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The Occurrence of Post-Conflict Skills in Captive Immature Chimpanzees (*Pan troglodytes*)

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The Occurrence of Post-Conflict Skills in Captive Immature Chimpanzees (*Pan troglodytes*)

Running title: Post-conflict Skills in immature chimpanzees

Abstract

Conflict management strategies can reduce costs of aggressive competition in group-living animals. Post-conflict behaviours such as reconciliation and third party post-conflict affiliation are widely accepted as social skills in primates and have been demonstrated in many species. Although immature primates possess a repertoire of species-specific behaviours, it is thought that they gradually develop appropriate social skills throughout prolonged juvenility to establish and maintain complex social relationships within their group. We examined the occurrence of post-conflict skills in five immature chimpanzees (*Pan troglodytes*) over 15 months focusing on interactions that were not with the subject’s mother. We observed reconciliation, with conciliatory tendencies comparable to adults, and provide the first evidence that captive immature chimpanzees commonly reconciled using social play. However, immatures were not more likely to reconcile valuable than non-valuable relationships. We also observed third party post-conflict affiliation although at a lower level than reported for adults. Our results provide evidence for post-conflict skills in immature chimpanzees but the lack of higher conciliatory tendency with valuable partners and low occurrence of third party affiliation indicates extended juvenility may be required refine these skills. Further work is needed to investigate whether these behaviours have the same function and effectiveness as those found in adults.

Key words: infant chimpanzees; social competence; reconciliation; consolation.

Introduction

Living in a group inevitably involves competition for limited resources between conspecifics. Investing in social relationships is one way for animals to increase their competitive ability and/or reduce the costs of competition. Where competition takes the form of aggressive conflict, costs can include risk of injury, increased stress, and potential damage to social relationships (Aureli et al 2002; Aureli & de Waal 2000). Conflict management strategies provide one way to alleviate these negative consequences. They include friendly post-conflict reunion between former opponents, known as reconciliation, and third party post-conflict affiliation between a bystander and victim of aggression, that has been referred to functionally as consolation (de Waal & Roosmalen 1979). Such behavioural strategies are viewed as part of a suite of social skills (Kempes et al 2009).
in primates that are learned during a ‘socialisation period’ in infancy (Bekoff 2001) and develop through a period of extended primate juvenility (de Waal 1989; Goodall 1986; Joffe 1997; Lonsdorf & Ross 2012; Pagel & Harvey 1993; Poirier & Smith 1974; Watts & Pusey 2002). For example, the play of orphaned chimpanzee (Pan troglodytes) juveniles was more likely to result in aggression than the play of mother-reared juveniles, strengthening the idea that social skills are learned in early infancy (Leeuwen et al 2014).

Since it was first documented in chimpanzees (de Waal & van Roosmalen 1979), studies have documented the occurrence of reconciliation in over 30 primate species (reviewed in Aureli et al 2002) across strepsirrhines (Verreaux’s sifaka Propithecus verreauxi, Palagi et al 2008), monkeys (e.g. Bonnet macaques Macaca radiata, Cooper et al 2007; white-faced capuchins Cebus capucinus, Leca et al 2002) and apes (e.g. bonobos Pan paniscus, Clay & de Waal 2014; mountain gorillas Gorilla gorilla beringei, Watts 1995) as well as a few non-primate species such as corvids (e.g. ravens Corvus corax, Fraser & Bugnyar 2011), domestic dogs (Canis familiaris, Cools et al 2008), bottlenose dolphins (Tursiops truncates, Yamamoto et al 2015), domestic goats (Capra hircus, Schino 1998), horses (Equus caballus, Cozzi et al 2010), spotted hyenas (Crocuta crocuta, Wahaj et al 2001), and wolves (Canis lupus, Baan et al 2014). Reconciliation has been shown to reduce the likelihood of renewed aggression and post-conflict stress (e.g. Aureli & van Schaik 1991; Cooper et al. 2007, Das 2000; Koski & Sterck 2007b; Fraser et al 2008; Watts et al 2000), and restore relationships (Cords 1992; Koyama 2001) in particular, relationships that are important to individuals, such as friendships and coalitions (the ‘valuable relationship hypothesis’: de Waal & Aureli 1997). Much less research has addressed reconciliation by immature primates (long tailed macaques, Macaca fascicularis: Cords, 1988, Cords & Aureli, 1993; stump-tailed macaques, M. arctoides and rhesus macaques, M. mulatta: de Waal & Johanowicz 1993; Japanese macaques, M. fuscata: Schino et al 1998; brown capuchins, Cebus apella: Weaver & de Waal, 2000, 2003; bonobos: Clay & de Waal 2013a). These studies, mostly in monkeys, have reported that juveniles are able to reconcile their conflicts. Unrelated juvenile long tailed macaques were more likely to reconcile than related pairs (Cords, 1988; Cords & Aureli, 1993) and juvenile females were more likely to reconcile with unrelated adult female opponents than juvenile males (Cords & Aureli 1993). These findings may relate to the value of the relationship with these partners, however, no studies have yet tested the valuable relationship hypothesis in immature primates using measures of affiliation to determine relationship value. Besides reconciliation other conflict management mechanisms can co-occur, for example, victims of aggression can receive solicited or unsolicited friendly contact from a third party or bystander not involved in the conflict (Verbeek & de Waal 1997). Such contact potentially functions as consolation (de Waal & Aureli 1996; Fraser et al 2008) and has been reported for great apes (e.g. Clay & de Waal 2013a,b; Cordoni & Palagi 2007; Fraser & Aureli 2008). However, reports for monkeys have been variable as studies have reported an absence of third party post-conflict affiliation in some macaque species (de Waal & Aureli 1996), an absence of functional consolation in stump-tailed macaques (Call et al 2002)
and mandrills (Schino & Marini 2012) but the occurrence of consolation (distress alleviation and preferential
direction towards friends) in Tonkean macaques M. tonkeana (Palagi et al 2014).

Chimpanzees are highly social animals with complex social behaviour related to the fission-fusion
structure of their society (e.g. Boesch & Boesch-Achermann 2000). Living in complex social groups,
chimpanzees require cognitive and behavioural skills to successfully maintain cooperative relationships (Boesch
et al 2003; Goodall 1986; Muller & Mitani 2005). Given that chimpanzees do not become sexually mature until the
age of 9 years, they have an extended period in which to acquire these skills such as reconciliation and third
party post-conflict affiliation. Both in the wild and in captivity, many studies have documented reconciliation
(Arnold & Whiten, 2001; Baker and Smuts, 1994; de Waal & Aureli, 1996; de Waal & van Roosmalen, 1979;
Fraser & Aureli, 2008; Fraser et al, 2010; Fuentes et al, 2002; Koski et al, 2007a; Preuschoft et al 2002; Wittig &
Boesch, 2003, 2005) and third party affiliation (de Waal and van Roosmalen, 1979; Fraser & Aureli 2008; Koski &
Sterck 2007, 2009; Palagi et al. 2006; Romero & de Waal 2010; Romero et al 2010; Wittig and Boesch 2003) in
adult chimpanzees. No studies have yet investigated the occurrence of post-conflict behaviour in immature
chimpanzees.

Determining which post-conflict skills chimpanzees have acquired by the beginning of juvenility is
important to understand the process of social skill acquisition. We investigated post-conflict behaviour in
immature chimpanzees and excluded mothers as social partners in our analyses as we were interested in the
occurrence of post-conflict behaviour as a means to contact other group members. We hypothesise that
reconciliation occurs in immature chimpanzees (Hypothesis 1a). Given the extended period of juvenility for the
development of social skills in chimpanzees, we predict that immature chimpanzees (up to 7 years) will not have
acquired conciliatory tendencies comparable to those previously reported for adults. As the immatures were likely
to have established play relationships with other immatures in the group, the greater compatibility or accessibility
(Cords & Aureli 2000) with immature opponents should facilitate post-conflict affiliation. Thus, opponent’s age
(immature/adult) category should affect conciliatory tendency (Hypothesis 1b). Further, if reconciliation functions
to repair bonds that have been strained during the previous conflict, it should be most predictable among
individuals that have a valuable relationship (de Waal & Aureli, 1997; de Waal & Yoshihara, 1983; Kappeler &
van Schaik, 1992). We, therefore, examined whether relationship quality affects conciliatory tendency
(Hypothesis 1c). The first affiliative post-conflict contact can take many forms in adult chimpanzees, for example
mouth-to-mouth kiss, sitting in contact or brief touch, with one of the most common being grooming (Arnold &
Whiten 2001; de Waal & van Roosmalen 1979). Indeed, in a previous report on the adults in our study group, the
most commonly occurring reconciliatory behaviour was grooming (Fraser & Aureli 2008). However, grooming is
used less frequently by infants and juveniles to contact group members other than their mother/siblings (Goodall
1986, Nishida 1988). Young chimpanzees are more likely to use play behaviour to acquire a central position in the group from which they can form affiliative relationships (Shimada & Sueur 2014). Play, rather than grooming, was also used by young chimpanzees to contact other group members during a period of greater tension (Palagi et al 2004). We therefore hypothesised that immatures would use specific behaviours to reconcile (Hypothesis 1d) and predict that immature chimpanzees will use social play rather than grooming to reconcile with former opponents.

Given that juvenile primates are capable of post-conflict reconciliation, we investigated whether immature chimpanzees engaged in other post-conflict behaviour such as third party contact with the recipient of aggression (Hypothesis 2a). Finally, we were interested in the co-occurrence of post-conflict skills and whether the tendency to perform reconciliation was related to tendency to perform third party affiliation with a recipient of aggression (Hypothesis 2b).

Methods

Subjects and Housing

The group of chimpanzees housed in Chester Zoo, UK, comprised 29 related and unrelated individuals (five adult and one adolescent male, 18 adult females, five infants/juveniles). Goodall (1986) defined infancy as less than 5 years and the juvenile period from 5-7 years although recent studies have grouped immatures as individuals younger than 12 years (e.g. Markham et al 2015). At the start of our study, four immatures were infants less than 5 years old and one was a juvenile. By the end of our study, two of the infants were 60 months and entering juvenility. For simplicity, we refer to the focal subjects as immatures (Table 1) throughout. They were all born and reared by their mothers in the zoo. Four of the immatures had relatives in the group, excluding their mothers, totalling seven dyads (relatedness coefficient $r = 0.25$ for two dyads and 0.125 for five dyads). Relatives were all adults. Group composition did not change during the study period with the exception of the birth of a female infant Tina in February 2009 and the death of a female infant Rhiannon in June 2008. All interactions with Rhiannon were excluded from the dataset.

The chimpanzee enclosure at Chester Zoo consisted of an outdoor grassed island, approximately 2000 m$^2$, separated from the public by a three metre moat and a 143 m$^2$ dome shaped indoor enclosure. The outdoor enclosure was enriched with trees, shrubs, rocks, logs, hammocks, and climbing structures. The indoor area had a 9m high iron frame with platforms, ropes and nets strung from the frame and walls. The chimpanzees were fed
two to three times a day and had *ad libitum* access to water both inside and outside. The observer was able to move easily between the two enclosures to maintain visibility of the subjects.

Table 1. The sex and age range (months) from the start to the end of the study (September 2008 – November 2009) of the five immature chimpanzees in Chester Zoo, UK.

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Sex</th>
<th>Age Range (months)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dona</td>
<td>F</td>
<td>40-55</td>
</tr>
<tr>
<td>Carlos</td>
<td>M</td>
<td>42-57</td>
</tr>
<tr>
<td>Dido</td>
<td>F</td>
<td>45-60</td>
</tr>
<tr>
<td>Frankie</td>
<td>F</td>
<td>45-60</td>
</tr>
<tr>
<td>Eric</td>
<td>M</td>
<td>63-78</td>
</tr>
</tbody>
</table>

Data Collection

S. Farooqi collected all data over 15 months (September 2008 – November 2009) recording the time (secs) immatures engaged in play and grooming during 15-minute continuous focal animal samples (Altmann, 1974) using Observer 5.0 (XT Noldus). We ensured focal samples were selected in random order and for approximately equal amounts of time and collected a total of 706 focal samples (mean±SD = 141.2 ±2.9).

Following de Waal & Yoshihara (1983), we recorded aggressive conflicts, noting the identities of the victim (the individual who first received aggression) and the main aggressor (the individual who attacked with the most intense aggression). We began a 5-minute post-conflict (PC) observation immediately after the conflict ended, noting the time/date and continuously recorded all social interactions using a dictaphone: proximity; kiss; play; grooming received; grooming given; mutual grooming; and sitting in contact (Table 2). If the conflict was renewed within two minutes of the start of the PC we abandoned the observation and restarted once the renewed conflict ceased. If the second conflict was more aggressive, we recorded the PC after this and ignored the initial conflict.

We recorded a matched-control (MC) observation the following, or next possible, day at the same time and under similar conditions i.e. when opponents were visible to each other (Koski et al 2007a) but when there had been no agonistic interaction between opponents for at least 15 minutes. If these conditions were not met, we postponed the MC until the next day or up to a maximum of one week. If we could not obtain a matched control within one week, we discarded the corresponding PC.
Table 2. Definitions of the behavioural categories for the chimpanzees at Chester Zoo, UK from September 2008 – November 2009.

<table>
<thead>
<tr>
<th>Behaviours</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Groom given</td>
<td>Picking through and/or slow brushing aside of the fur of another individual with one or more hands.</td>
</tr>
<tr>
<td>Groom receive</td>
<td>Another individual(s) picks through and/or slowly brushes aside the fur of the focal individual with one or more hands,</td>
</tr>
<tr>
<td>Groom mutual</td>
<td>Two chimpanzees pick through and/or slowly brush aside the fur of each other simultaneously.</td>
</tr>
<tr>
<td>Sitting in contact</td>
<td>Huddling with another individual or with a significant portion of body contact. Includes embraces with open arms.</td>
</tr>
<tr>
<td>Proximity</td>
<td>The focal animal is within an arm’s length from another animal or animals, no touching of body parts.</td>
</tr>
<tr>
<td>Aggression</td>
<td>A threat, charging display, chase, grasp, push or throwing of an object and any contact with another involving kick, hit, stamp, drag, tug hair, bite or scratch.</td>
</tr>
<tr>
<td>Play</td>
<td>Relaxed slow movements of single animal, lying in hammock, playing with ropes, rags and blankets, somersaulting or tickling or slow grappling between two or more individuals. No running or chasing. Behavioural elements of play including fast grappling, tumbling, wrestling, moving across circles, tackling, stomping, slapping, dragging by limbs and slamming on the ground.</td>
</tr>
<tr>
<td>Kiss</td>
<td>Mouth-to-mouth contact</td>
</tr>
</tbody>
</table>

We also applied the PC-MC method to record third party affiliative contact (e.g. Call et al, 2002) from these conflicts involving at least one immature. We considered contact when an immature third party initiated affiliative contact with a recipient of aggression (also known as true consolation: Verbeek & de Waal, 1997).

Third party affiliative contact was considered ‘solicited’ (Verbeek & de Waal, 1997) when the recipient approached or stretched a hand towards the third party prior to the interaction (Fraser & Aureli, 2008).

Data Analysis

Our sample included an older male infant that transitioned to juvenility during the study. We checked that his behaviour was not consistently higher than the other immatures so that we could include him in our analysis. We analysed differences using paired t-tests (df=4) and where necessary transformed data to meet assumptions of normality. When comparing the proportion of dispersed pairs (all zeros) with attracted pairs, we used a one-sample t-test. Performing non-parametric statistics did not alter the significance of the results. Where appropriate, we report mean (±SD) values in the text. We performed statistical analyses using SPSS 20 and all tests were two-tailed with the significance level set at p < 0.05.

We collected a total of 176 PC observations, excluding conflicts with mothers, of which seven were discarded because no matched-controls were obtained within the following seven days. A mean number of 33.8±18.3 PC-MC pairs per focal subject were recorded from 61 conflicts between immatures and 108 conflicts between immatures and adults. Each PC-MC pair was labelled: attracted, if the first affiliative interaction between opponents occurred earlier, or only in the PC relative to the MC; dispersed, if it occurred earlier or only in the MC;
and 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. To test whether immatures reconciled their conflicts (Hypothesis 1a),
we compared the proportion of attracted and dispersed pairs (Fraser & Aureli, 2008). We tested this for all PC-MC pairs and then separated conflicts between immatures and those between immatures and adults to test
whether immatures reconciled conflicts amongst themselves, as well as those with adults. In order to test
whether the occurrence of reconciliation was not due to one or two immatures, we calculated the corrected
conciliatory tendency that controls for baseline levels of affiliation (Veneema et al, 1994) for each individual as
100*[(number of attracted pairs – number of dispersed pairs)/ total PC-MC pairs]. We then tested for a difference
between individuals’ corrected conciliatory tendency with other immatures and with adults (Hypothesis 1b).

We used the adult-immature conflicts only (n=108) and excluded the adult-initiated reconciliations
(n=101) to test the effects of kinship and valuable relationships on corrected conciliatory tendencies (Hypothesis 1c). As there were only four PC-MC pairs for two kin dyads we could not compare corrected conciliatory
tendencies between kin and nonkin. In order to test the valuable relationship hypothesis, we excluded PCs
between kin (n=97, mean±SD number of PCs per immature = 19.4±11.8 and mean number of opponents per
immature = 9 ±3.8) and for immatures, compared the corrected conciliatory tendency with their valuable partners
to the corrected conciliatory tendency with their non-valuable partners (Hypothesis 1c). We defined valuable
partners as those that were grooming or play partners. Given that this is a captive group living in close quarters,
proximity relationships may not accurately reflect relationship quality. Due to the low occurrence of grooming (9 of
the 44 PC adult-immature dyads groomed at some point but at low rates), we labelled any adult with whom an
immature exchanged grooming as a grooming partner. As play is one of the most important social interactions for
immatures to contact other group members we incorporated play behaviour. Thirty-two of the 44 immature-adult
PC dyads played with each other at some point. We therefore defined valuable play partners as those that played
above an individual’s mean and non-valuable play partners as those that never groomed or played above an
individual’s mean.

We tested the most commonly used reconciliatory behaviours to see whether they were more likely to
occur in the PC than the MC. To assess whether grooming or play were used preferentially as reconciliatory
behaviour by immatures, we compared the proportions of first PC contacts that were play with those that were
grooming (Hypothesis 1d).

We investigated the occurrence of unsolicited and solicited third party affiliative contact separately
(Hypothesis 2a). For unsolicited contact we identified where each immature acted as a third party initiating PC
affiliative contact with the recipient of aggression and compared this to the occurrence and timing of affiliative

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contact between the same third party and recipient of aggression in the PC. We then labelled PC-MC pairs as:

- attracted, if contact occurred only in the PC or earlier in the PC than in the MC; dispersed, if it occurred only in
- the MC or earlier in the MC than in the PC; and neutral, if there was no affiliative interaction in either the PC or
- the MC, or it occurred at the same time in both. We then tested for a difference between the proportion of
- attracted and dispersed pairs to determine the occurrence of third party PC affiliation. Solicited third party PC
- affiliative contact occurred too rarely to be analysed. For comparison with previous analyses, we calculated
- individual triadic conciliatory tendency (Call et al 2002) for each immature as a measure of third party post-
- conflict affiliation received: 100*([number of attracted pairs – number of dispersed pairs]/ total PC-MC pairs).

Triadic conciliatory tendency is an index that is calculated for individual victims and reflects contact received or
- solicited. Thus to examine third party affiliative contact offered by immatures we present the mean frequency of
- contact given by immature third parties and give the proportions offered to adult and immature victims. We
- compared the latency to first affiliative contact between the victim and third party in PC-MC observations in a five
- minute time window. To investigate whether corrected conciliatory tendency and triadic conciliatory tendency co-
- occurred, we used a Pearson correlation to test for a relationship (Hypothesis 2b).

Results

Following the PC-MC method, we found the proportion of attracted pairs (0.43±0.07) was significantly
- higher than the proportion of dispersed pairs (0.12±0.03, t=8.2, p<0.001), indicating that the majority of affiliative
- contacts between the opponents occurred earlier in the PC than in the MC and demonstrating the occurrence of
- reconciliation (Hypothesis 1a). Former opponents were more likely to make affiliative contact in the first minute of
- observation (Fig. 1). Overall, the mean group corrected conciliatory tendency for the immature chimpanzees was
- 31.4% ±4.3 (Table 3). When we selected only conflicts between immatures (n=61) we found that the proportion of
- attracted pairs (0.53±0.12) remained higher than the proportion of dispersed pairs (0.18±0.05, t= 4.89, p=0.008),
- demonstrating the occurrence of reconciliation between immatures. Likewise for conflicts between immatures and
- adults (n=108), the proportion of attracted pairs (0.33±0.09) was higher than the proportion of dispersed pairs
- (0.07±0.06, t=8.33, p<0.001).

Within the 70 attracted pairs, affiliative contact was initiated by immatures in 63 PCs and by adults in
- only seven PCs. Excluding the adult-initiated contacts, the proportion of attracted pairs (0.27±0.15) remained
- higher than the proportion of dispersed pairs (0.07±0.06, t=3.12, p=0.036). The mean individual corrected
- conciliatory tendency for immature-immature conflicts (36%±13.8) did not differ from that for immature-adult
- conflicts (26%±3.9, t=1.02, p=0.4, Hypothesis 1b). Neither did we find any difference in mean individual corrected
conciliatory tendencies with valuable partners (39%±22.5) and non-valuable partners (24%±18.3, t=2.0, p=0.19) as only three (Dona and Carlos, the youngest and Eric, the oldest) immatures had higher corrected conciliatory tendencies for valuable than non-valuable partners.

Fig. 1 The frequency of first affiliative contact between former chimpanzee opponents during each minute of the post-conflict (PC) and matched control (MC) observations collected at Chester Zoo, U.K. from September 2008 – November 2009.

Table 3 Individual corrected conciliatory tendencies (CCT), triadic contact tendencies (TCT) for each immature chimpanzee over the course of PC data collection at Chester Zoo, U.K. from September 2008 – November 2009.

<table>
<thead>
<tr>
<th>Immature</th>
<th>CCT (%)</th>
<th>TCT (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dona</td>
<td>26.3</td>
<td>10.5</td>
</tr>
<tr>
<td>Carlos</td>
<td>25.4</td>
<td>11.3</td>
</tr>
<tr>
<td>Dido</td>
<td>46.2</td>
<td>7.7</td>
</tr>
<tr>
<td>Frankie</td>
<td>28.9</td>
<td>8.7</td>
</tr>
<tr>
<td>Eric</td>
<td>30</td>
<td>11.5</td>
</tr>
<tr>
<td>Mean(±SD)</td>
<td>31.4 ±8.5</td>
<td>10.0 ±1.7</td>
</tr>
</tbody>
</table>

The most frequently occurring reconciliatory behaviours were social play (37%), arm’s length proximity (30%), and sit in contact including embrace (24%). Play was significantly more likely to occur after a conflict compared to the control period (play: t=4.5, p<0.02), however, proximity (t = 1.6, p>0.1) and sit in contact including embrace (t = 2.1, p>0.1) were not more likely to occur relative to the control. Other behaviours used for reconciliation were grooming (6%), that occurred much less frequently, and kissing, that only occurred twice (3%). The first case of kissing was after aggression between Carlos and an adult male, Carlos approached the adult and both kissed. In the second case, Eric kissed Dido after he had hit her hard. Immature chimpanzees
were significantly more likely to use play rather than grooming as a reconciliatory behaviour, supporting our prediction for Hypothesis 1d \( t = 5.87, p = 0.004 \).

Considering third party post-conflict contact, the proportion of attracted pairs \((0.1±0.06)\) was significantly higher than the proportion of dispersed pairs \((0.0±0.0)\) demonstrating the occurrence of third party post-conflict affiliation \( t = 3.8, p<0.02 \), Hypothesis 2a. All immatures offered this behaviour with the exception of one female immature \((\text{mean}±\text{SD frequency given by immatures was } 3.8±1.3)\). Only immature victims were the recipients of third party post-conflict affiliation. As victims of aggression, all immatures received post-conflict affiliation from bystanders and the mean triadic conciliatory tendency for the immatures was 10\% (Table 3). The temporal distribution of the frequency of first affiliative contacts from immature third parties to the recipients of aggression showed that all contacts occurred during the first minute of the PC (Figure 2). Solicited third party post-conflict affiliation occurred too rarely to be analysed (two cases).

When we tested for an association between triadic conciliatory tendency and corrected conciliatory tendency (Hypothesis 2b) we found no significant association \( r = -0.27, p=0.9 \).

Fig. 2. Frequency of first affiliative contact by immature third party to a recipient of aggression in each minute of the post-conflict (PC) and matched-control (MC) periods collected at Chester Zoo, U.K. from September 2008 – November 2009.
Discussion

We quantitatively demonstrated the occurrence of reconciliation and third party post-conflict affiliation in immature chimpanzees. As sample size was small and included four infants and one older infant who became a juvenile within the study period, our findings should be interpreted with caution and await replication, nonetheless, the presence of these behaviours suggests that by the end of infancy and beginning of juvenility (5-6 years) chimpanzees have acquired post-conflict social skills commonly reported in adults (e.g. Fraser et al 2010; Preston & de Waal 2002). We did not find evidence for solicited third party post-conflict affiliation.

We found that immature chimpanzees were capable of reconciling their conflicts (corrected conciliatory tendency = 31.4%) and they did so at a comparable, although lower level to that reported for adults in the same group (corrected conciliatory tendency = 47.5%) around 18 months before our study (Fraser et al 2008). Although variable, lower corrected conciliatory tendencies have often been reported for wild (14.4-21.6%) chimpanzees (Arnold & Whiten 2001, Kutsukake & Castles, 2004, Wittig & Boesch, 2005) than for captive (21.6 – 41.2%) chimpanzees (Fraser et al 2008; Koski et al 2007a; Preuschoft et al., 2002; but see Fuentes et al., 2002 and Webb et al 2014). A higher conciliatory behaviour has been associated with particularly tolerant populations (de Waal & Roosmalen, 1979).

Post-conflict reconciliation has several functions such as reducing levels of post-conflict anxiety (e.g. Aureli & van Schaik, 1991), and restoring tolerance levels and valuable social relationships damaged by the aggressive conflict (de Waal & Aureli 1997). Our results do not address which of these functions reconciliation fulfils in immatures, for example, we did not collect any measures of post-conflict anxiety. In contrast to the finding that same aged dyads (adult-adult and adolescent-adolescent) were more likely to reconcile than mixed-aged dyads (Webb et al 2014), we did not find any difference in the corrected conciliatory tendencies of immatures with their peers or with adults. Neither did we find an effect of relationship value on immatures conciliatory tendency. This could suggest that immatures had acquired the behaviour of post-conflict affiliation with former opponents but not the selectivity in reconciling with valuable partners, perhaps due to a lack of differentiated relationships at this age. Further research is needed to investigate the functional aspects of reconciliation in immature chimpanzees.

Our study is the first to demonstrate that immature chimpanzees preferentially use social play to reconcile with former opponents. In the study group, adult chimpanzees have been previously reported to most commonly reconcile using grooming behaviour (nearly 40%) with behavioural specificity (de Waal, 1993) demonstrated for kiss and embrace (Fraser and Aureli, 2008). Grooming was used rarely by immature chimpanzees and their preference for play likely reflects their most common form of social interaction with
conspecifics at this age (e.g. Bloomsmith et al 1994; Shimada & Sueur 2014), despite the fact that play
decreases markedly in late infancy (Lonsdorf et al 2014b). Play has also been reported to function in reducing
tension and confrontations during stressful situations in chimpanzees and bonobos (Palagi et al 2005; Paquette
1994) which adds to its suitability as a reconciliatory behaviour. Kissing only occurred twice, suggesting that
these may be adult forms of reconciliatory behaviour that further develop during juvenility and adolescence.
Unfortunately the frequency of embracing could not be determined as it had been combined with sitting in
contact, however, sitting in contact occurred at a much lower rate than play.

Reconciliation merely requires an ability to recognize individuals and remember past interactions, and a
conciliatory disposition (De Waal & Yoshihara 1979). In contrast, consolation is proposed to be cognitively more
demanding as it requires some form of sympathetic concern about another’s state, including attempts to
ameliorate another’s state (de Waal & Aureli 1996, 2002; Preston & de Waal 2002; cf Bolhuis 2015 and
Palagi et al 2006). Our analysis of third party post-conflict affiliation did not include any measure of stress
alleviation in the victim and so we cannot interpret this behaviour as consolation, nonetheless we can compare
the occurrence of the operational definition with other studies. The mean triadic conciliatory tendency for
immatures in our study was 10%, lower than that reported previously for adults: in the same group (29.4%,
Fraser et al 2008); for other captive groups (16.5% and 10.8%, Romero & de Waal 2010; 49.5%, Palagi et al
2006); or in the wild (15.1%, Kustukake & Castles 2004). However, we restricted our data collection to conflicts
involving an immature and did not collect conflicts between adults. This may have biased our analysis to lower
values of triadic conciliatory tendency and restricted to whom immatures offered affiliation. Unlike previous
findings, we did not find that immatures had high rates of third party post-conflict affiliation with both adults and
infants/juveniles (Clay & de Waal 2013a), but found that immatures only offered third party post-conflict affiliation
to other immatures. In another group of captive chimpanzees (Palagi et al 2006), there was no difference in adult-
adult, adult-juvenile, or juvenile-juvenile triadic conciliatory tendencies (juveniles were aged between 6-8 years)
suggesting that third party post-conflict affiliation is fully acquired and expressed after 6 years of age. However,
they did not include an analysis of the functional aspect of consolation.

It is possible that third party post-conflict affiliation in immatures may be functionally different to
consolation in adults. The benefits of ‘true’ consolation are still debated but possible functions include stress
reduction (Fraser et al 2008) and distress alleviation, where contact is more likely between friends than non-
friends (Fraser et al 2008; Romero & de Waal 2010). There are different levels of empathy (de Waal 2008), from
emotional contagion (being affected by another’s emotional or arousal state), to sympathetic concern (appraisal
of another’s situation) and empathic perspective taking. It is possible that consolation in immatures and adults
may reflect these different levels. Given that infant chimpanzees (aged 36-54 months) appear to be capable of
instrumental helping i.e. knowing something about the goal another individual is attempting to achieve as well as the current obstacles to that goal (Warneken & Tomasello 2006), it seems reasonable that they may be capable of recognizing and responding to another's distress (i.e. sympathetic concern).

Future studies should address whether the variation in individual triadic conciliatory tendency (7.7 to 11.5%) reflects stable individual variation or underlying cognitive capacity, ideally by combining experimental and social behavioural data. Consistent individual differences in post-conflict behaviour have been reported for adult and adolescent chimpanzees, where an individual’s conciliatory tendency was associated with social switching behaviour that was indexed by changes or switches in social behavioural state or partner (Webb et al 2014). Further, individual emotion regulation is an important component of social competence (Clay & de Waal 2013b). Juvenile bonobos that were better able to manage their own emotions (faster recovery from self-distress and baseline levels of anxiety-related behaviour) showed greater social competence (number of friendships, amount of sustained play and a composite index of sociality) and were more likely to offer consolation.

Finally, we were interested in whether the expression of reconciliation would be associated with the prevalence of third party post-conflict affiliation. However, we did not find any association between corrected conciliatory tendency and triadic conciliatory tendency across immatures. The lack of any association is difficult to explain, as possible interpretations could relate to our small sample size or point to different, underlying capacities associated with reconciliation, consolation and general sociability.

In summary, our findings provide data on the occurrence of post-conflict behaviour in immature chimpanzees. We found that immatures were able to perform reconciliation however, functional aspects, such as reconciling valuable relationships and post-conflict behavioural specificity, were not fully developed. Immatures performed third party affiliative contact, albeit at lower levels than report in adults. Our findings support the idea that post-conflict skills are refined, gradually, through an extended juvenile period. Further work is needed to explore these post-conflict behaviours in immatures and determine whether the expression of these skills is influenced by individual differences and the emergence of underlying cognitive capacities and if they are functionally different to post-conflict skills found in adults.

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References


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