition we included the random variable 'PC-MC pair' for which each PC and its corresponding MC were given a unique number. The occurrence of consolation (PC with consolation=1 and PC without consolation or reconciliation=0) or type of observation (PC=1 and MC=0) was entered as a fixed explanatory variable depending on the analysis.

6.2.2.2. Determinants of Consolation

Following de Waal & Yoshihara's (1983) procedure, PC-MC pairs were labelled attracted if affiliative interaction occurred earlier in the PC than in the MC, or only in the PC. Neutral pairs had no affiliative interaction in either the PC or the MC, or at the same time in both. Pairs in which affiliative interaction occurred earlier, or only in MC, were labelled dispersed. For reconciliation the affiliative interaction was between the former opponents and for consolation the affiliative interaction was directed from a third party to the initial recipient of aggression. PC-MC pairs in which it was unclear who had initiated the contact were not considered. As the operational definition of consolation used for demonstrating its function would be too conservative leading to an excessive reduction in sample size, a different definition was used. Consolation was considered to have taken place when the PC-MC pair was attracted. A similar operational definition for reconciliation was used. For these analyses, neutral or dispersed pairs indicated an absence of reconciliation or consolation.

Table 6.1. Variables used in GLMM (binomial dependent variables) and LMM (continuous dependent variables) analyses for the determinants of consolation.

Name	**Type**
Dependent variables	
Consolation	Binomial (1=yes, 0=no)
Consolation Index	Continuous
TCT	Continuous
Fixed explanatory variables (relationship characteristics)	
Value	Continuous
Compatibility	Continuous
Security	Continuous
Sex-dyad combination	Binomial (1=including males, 0=no males)
Kinship	Binomial (1=yes, 0=no)
Fixed explanatory variables (conflict characteristics)	
Outcome	Binomial (1=decided, 0=undecided)
Intensity	Ordinal (1=low, 2=medium, 3=high)
Directionality	Binomial (1=bi-directional, 0=unidirectional)
Bluff	Binomial (1=starts with bluff display, 0= no bluff display)
Reconciliation	Binomial (1=yes, 0=no)

Random variables	
Recipient	Nominal
Aggressor	Nominal
Consoler	Nominal

Factors affecting the occurrence of reconciliation were investigated at the PC level using generalised linear mixed models (GLMMs) fitted with a binomial dependent variable, the presence or absence of consolation. Conflict characteristics (directionality, outcome, intensity, and initiation with a bluff display), characteristics of the relationship between the recipient and the aggressor (value, compatibility, security, kinship and sex combination) and the occurrence of reconciliation were entered as fixed variables (see Table 6.1 for descriptions of variables). Value, compatibility and security were composite variables derived from 9 behavioural categories using principal component analysis (Chapter 4). The identity of the recipient and aggressor were evaluated as random variables.

In order to investigate the effects of the characteristics of the relationship between third parties and recipients on the occurrence of consolation, the following consolation index was devised for each dyad: frequency of consolation / opportunity to console. The frequency of consolation was the number of times each potential consoler initiated the first affiliative interaction directed towards the recipient of aggression. The opportunity to console was the number of PCs in which one individual was the recipient, excluding those in which the partner was an aggressor. A LMM was run with the consolation index as a continuous dependent variable. Relationship characteristics (value, compatibility, security, sex-dyad combination and kinship) between potential consolers and recipients were input as fixed variables, and the identities of potential consolers and recipients were entered as random variables (Table 6.1).

As the consolation index does not control for baseline levels of affiliation between partners, a further analysis was conducted using the 'triadic contact tendency' (TCT) (Call et al., 2002) for the recipient and each potential consoler. The TCT was calculated for each dyad as follows: (attracted pairs – dispersed pairs)/(attracted + dispersed + neutral pairs). PC-MC pairs in which it was unclear who had initiated the contact were not considered for that dyad. The LMM was then rerun using TCT as the continuous dependent variable. It would not have been sufficient to have only run this analysis without running the LMM with the consolation index as the TCT is based on the first affiliative interaction between the recipient and *each* potential consoler, regardless of whether affiliative interaction has already occurred with another partner. As the function and demonstration of consolation are based only on the first affiliative interaction initiated by *any* third party, we cannot know whether further contacts function as consolation. The two analyses are thus viewed as complementary. An alpha level of 0.05 was adopted for all tests.

6.3. Results

6.3.1. Function of Consolation

Levels of self-grooming and self-scratching were not significantly different for PCs after consolation and MCs (self-grooming: β=3.24 s per min, 95%C.I.:0.35, 7.14, P=0.151; self-scratching: β=0.03 bouts per min, 95%C.I.:-0.07, 0.13, P=0.531; Table 6.2). PCs after consolation had a significantly lower level of self-grooming than PCs without consolation or reconciliation (β=-8.65 s per min, 95%C.I.:-15.53, 2.55, P=0.008), but no significant difference was found for levels of self-scratching (β=-0.04 bouts per min, 95%C.I.:-0.15, 0.06, P=0.400; Table 6.3), although the pattern was in the same direction (Fig. 6.1).

6.3.2. Determinants of Consolation

When the factors determining the occurrence of consolation were analysed, the best model from the GLMM analysis (Table 6.4) showed that reconciliation had a negative effect on consolation (Odds ratio=0.43, 95% C.I.: 0.22, 0.85, P=0.013), indicating that consolation was more likely to occur in the absence of reconciliation. This model also included a non-significant trend towards recipients of aggression from more compatible opponents (Odds ratio=1.28, 95% C.I.: 0.95, 1.67, P=0.061) and participants of bi-directional conflicts (Odds ratio=1.88, 95% C.I.: 0.95, 3.74, P=0.065) being more likely to receive consolation.

Fig. 6.1 Mean (+S.E.) time spent self-grooming (A) and mean (+S.E.) rate of self-scratching (B) during minutes 2-10 of PCs without consolation or reconciliation and PCs with consolation, and during MCs. *P<0.05

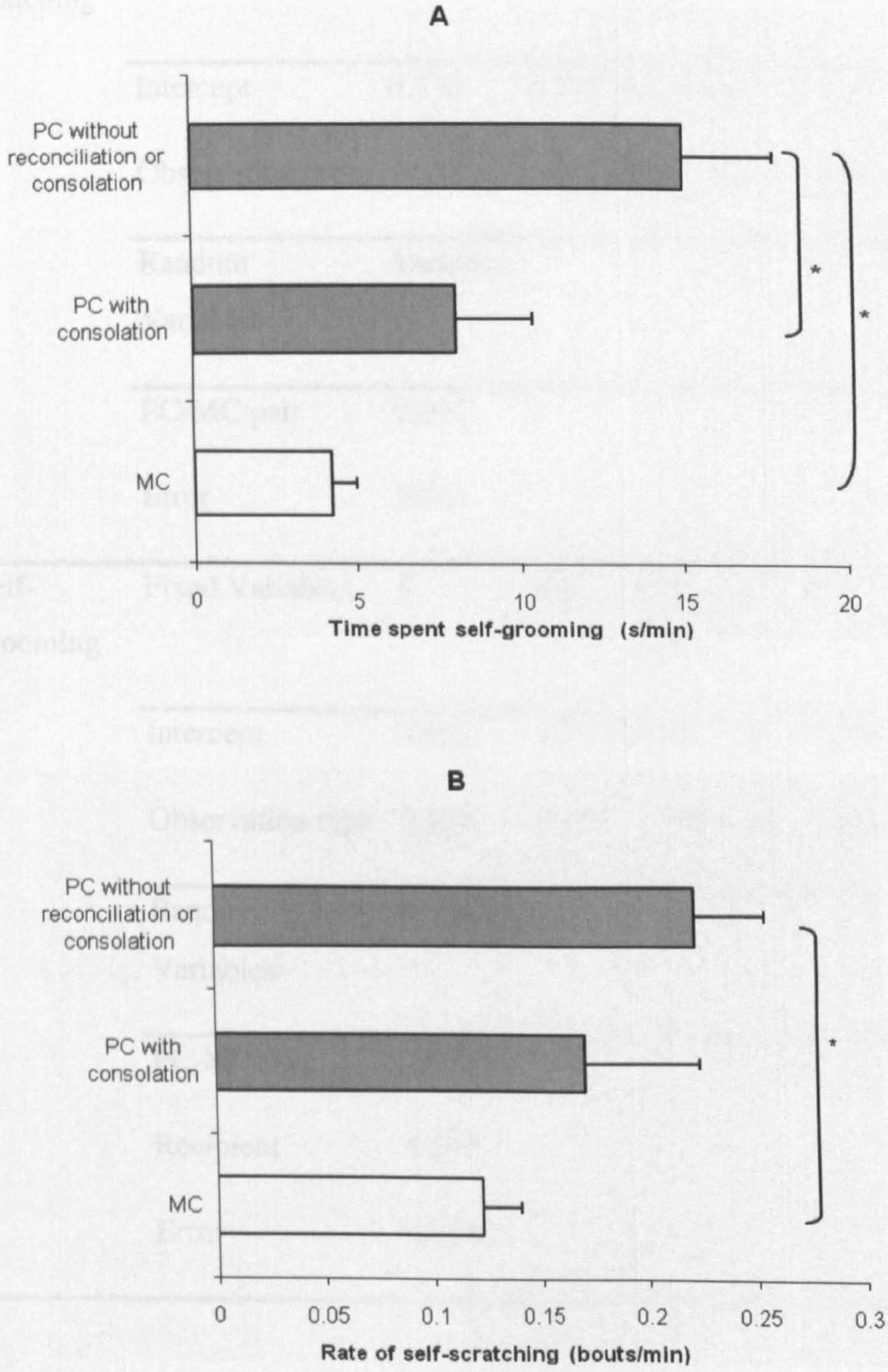


Table 6.2. Variables in the best LMM showing the effects of observation type (PC with consolation or MC) on levels of self-scratching and self-grooming.

Self-scratching	Fixed Variables	β	S.E.	95% C.I. of β	t	P
	Intercept	0.170	0.035	0.10, 0.24	4.836	<0.001
	Observation type	0.031	0.049	-0.07, 0.13	0.629	0.531
	Random Variables	Variance				
	PC-MC pair	0.002				
	Error	0.044				
Self-grooming	Fixed Variables	β	S.E.	95% C.I. of β	t	P
	Intercept	3.838	1.728	0.35, 7.14	2.221	0.030
	Observation type	3.238	2.222	-1.48, 7.99	1.453	0.151
	Random Variables	Variance				
	PC-MC pair	12.337				
	Recipient	1.893				
	Error	91.304				

Table 6.3. Variables in the best LMM showing the effect of consolation on self-scratching and self-grooming levels in PCs with and without consolation.

Self-scratching	Fixed Variables	β	S.E.	95% C.I. of β	t	P
	Intercept	0.233	0.037	0.16, 0.31	6.300	<0.001
	Consolation	-0.044	0.052	-0.15, 0.06	-0.846	0.400
	Random Variables	Variance				
	Recipient	<0.001				
	Error	0.059				
Self-grooming	Fixed Variables	β	S.E.	95% C.I. of β	t	P
	Intercept	15.165	2.262	10.83, 9.54	6.706	<0.001
	Consolation	-8.651	3.198	-15.53, -2.55	-2.705	0.008
	Random Variables	Variance				
	Recipient	<0.001				
	Error	219.93				

Table 6.4. Variables in the best GLMM explaining the occurrence of consolation, using attracted PC-MC pairs.

Fixed Variables	β	S.E.	z	P	Odds Ratio	95% C.I. of Odds Ratio
Intercept	0.157	0.369	0.447	0.662		
Reconciliation	-0.839	0.348	-2.483	0.013	0.43	0.22, 0.85
Directionality	0.632	0.343	1.843	0.065	1.88	0.95, 3.74
Compatibility	0.245	0.131	1.887	0.061	1.28	0.98, 1.67
Random Variables	**Variance**					
Recipient	0.447					

Error variance for random variables is not available for GLMMs.

When the impact of the quality of the relationship between the initial recipient of aggression and possible consolers on the occurrence of consolation was analysed using LLMs with the consolation index as a dependent variable, the only variable remaining in the best model was relationship value (β=0.01, 95%C.I.:<0.01, 0.02, P=0.018; Table 6.5). This result was confirmed when TCT was used as the dependent variable (β=0.01, 95%C.I.:0.01, 0.02, P=0.002; Table 6.5). Thus, recipients of aggression were more likely to be consoled by individuals with whom they had a more valuable relationship.

Table 6.5. Variables in the best LMMs explaining the occurrence of consolation, using the consolation index and TCT.

Consolation Index	Fixed Variables	β	Bootstrap S.E.	95% C.I. of β	z	P
	Intercept	0.024	0.003	0.02, 0.03	6.84	<0.001
	Value	0.010	0.004	<0.01, 0.02	2.37	0.018
	Random Variables	Variance				
	Consoler	0.005				
TCT	Fixed Variables	β	Bootstrap S.E.	95% C.I. of β	z	P
	Intercept	0.017	0.004	0.01, 0.03	3.96	<0.001
	Value	0.013	0.004	0.01, 0.02	3.08	0.002
	Random Variables	Variance				
	Consoler	0.015				

Error variance for random variables is not available for bootstrap models.

6.4. Discussion

The present study provides strong indications that consolation does have a calming function, as its name suggests. The findings support the notion that consolation can be an alternative to reconciliation as a stress alleviation mechanism when the latter fails to occur. Its beneficial nature is further supported by the result that consolation was more likely to be offered by valuable partners.

Chimpanzees spent less time self-grooming following conflicts when consolation occurred than when it did not, and levels of self-grooming following consolation were not different from baseline levels. These results imply that consolation reduced levels of post-conflict self-grooming and thus had a stress-alleviating effect. Although the reduction in self-scratching did not reach significance, the data trend was similar to that of self-grooming (Fig. 2b), and self-scratching rates after consolation did not differ from baseline levels. As levels of self-directed behaviour are an indirect measure of stress, the use of additional measures of stress is recommended in future studies in order to confirm these findings. High levels of stress may be experienced by recipients of aggression after the cessation of conflict due to uncertainty as a result of possible disruption to the inter-opponent relationship and the loss of its potential benefits, in addition to risks of renewed aggression (Aureli & van Schaik, 1991). Long-term high stress levels may have negative consequences (Sapolsky, 2004), which may thus be mitigated by consolation. The only other study that has investigated the stress-alleviating function of consolation, also in captive chimpanzees, focused only on self-scratching rates and found no support for this function (Koski & Sterck, 2007). However, Koski & Sterck (2007) compared self-scratching rates before and after consolation, which is quite different from my comparison with post-conflict periods without consolation and baseline levels.

Consolation was more likely to occur when reconciliation did not, a result that confirms previous studies (Palagi et al., 2004; Palagi et al., 2006a). This suggests that consolation may act as an alternative to reconciliation, serving a similar stress-alleviating function (see Chapter 5 for evidence of this function of reconciliation in the study group). Since reconciliation may also serve to repair the relationship between former opponents, however, it is likely that reconciliation would have first priority for former opponents, and thus consolation would be an alternative to reconciliation only if the latter fails to occur (Watts et al., 2000; Wittig & Boesch, 2003a; Palagi et al., 2006a). Consolation may be preferable when it may not be worth reconciling if the relationship between opponents is of low value and/or the risks of approaching the former opponent are too high (Wittig & Boesch, 2003a).

The mechanisms underlying consolation may explain the interspecific variation found in the occurrence of consolation in primates. Consolation has been documented in great apes, but not in monkeys. Although third-party initiated affiliation has been demonstrated in stump-tailed macaques (*Macaca arctoides*), it seems behaviourally different from consolation among apes, and has been suggested to serve a protective or appeasement function (i.e. prevention of further aggression: Call et al., 2002). Interspecific variation in consolation patterns might reflect differences in the perception of distress, that is, apes may be more sensitive to or more accurate in evaluating the stress levels of others (de Waal & Aureli, 1996; Aureli, 1997). Japanese macaque (*Macaca fuscata*) mothers, for example, do not display signs of distress when their offspring are targets of aggression nor do they increase post-conflict affiliative contacts with their offspring, suggesting that they may be unable to perceive their offspring's need for distress alleviation (Schino et al., 2004). For a bystander to provide reassuring contact to a recipient of aggression, thus helping the recipient reduce its post-conflict stress, the bystander may be required to perceive the distress of the recipient and act empathically. All mammals are capable of basic empathy, such as emotional contagion (Preston & de Waal, 2002), but there is an ongoing debate about the level reached by chimpanzees, which seems to exceed this level (Preston & de Waal, 2002; Silk et al., 2005; Jensen et al., 2006; Warneken et al., 2007; Penn & Povinelli, 2007; de Waal, 2008). Consolation may be one of the best-documented examples of so-called 'sympathetic concern', i.e., concern about another's state and attempts to ameliorate this state (de Waal, 2008), and yet, until now, there was no evidence that consolation reduces distress. This study therefore lends support for consolation being a critical behaviour in this debate.

Relationships between different group members vary considerably, and this variation may affect the way each individual behaves with a specific partner. The flexibility in behaviour according to relationship quality allows individuals to maximize the benefits and minimize the costs of each relationship (Kummer, 1978; Aureli & Schaffner, 2002b). Aureli & Schaffner (2002a) suggested that the quality of relationship between individuals is likely to affect their empathic response. Indeed, a number of studies found that similarity and closeness between individuals promotes empathy (Cialdini et al., 1997; Langford et al., 2006; Preston & de Waal, 2002). Similarly, we found that consolation was more likely between individuals with a valuable relationship, suggesting that chimpanzees are particularly responsive to the distress of valuable partners. Although it is the first time that this has been shown in primates, post-conflict third party affiliation has been reported between valuable partner, such as mating partners, in rooks (*Corvis frugilegus*) (Seed et al., 2007).

As consolation was more likely to occur between valuable partners, it is likely that bystanders derived greater benefits from consoling such partners. It is possible that consolation is part of a behavioural exchange between partners, either through reciprocity or interchange (de Waal, 1997; Watts, 2002), and thus the consoler may derive benefits by receiving consolation or other valuable behaviour in the future. It has also been suggested that consolation reduces the likelihood of further attacks among all group members, and is therefore advantageous to both consoler and recipient (Palagi et al., 2006a). Koski (2007) suggested that consolation in chimpanzees may serve a protection function by specifically reducing the risk of the consoler becoming the target of further aggression from the original recipient of aggression. Given how rare redirected aggression (i.e., further aggression initiated by the recipient of aggression and directed towards a third party) is among chimpanzees (de Waal & Hoeskstra, 1980; de Waal & van Hooff, 1981; Arnold & Whiten, 2001), the 'protection hypothesis' (Koski, 2007) is however unlikely to account for the primary function of consolation. Furthermore, since consolation was more likely to be provided by valuable partners in this study, these partners are unlikely targets of redirected aggression. Indeed the high value of the relationship between the recipient and consoler makes it more likely that consolation is a mutualistic behaviour, providing distress alleviation and improving well being, thus maintaining the benefits afforded by the relationship to both parties.

The results of this study suggest that chimpanzees respond empathically to valuable partners by consoling recipients of aggression, thus reducing recipient post-conflict stress levels particularly when reconciliation fails to occur. These findings provide support for consolation being a critical behaviour in the debate about the degree of empathic tendencies in great apes. Further research should focus on consolation not simply as a post-conflict event, but also as a possible empathic behaviour mediated by variation in relationship quality and emotional state.

CHAPTER 7

General Discussion

7.1. Post-Conflict Behaviour of Chimpanzees at Chester Zoo

This study demonstrated the occurrence of both reconciliation and consolation in the chimpanzees at Chester Zoo and furthermore demonstrated that both reconciliation and consolation reduce post-conflict stress levels in recipients of aggression and may function as alternatives to each other. The post-conflict behaviour of the chimpanzees was characterised by the use of context specific behaviours, indicative of an explicit post-conflict style, which is expected when reconciliation and consolation rates are high as it was the case in this study. Relationships between partners were found to consist of three separate components: Value, Compatibility and Security. Individuals were found to be more likely to receive consolation from those partners with whom they shared a valuable relationship, suggesting that chimpanzees responded empathically to valuable partners by consoling recipients of aggression, thereby reducing their post-conflict stress levels, especially when reconciliation failed to occur.

One of the most frequent investigations into the intra-group variation of conciliatory tendencies is the effect of sex combination on the occurrence of reconciliation (e.g. de Waal, 1986; Watts, 1995a; Schino et al., 1998; Cooper &

Bernstein, 2002; Palagi et al., 2004). In many cases, inferences are made about the quality of the relationship represented by the different sex-combinations (reviewed in Cords & Aureli, 2000; Watts, 2006). In baboon and macaque societies typically characterised by matrilineal structures, relationships between adult females are considered to be of higher value than relationships between males or mixed sex dyads, as females, particularly kin, cooperate to defend access to resources, form coalitions, and preferentially groom other females (Sterck et al., 1997; Widdig et al., 2001; Silk et al., 2004). It should be noted, however, that relationships among female dyads within a group may be subject to considerable variation (van Schaik & Aureli, 2000; Silk, 2002c). In chimpanzees, male philopatry and the high degree of cooperation between males in the wild are often used to infer more valuable relationships for male-male dyads (Arnold & Whiten, 2001; de Waal, 1986; Koski et al., 2007b; Kutsukake & Castles, 2004). In this study, however, dyads including males were not found to be more valuable (Chapter 4), and nor were they found to be more likely to reconcile than other dyads. In fact, female-female dyads showed higher conciliatory tendencies than male-male dyads (Chapter 3). All effect of sex combination on the occurrence of reconciliation was removed, however, when stronger predictors of reconciliation, such as the occurrence of consolation and initiation of the conflict with a bluff display, were included in the analyses (Chapter 5). These findings suggest that male-male dyads are not therefore necessarily the most valuable sex-combination in chimpanzees. Furthermore, the sex-combination of the dyad might not be one of the critical factors in determining the occurrence of reconciliation. Thus, it is imperative to investigate the determinants of reconciliation, in particular the quality of the relationship between opponents, in greater detail than simply attributing levels of relationship value to broad categories of partners (van Schaik & Aureli, 2000), especially if those attributions are based on assumptions without prior testing. This was achieved in the present study by using composite behavioural measures of each component of relationship quality. Although no effect of any aspect of relationship quality on reconciliation was found, it must be noted that the sample sizes of this study were limited despite the research effort of up to 6 hours a day, 5 days a week for 18 months. The significant effect of relationship quality on consolation clearly shows that this approach can be successful even with my sample size, but all tests would benefit from being conducted on a larger sample size.

Initiation of a conflict with a bluff display was one of the variables that had a sufficiently strong effect on the occurrence of reconciliation to remove the effects of sex and relationship value (see Chapter 5). It was concluded that bluff displays most likely do not damage the relationship between opponents and thus reconciliation may not be necessary. However, recipients of conflicts initiated with a bluff display were equally likely to be consoled as recipients of other conflicts (Chapter 6). This suggests that potential consolers nevertheless may perceive the recipient of aggression to be distressed. Even if the bluff display did not disrupt the relationship between opponents, it is likely that the conflict was nevertheless stressful, possibly as a result of the risks of injury and of renewed aggression. Thus, although the relationship repair function of reconciliation may be redundant, the stress-alleviating function may still be necessary. Consolation, however, can also fulfil this function, and thus may be preferable to reconciliation if the risks of renewed aggression are high (Wittig & Boesch, 2003a).

My findings show that consolation may act as an alternative to reconciliation. Chapter 3 showed that reconciliation was less likely to occur after consolation, and that consolation was less likely to occur after reconciliation. Moreover, Chapters 5 and 6 showed that consolation was more likely in the absence of reconciliation and that reconciliation was more likely in the absence of consolation, confirming that they may function as alternatives in distress alleviation, although reconciliation may be preferable over consolation whenever possible because of its function in repairing the relationship between opponents. Furthermore, reconciliation and consolation may occur under opposing conditions (Wittig & Boesch, 2003a), as conflicts between mixed-sex dyads in wild chimpanzees were most likely to be reconciled, but least likely to be followed by consolation, and whereas reconciliation was more likely to occur after conflicts between valuable partners, consolation was more likely to occur after conflicts between partners with low value relationships. These findings suggest that reconciliation and consolation may represent separate, opposing, strategies for the post-conflict management of aggressive conflict.

One of mysteries surrounding post-conflict behaviour is why many studies have been unable to demonstrate solicited consolation in apes (Fuentes et al., 2002; Wittig & Boesch, 2003a; Kutsukake & Castles, 2004; Koski & Sterck, 2007; this study, Chapter 3). Solicited consolation has been demonstrated in a number of species of Old and New World monkeys (York & Rowell, 1988; Verbeek & de

Waal, 1997; Arnold & Barton, 2001b; Call et al., 2002), and, although its function has not been tested, may serve a stress-alleviating function similar to that of consolation (Watts et al., 2000). Thus, why do monkeys initiate affiliative interactions with third parties while apes appear to wait for third parties to take the initiative? According to the social cognition hypothesis (de Waal & Aureli, 1996), the cognitive abilities of monkeys do not reach the threshold above which individuals are able to perceive and respond to distress in others. This might explain why monkeys do not exhibit consolation, but tells us nothing about why solicited consolation is not ubiquitous in apes. It may be that reconciliation and consolation are both so effective that there is no need to solicit affiliation from others. In this study, only 20.3% of aggressive conflicts did not result in either reconciliation or consolation in the ten minutes following the end of the conflict (Chapter 3), leaving little opportunity for another post-conflict interaction to occur. That is not to say that the chimpanzees never solicit consolation, but that the relative frequency of contacts in post-conflict periods is not significantly different from that in control periods. As a consequence, solicited consolation cannot be demonstrated as a post-conflict interaction. The high baseline frequency of affiliative interactions characteristic of chimpanzees (Goodall, 1986; de Waal, 1986, 1994; Nishida et al., 1999; Watts, 2002) may make it particularly difficult to detect a difference in affiliation in post-conflict and control periods when there are only a limited number of cases when reconciliation and consolation did not occur. Conversely, solicited consolation has been demonstrated in other studies that have reported high rates of both reconciliation and consolation (Cordoni et al., 2006; Mallavarapu et al., 2006; Palagi et al., 2004; Palagi et al., 2006a), although only one of those is on chimpanzees (Palagi et al., 2006a).

The chimpanzees in this study displayed an explicit style of post-conflict behaviour in that they utilised context-specific behaviours, kiss and embrace, for reconciliation and consolation. While this style is characteristic of species with tolerant societies (de Waal & Ren, 1988), within those species, there may be a differential use of behaviours for post-conflict interactions, as context-specific behaviours only make up a proportion of all cases (Chapter 3). This study has shown that consolers are likely to be valuable partners of recipients of aggression (Chapter 6). Those consolers may draw benefits from alleviating post-conflict stress in valuable partners (Watts et al., 2000), and thus may be motivated to maximise the effectiveness of consolation. As for species for which affiliative interactions are common, context-specific behaviour may enable the actor's intentions to be made more explicit, especially for individuals who interact regularly. Thus, valuable partners may be able to maximise the effectiveness of consolation by using explicit gestures. Whether this is the case, however, remains to be tested, as currently we do not know whether consolers draw benefits from consolation, or whether the type of behaviour used or the relationship between the consoler and recipient influence the effectiveness of consolation in reducing post-conflict stress levels in the recipient of aggression.

The results of this study fit the general pattern for post-conflict behaviour in chimpanzees, although the considerable variation in the occurrence and patterns of reconciliation and consolation across studies on chimpanzees (see Table 7.1) makes it difficult to generalise findings for the species. This variation is unlikely to be due to the behaviour of the chimpanzees in captive versus wild settings, but is most likely influenced by the different variables and methods used and differences in group composition (Colmenares, 2006). The stability of dominance relationships as a function of the time since the group was established has been suggested to be a factor in the variation in conciliatory tendencies (Baker & Smuts, 1994). As reconciliation may reflect a need for social stability and tension reduction when relationships are threatened by high levels of competition and aggression, reconciliation may be expected to occur at higher rates in recently established captive groups where competition is likely to be high and dominance positions unstable (Baker & Smuts, 1994). The high conciliatory tendencies reported for a very well-established group in this study, however, suggest that this may not be the case. Despite some variation in findings among studies, a striking similarity exists between the overall patterns of post-conflict behaviour between chimpanzees and young children. Reconciliation is more likely to occur between friends in children, and conciliatory tendencies were similar to those reported in this study (Butovskaya & Kozintsev, 1999; Ljungberg et al., 1999; Verbeek & de Waal, 2001; Fujisawa et al., 2005; reviewed in Butovskaya et al., 2000). The notion of consolation as an alternative to reconciliation was also supported in Japanese school children, as consolation was more likely to occur in the absence of reconciliation, and was likely to be explicit (Fujisawa et al., 2006). Despite the very similar conditions in which children were observed across studies, patterns of post-conflict behaviour nevertheless varied among groups of children, most likely as a result of cultural variation (Butovskaya et al., 2000) and similar cultural variation has been observed in the post-conflict behaviour of adult humans (Fry, 2000). Could some of the variation in findings between chimpanzee studies also be attributed to cultural variation? Variants of certain behaviours used for reconciliation and consolation, such as the mouth-to-mouth kiss observed among the Arnhem Zoo chimpanzees (de Waal & van Roosmalen, 1979) are possibly due to cultural differences between the groups, as such a variant was never observed in any other group (Arnold & Whiten, 2001; Fuentes et al., 2002; Kutsukake & Castles, 2004; Chapter 3). The mouth-to-mouth kiss of the Arnhem Zoo chimpanzees and the mouth-to-body kiss (directed to any part of the body except the mouth) of the Chester Zoo chimpanzees are likely to be socially learned variants that fulfil similar functions under similar conditions. Little is known, however, about what aspects of post-conflict behaviour in non-human primates may be subject to cultural variation.

7.2. Future Directions for Conflict Management Research

This thesis has attempted to address some of the questions surrounding reconciliation, consolation and relationship quality in chimpanzees. While answering some, it also highlighted that there are more questions to be answered and probably yet more to be asked.

Table 7.1. Post-conflict behaviour in chimpanzees.

	Reconciliation		Consolation		Solicited Consolation	Setting
	CCT	Determinants	TCT	Determinants	TCT	
de Waal & van Roosmalen, 1979	Yes		Yes, but did not differentiate between initiators			C
de Waal, 1986	Yes	Sex (MM>MF>FF)				C
Baker & Smuts, 1994	14.4%	Sex (FF>MF>MM)				C
de Waal & Aureli, 1996			Yes	Strictly aggressive conflicts		C
Arnold & Whiten, 2001	12.3%	Sex (MF and MM > FF) High affiliation score	No		Yes	W
Preuschoft et al., 2002	41.2%	High grooming rates				C
Fuentes et al., 2002	17.3%	Sex (FF>MF>MM)	No, but did not differentiate initiator			C

Wittig & Boesch, 2003	15.9%	Sex (MF>FF or MM) High association index High opponent food sharing with agonistic support	Yes	Sex (MF<FF or MM) Few competitors Low opponent food sharing with agonistic support	No	W
Kutsukake & Castles, 2004	14.4%	None	Yes		No	W
Palagi et al., 2006	28.9%		49.5%	Absence of reconciliation Screaming	53.0%	C
Watts, 2006	Yes	High coalitionary support				W
Koski et al. 2007	21.6%	Sex (MM>FF) High compatibility	12.7%	None	No	C
This study	47.5%	Occurrence of consolation Initiation of conflict with bluff display	29.4%	Absence of reconciliation Value of recipient-consoler relationship	No	C

CCT= corrected conciliatory tendency; TCT= triadic contact tendency; When CCT or TCT were not available, Yes or No indicates that the occurrence of the post-conflict interaction was, or was not, demonstrated. W= wild; C= captive; MM= male-male dyads, MF= mixed-sex dyads, FF= female-female dyads.

While the influence of the quality of relationship between opponents on post-conflict interactions has been the focus of a number of studies (Cords & Aureli, 2000; Watts, 2006; Chapter 5, Chapter 6), it is likely that the quality of the relationship between potential opponents also has an influence on whether conflicts of interest escalate into aggression (de Waal, 1996; de Waal, 2000a; Wittig & Boesch, 2003b). Wild chimpanzees have been found to make their decisions on whether to initiate aggression according to the relative dominance status of the opponents and the benefits afforded by their relationship (Wittig & Boesch, 2003b). The findings of this study, however, suggest that the quality of relationships is composed of several independent components (Chapter 4). If these components influence the occurrence of post-conflict interactions in different ways (Cords & Aureli, 2000), they may also have different effects on the escalation of aggression. Thus, further work is needed to understand how different aspects of the quality of the relationship between opponents affect what happens once a conflict of interest arises.

This study has shown that valuable partners are more likely to console recipients of aggression. Relationship quality has been shown to be linked to emotional responses (Aureli & Schaffner, 2002b), as, for example, levels of self-directed behaviour may be higher after conflicts with valuable partners (Aureli & Smucny, 2000). Moreover, social buffering, i.e., the reduction of a stress response to a stressor as the result of the presence of other conspecifics, has been shown to be more effective between familiar partners (Coe et al., 1982; Hennessy et al., 1995; de Vries, 2002). Hence, the degree of affiliation and attachment between partners has been suggested to influence the efficacy of social buffering (Kikusui et al., 2006). Could the relationship between the consoler and the recipient therefore also influence the effectiveness of consolation, i.e., are valuable partners more effective at alleviating post-conflict stress than less valuable partners? Unfortunately the limited sample size in this study precluded this hypothesis from being tested. As levels of self-directed behaviour were not significantly different from baseline levels following consolation, however, it is possible that either consolation was always performed by partners with a high enough value for consolation to be entirely effective, or that the relationship between the consoler and recipient did not affect the effectiveness of the interaction in reducing post-conflict stress. If variation does exist in the effectiveness of consolation, it may also be due to differences in effectiveness of the behaviours employed for consolation, but these too are likely to be influenced by the quality of the relationship between partners (Call et al., 1999). Thus, further investigation into the effect of the quality of the relationship between consoler and recipient, and of the behaviours used for consolation, on the efficacy of consolation is recommended.

An example of the absence of the necessary degree of empathy required to perceive others' need for distress-alleviation in monkeys is the lack of response by Japanese macaque mothers to the distress of their offspring following aggression (Schino et al., 2004). This study, however, has not been replicated in apes, and we do not know, therefore, how mothers respond to conflicts involving their offspring in primates that do presumably have the prerequisite empathic abilities for distress alleviation. It is not known whether consolers themselves experience high levels of stress (Watts et al., 2000), but mothers of recipients of aggression are likely to be the most susceptible to raised stress levels if third parties are emotionally affected by aggressive conflict (Schino et al., 2004). Thus investigating the response of chimpanzee mothers when their offspring receive aggression, would not only clarify the dichotomy in empathic abilities between monkeys and apes, but, if chimpanzee mothers do show signs of distress as would be expected, may help us understand more about how third parties are affected by aggressive conflict between others. Furthermore, it would be interesting to compare the responses of potential consolers to aggressive conflicts between others and relate it to the quality of their relationship with the recipient of aggression and the likelihood that they will provide consolation

While this study has focussed on interactions between recipients of aggression and third-parties, post-conflict affiliation may also occur between aggressors and third parties. Although such interactions may fulfil different functions to consolation, they may form an important part of conflict management (Das, 2000). Post-conflict affiliation with the aggressor may have multiple functions. It may appease the aggressor and thus reduce the likelihood of renewed aggression, either between the former opponents or between the aggressor and third parties (Kutsukake & Castles, 2004; Koski et al., 2007a). It may serve as a form of triadic reconciliation with opponents' kin (Judge, 1991; Wittig et al., 2007), or as signal of support from their own kin (Call et al., 2002), or as signal to strengthen bonds between potential coalition parters (Das et al., 1997). The variety of functions shown or proposed suggests that the function of post-conflict affiliation between aggressors and third parties may vary according to the behaviours used (Call et al., 2002), the identity of the third party (Das, 2000) and the species. The functions of post-conflict affiliation between aggressors and third parties must, therefore, be investigated in all species and within each study group, so that variations within groups and species can be thoroughly understood. Furthermore, in order to understand post-conflict behaviour as a whole, all aspects of post-conflict interactions must be investigated, whether they occur between opponents, between recipients of aggression and third parties, between aggressors and third parties, or just even among bystanders (e.g. Judge & Mullen, 2005).

This study showed that kiss and embrace were context-specific behaviours used for reconciliation and consolation. If these behaviours function to signal reconciliation or consolation in a post-conflict context, they may be used in other contexts to signal similar intentions. The meaning of a signal has been shown to be modulated by context in pigtailed macaques (*Macaca nemestrina*), where silent-bared-teeth displays indicated submission in a post-conflict context, but in other contexts, where submission was unwarranted, signalled subordination (Flack & de Waal, 2007). Thus, out of a post-conflict context, it would not be appropriate for chimpanzees to signal reconciliation or consolation, but kiss and embrace could be adapted to signal peaceful intentions and thus reduce uncertainty about interaction between partners. Brief affiliative behaviours, such as kiss and embrace, may therefore form part of conflict avoidance strategies by reinforcing relationships and making intentions explicit. Predictions about the functions of brief affiliative behaviours, however, in addition to other possible conflict avoidance strategies, such as pant-grunt greetings, remain to be tested.

The benefits of group living are thus maintained through a complex system of negotiation, conflict avoidance, conflict resolution, relationship repair and damage limitation strategies that, despite ubiquitous conflicts of interest between group members, enable valuable, cooperative relationships to be maintained, thus preserving group cohesion and its associated benefits. In understanding these strategies as mechanisms for the maintenance of group cohesion and cooperation, we can also learn about cognitive abilities, cultural differences, and the evolution and development of communicatory signals. Hence, conflict management is a hugely important avenue for continued research effort, with particular emphasis placed on the importance of integrating studies from different areas of conflict management and on systematic comparisons of conflict-avoidance and post-conflict behaviour in groups within and between species.

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