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Farooqi, S and Koyama, NF (2016) The Occurrence of Postconflict Skills in Captive Immature Chimpanzees (Pan troglodytes). International Journal of Primatology, 37 (2). pp. 185-199. ISSN 1573-8604

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

2

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14

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

16 Running title: Post-conflict Skills in immature chimpanzees

17

18 **Abstract**

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

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

34

35 **Introduction**

36 Living in a group inevitably involves competition for limited resources between conspecifics. Investing in
37 social relationships is one way for animals to increase their competitive ability and/or reduce the costs of
38 competition. Where competition takes the form of aggressive conflict, costs can include risk of injury, increased
39 stress, and potential damage to social relationships (Aureli et al 2002; Aureli & de Waal 2000). Conflict
40 management strategies provide one way to alleviate these negative consequences. They include friendly post-
41 conflict reunion between former opponents, known as reconciliation, and third party post-conflict affiliation
42 between a bystander and victim of aggression, that has been referred to functionally as consolation (de Waal &
43 Roosmalen 1979). Such behavioural strategies are viewed as part of a suite of social skills (Kempes et al 2009)

44 in primates that are learned during a 'socialisation period' in infancy (Bekoff 2001) and develop through a period
45 of extended primate juvenility (de Waal 1989; Goodall 1986; Joffe 1997; Lonsdorf & Ross 2012; Pagel & Harvey
46 1993; Poirier & Smith 1974; Watts & Pusey 2002). For example, the play of orphaned chimpanzee (*Pan*
47 *trogodytes*) juveniles was more likely to result in aggression than the play of mother-reared juveniles,
48 strengthening the idea that social skills are learned in early infancy (Leeuwen *et al* 2014).

49 Since it was first documented in chimpanzees (de Waal & van Roosmalen 1979), studies have
50 documented the occurrence of reconciliation in over 30 primate species (reviewed in Aureli *et al* 2002) across
51 strepsirrhines (Verreaux's sifaka *Propithecus verreauxi*, Palagi *et al* 2008), monkeys (e.g. Bonnet macaques
52 *Macaca radiata*, Cooper *et al* 2007; white-faced capuchins *Cebus capucinus*, Leca *et al* 2002) and apes (e.g.
53 bonobos *Pan paniscus*, Clay & de Waal 2014; mountain gorillas *Gorilla gorilla beringei*, Watts 1995) as well as a
54 few non-primate species such as corvids (e.g. ravens *Corvus corax*, Fraser & Bugnyar 2011), domestic dogs
55 (*Canis familiaris*, Cools *et al* 2008), bottlenose dolphins (*Tursiops truncatus*, Yamamoto *et al* 2015), domestic
56 goats (*Capra hircus*, Schino 1998), horses (*Equus caballus*, Cozzi *et al* 2010), spotted hyenas (*Crocuta crocuta*,
57 Wahaj *et al* 2001), and wolves (*Canis lupus*, Baan *et al* 2014),. Reconciliation has been shown to reduce the
58 likelihood of renewed aggression and post-conflict stress (e.g. Aureli & van Schaik 1991; Cooper *et al.* 2007, Das
59 2000; Koski & Sterck 2007b; Fraser *et al* 2008; Watts *et al* 2000), and restore relationships (Cords 1992; Koyama
60 2001) in particular, relationships that are important to individuals, such as friendships and coalitions (the 'valuable
61 relationship hypothesis': de Waal & Aureli 1997). Much less research has addressed reconciliation by immature
62 primates (long tailed macaques, *Macaca fascicularis*: Cords, 1988, Cords & Aureli, 1993; stumptailed macaques,
63 *M. arctoides* and rhesus macaques, *M. mulatta*: de Waal & Johanowicz 1993; Japanese macaques, *M. fuscata*:
64 Schino *et al* 1998; brown capuchins, *Cebus apella*: Weaver & de Waal, 2000, 2003; bonobos: Clay & de Waal
65 2013a). These studies, mostly in monkeys, have reported that juveniles are able to reconcile their conflicts.
66 Unrelated juvenile long tailed macaques were more likely to reconcile than related pairs (Cords, 1988; Cords &
67 Aureli, 1993) and juvenile females were more likely to reconcile with unrelated adult female opponents than
68 juvenile males (Cords & Aureli 1993). These findings may relate to the value of the relationship with these
69 partners, however, no studies have yet tested the valuable relationship hypothesis in immature primates using
70 measures of affiliation to determine relationship value. Besides reconciliation other conflict management
71 mechanisms can co-occur, for example, victims of aggression can receive solicited or unsolicited friendly contact
72 from a third party or bystander not involved in the conflict (Verbeek & de Waal 1997). Such contact potentially
73 functions as consolation (de Waal & Aureli 1996; Fraser *et al* 2008) and has been reported for great apes (e.g.
74 Clay & de Waal 2013a,b; Cordoni & Palagi 2007; Fraser & Aureli 2008). However, reports for monkeys have
75 been variable as studies have reported an absence of third party post-conflict affiliation in some macaque
76 species (de Waal & Aureli 1996), an absence of functional consolation in stumptailed macaques (Call *et al* 2002)

77 and mandrills (Schino & Marini 2012) but the occurrence of consolation (distress alleviation and preferential
78 direction towards friends) in Tonkean macaques *M. tonkeana* (Palagi et al 2014).

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

91 Determining which post-conflict skills chimpanzees have acquired by the beginning of juvenility is
92 important to understand the process of social skill acquisition. We investigated post-conflict behaviour in
93 immature chimpanzees and excluded mothers as social partners in our analyses as we were interested in the
94 occurrence of post-conflict behaviour as a means to contact other group members. We hypothesise that
95 reconciliation occurs in immature chimpanzees (Hypothesis 1a). Given the extended period of juvenility for the
96 development of social skills in chimpanzees, we predict that immature chimpanzees (up to 7 years) will not have
97 acquired conciliatory tendencies comparable to those previously reported for adults. As the immatures were likely
98 to have established play relationships with other immatures in the group, the greater compatibility or accessibility
99 (Cords & Aureli 2000) with immature opponents should facilitate post-conflict affiliation. Thus, opponent's age
100 (immature/adult) category should affect conciliatory tendency (Hypothesis 1b). Further, if reconciliation functions
101 to repair bonds that have been strained during the previous conflict, it should be most predictable among
102 individuals that have a valuable relationship (de Waal & Aureli, 1997; de Waal & Yoshihara, 1983; Kappeler &
103 van Schaik, 1992). We, therefore, examined whether relationship quality affects conciliatory tendency
104 (Hypothesis 1c). The first affiliative post-conflict contact can take many forms in adult chimpanzees, for example
105 mouth-to-mouth kiss, sitting in contact or brief touch, with one of the most common being grooming (Arnold &
106 Whiten 2001; de Waal & van Roosmalen 1979). Indeed, in a previous report on the adults in our study group, the
107 most commonly occurring reconciliatory behaviour was grooming (Fraser & Aureli 2008). However, grooming is
108 used less frequently by infants and juveniles to contact group members other than their mother/siblings (Goodall

109 1986, Nishida 1988). Young chimpanzees are more likely to use play behaviour to acquire a central position in
110 the group from which they can form affiliative relationships (Shimada & Sueur 2014). Play, rather than grooming,
111 was also used by young chimpanzees to contact other group members during a period of greater tension (Palagi
112 *et al* 2004). We therefore hypothesised that immatures would use specific behaviours to reconcile (Hypothesis
113 1d) and predict that immature chimpanzees will use social play rather than grooming to reconcile with former
114 opponents.

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

120

121 **Methods**

122 **Subjects and Housing**

123 The group of chimpanzees housed in Chester Zoo, UK, comprised 29 related and unrelated individuals (five adult
124 and one adolescent male, 18 adult females, five infants/juveniles). Goodall (1986) defined infancy as less than 5
125 years and the juvenile period from 5-7 years although recent studies have grouped immatures as individuals
126 younger than 12 years (e.g. Markham *et al* 2015). At the start of our study, four immatures were infants less than
127 5 years old and one was a juvenile. By the end of our study, two of the infants were 60 months and entering
128 juvenility. For simplicity, we refer to the focal subjects as immatures (Table 1) throughout. They were all born and
129 reared by their mothers in the zoo. Four of the immatures had relatives in the group, excluding their mothers,
130 totalling seven dyads (relatedness coefficient $r = 0.25$ for two dyads and 0.125 for five dyads). Relatives were all
131 adults. Group composition did not change during the study period with the exception of the birth of a female infant
132 Tina in February 2009 and the death of a female infant Rhiannon in June 2008. All interactions with Rhiannon
133 were excluded from the dataset.

134 The chimpanzee enclosure at Chester Zoo consisted of an outdoor grassed island, approximately 2000 m²,
135 separated from the public by a three metre moat and a 143 m² dome shaped indoor enclosure. The outdoor
136 enclosure was enriched with trees, shrubs, rocks, logs, hammocks, and climbing structures. The indoor area had
137 a 9m high iron frame with platforms, ropes and nets strung from the frame and walls. The chimpanzees were fed

138 two to three times a day and had *ad libitum* access to water both inside and outside. The observer was able to
139 move easily between the two enclosures to maintain visibility of the subjects.

140 Table 1. The sex and age range (months) from the start to the end of the study (September 2008 – November
141 2009) of the five immature chimpanzees in Chester Zoo, UK.

142

Subjects	Sex	Age Range (months)
Dona	F	40-55
Carlos	M	42-57
Dido	F	45-60
Frankie	F	45-60
Eric	M	63-78

143

144

145 Data Collection

146 S. Farooqi collected all data over 15 months (September 2008 – November 2009) recording the time
147 (secs) immatures engaged in play and grooming during 15- minute continuous focal animal samples (Altmann,
148 1974) using Observer 5.0 (XT Noldus). We ensured focal samples were selected in random order and for
149 approximately equal amounts of time and collected a total of 706 focal samples (mean \pm SD = 141.2 \pm 2.9).
150 Following de Waal & Yoshihara (1983), we recorded aggressive conflicts, noting the identities of the victim (the
151 individual who first received aggression) and the main aggressor (the individual who attacked with the most
152 intense aggression). We began a 5-minute post-conflict (PC) observation immediately after the conflict ended,
153 noting the time/date and continuously recorded all social interactions using a dictaphone: proximity; kiss; play;
154 grooming received; grooming given; mutual grooming; and sitting in contact (Table 2). If the conflict was renewed
155 within two minutes of the start of the PC we abandoned the observation and restarted once the renewed conflict
156 ceased. If the second conflict was more aggressive, we recorded the PC after this and ignored the initial conflict.

157 We recorded a matched-control (MC) observation the following, or next possible, day at the same time
158 and under similar conditions i.e. when opponents were visible to each other (Koski et al 2007a) but when there
159 had been no agonistic interaction between opponents for at least 15 minutes. If these conditions were not met,
160 we postponed the MC until the next day or up to a maximum of one week. If we could not obtain a matched
161 control within one week, we discarded the corresponding PC.

162 Table 2. Definitions of the behavioural categories for the chimpanzees at Chester Zoo, UK from September 2008
 163 – November 2009.

Behaviours	Definition
Groom given	Picking through and/or slow brushing aside of the fur of another individual with one or more hands.
Groom receive	Another individual(s) picks through and/or slowly brushes aside the fur of the focal individual with one or more hands,
Groom mutual	Two chimpanzees pick through and/or slowly brush aside the fur of each other simultaneously.
Sitting in contact	Huddling with another individual or with a significant portion of body contact. Includes embraces with open arms.
Proximity	The focal animal is within an arm's length from another animal or animals, no touching of body parts.
Aggression	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.
Play	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.
Kiss	Mouth-to-mouth contact

164 We also applied the PC-MC method to record third party affiliative contact (e.g. Call *et al*, 2002) from
 165 these conflicts involving at least one immature. We considered contact when an immature third party initiated
 166 affiliative contact with a recipient of aggression (also known as true consolation: Verbeek & de Waal, 1997).
 167 Third party affiliative contact was considered 'solicited' (Verbeek & de Waal, 1997) when the recipient
 168 approached or stretched a hand towards the third party prior to the interaction (Fraser & Aureli, 2008).

169

170 Data Analysis

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

178 We collected a total of 176 PC observations, excluding conflicts with mothers, of which seven were
 179 discarded because no matched-controls were obtained within the following seven days. A mean number of
 180 33.8 ± 18.3 PC-MC pairs per focal subject were recorded from 61 conflicts between immatures and 108 conflicts
 181 between immatures and adults. Each PC-MC pair was labelled: attracted, if the first affiliative interaction between
 182 opponents occurred earlier, or only in the PC relative to the MC; dispersed, if it occurred earlier or only in the MC;

183 and neutral, if there was no affiliative interaction between the opponents in either observation or if it occurred at
184 the same time in both the PC and the MC. To test whether immatures reconciled their conflicts (Hypothesis 1a),
185 we compared the proportion of attracted and dispersed pairs (Fraser & Aureli, 2008). We tested this for all PC-
186 MC pairs and then separated conflicts between immatures and those between immatures and adults to test
187 whether immatures reconciled conflicts amongst themselves, as well as those with adults. In order to test
188 whether the occurrence of reconciliation was not due to one or two immatures, we calculated the corrected
189 conciliatory tendency that controls for baseline levels of affiliation (Veneema et al, 1994) for each individual as
190 $100 * ([\text{number of attracted pairs} - \text{number of dispersed pairs}] / \text{total PC-MC pairs})$. We then tested for a difference
191 between individuals' corrected conciliatory tendency with other immatures and with adults (Hypothesis 1b).

192 We used the adult-immature conflicts only (n=108) and excluded the adult-initiated reconciliations
193 (n=101) to test the effects of kinship and valuable relationships on corrected conciliatory tendencies (Hypothesis
194 1c). As there were only four PC-MC pairs for two kin dyads we could not compare corrected conciliatory
195 tendencies between kin and nonkin. In order to test the valuable relationship hypothesis, we excluded PCs
196 between kin (n=97, mean±SD number of PCs per immature = 19.4±11.8 and mean number of opponents per
197 immature = 9 ±3.8) and for immatures, compared the corrected conciliatory tendency with their valuable partners
198 to the corrected conciliatory tendency with their non-valuable partners (Hypothesis 1c). We defined valuable
199 partners as those that were grooming or play partners. Given that this is a captive group living in close quarters,
200 proximity relationships may not accurately reflect relationship quality. Due to the low occurrence of grooming (9 of
201 the 44 PC adult-immature dyads groomed at some point but at low rates), we labelled any adult with whom an
202 immature exchanged grooming as a grooming partner. As play is one of the most important social interactions for
203 immatures to contact other group members we incorporated play behaviour. Thirty-two of the 44 immature-adult
204 PC dyads played with each other at some point. We therefore defined valuable play partners as those that played
205 above an individual's mean and non-valuable play partners as those that never groomed or played above an
206 individual's mean.

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

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

214 contact between the same third party and recipient of aggression in the MC. We then labelled PC-MC pairs as:
215 attracted, if contact occurred only in the PC or earlier in the PC than in the MC; dispersed, if it occurred only in
216 the MC or earlier in the MC than in the PC; and neutral, if there was no affiliative interaction in either the PC or
217 the MC, or it occurred at the same time in both. We then tested for a difference between the proportion of
218 attracted and dispersed pairs to determine the occurrence of third party PC affiliation. Solicited third party PC
219 affiliative contact occurred too rarely to be analysed. For comparison with previous analyses, we calculated
220 individual triadic conciliatory tendency (Call et al 2002) for each immature as a measure of third party post-
221 conflict affiliation received: $100 * ([\text{number of attracted pairs} - \text{number of dispersed pairs}] / \text{total PC-MC pairs})$.
222 Triadic conciliatory tendency is an index that is calculated for individual victims and reflects contact received or
223 solicited. Thus to examine third party affiliative contact offered by immatures we present the mean frequency of
224 contact given by immature third parties and give the proportions offered to adult and immature victims. We
225 compared the latency to first affiliative contact between the victim and third party in PC- MC observations in a five
226 minute time window. To investigate whether corrected conciliatory tendency and triadic conciliatory tendency co-
227 occurred, we used a Pearson correlation to test for a relationship (Hypothesis 2b).

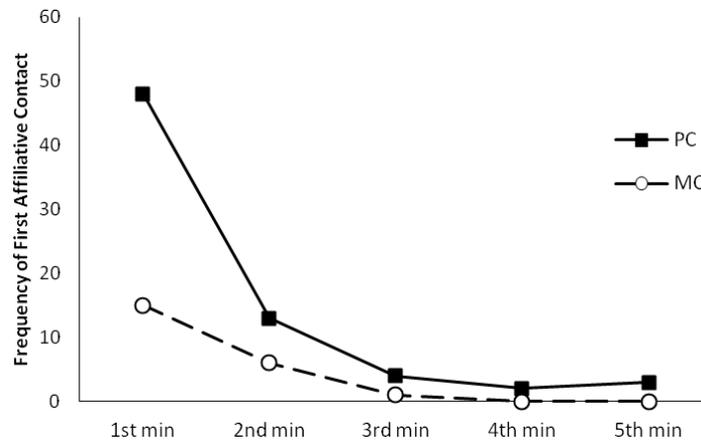
228

229 **Results**

230 Following the PC-MC method, we found the proportion of attracted pairs (0.43 ± 0.07) was significantly
231 higher than the proportion of dispersed pairs (0.12 ± 0.03 , $t=8.2$, $p<0.001$), indicating that the majority of affiliative
232 contacts between the opponents occurred earlier in the PC than in the MC and demonstrating the occurrence of
233 reconciliation (Hypothesis 1a). Former opponents were more likely to make affiliative contact in the first minute of
234 observation (Fig. 1). Overall, the mean group corrected conciliatory tendency for the immature chimpanzees was
235 $31.4\% \pm 4.3$ (Table 3). When we selected only conflicts between immatures ($n=61$) we found that the proportion of
236 attracted pairs (0.53 ± 0.12) remained higher than the proportion of dispersed pairs (0.18 ± 0.05 , $t= 4.89$, $p=0.008$),
237 demonstrating the occurrence of reconciliation between immatures. Likewise for conflicts between immatures and
238 adults ($n=108$), the proportion of attracted pairs (0.33 ± 0.09) was higher than the proportion of dispersed pairs
239 (0.07 ± 0.06 , $t=8.33$, $p<0.001$).

240 Within the 70 attracted pairs, affiliative contact was initiated by immatures in 63 PCs and by adults in
241 only seven PCs. Excluding the adult-initiated contacts, the proportion of attracted pairs (0.27 ± 0.15) remained
242 higher than the proportion of dispersed pairs (0.07 ± 0.06 , $t_4=3.12$, $p=0.036$). The mean individual corrected
243 conciliatory tendency for immature-immature conflicts ($36\% \pm 13.8$) did not differ from that for immature-adult
244 conflicts ($26\% \pm 3.9$, $t=1.02$, $p=0.4$, Hypothesis 1b). Neither did we find any difference in mean individual corrected

245 conciliatory tendencies with valuable partners ($39\% \pm 22.5$) and non-valuable partners ($24\% \pm 18.3$, $t=2.0$, $p=0.19$)
 246 as only three (Dona and Carlos, the youngest and Eric, the oldest) immatures had higher corrected conciliatory
 247 tendencies for valuable than non-valuable partners.



248

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

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

Immatures	CCT (%)	TCT (%)
Dona	26.3	10.5
Carlos	25.4	11.3
Dido	46.2	7.7
Frankie	28.9	8.7
Eric	30	11.5
Mean(\pm SD)	31.4 \pm 8.5	10.0 \pm 1.7

254

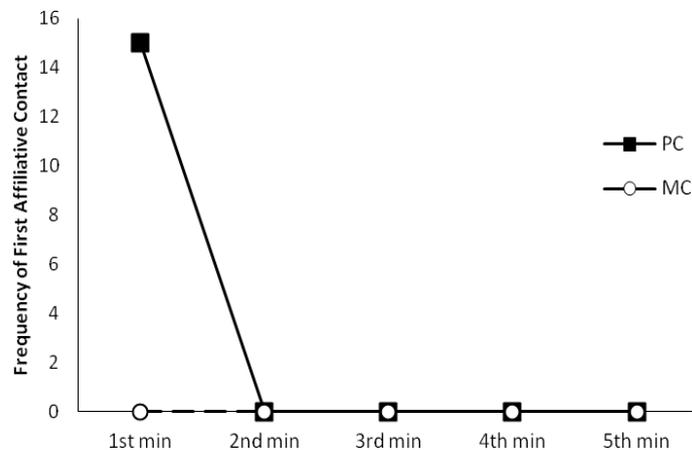
255 The most frequently occurring reconciliatory behaviours were social play (37%), arm's length proximity
 256 (30%), and sit in contact including embrace (24%). Play was significantly more likely to occur after a conflict
 257 compared to the control period (play: $t=4.5$, $p<0.02$), however, proximity ($t = 1.6$, $p>0.1$) and sit in contact
 258 including embrace ($t = 2.1$, $p>0.1$) were not more likely to occur relative to the control. Other behaviours used for
 259 reconciliation were grooming (6%), that occurred much less frequently, and kissing, that only occurred twice
 260 (3%). The first case of kissing was after aggression between Carlos and an adult male, Carlos approached the
 261 adult and both kissed. In the second case, Eric kissed Dido after he had hit her hard. Immature chimpanzees

262 were significantly more likely to use play rather than grooming as a reconciliatory behaviour, supporting our
263 prediction for Hypothesis 1d ($t = 5.87, p = 0.004$).

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

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

275



276

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

280

281

282 **Discussion**

283 We quantitatively demonstrated the occurrence of reconciliation and third party post-conflict affiliation in
284 immature chimpanzees. As sample size was small and included four infants and one older infant who became a
285 juvenile within the study period, our findings should be interpreted with caution and await replication,
286 nonetheless, the presence of these behaviours suggests that by the end of infancy and beginning of juvenility (5-
287 6 years) chimpanzees have acquired post-conflict social skills commonly reported in adults (e.g. Fraser et al
288 2010; Preston & de Waal 2002). We did not find evidence for solicited third party post-conflict affiliation.

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

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

308 Our study is the first to demonstrate that immature chimpanzees preferentially use social play to
309 reconcile with former opponents. In the study group, adult chimpanzees have been previously reported to most
310 commonly reconcile using grooming behaviour (nearly 40%) with behavioural specificity (de Waal, 1993)
311 demonstrated for kiss and embrace (Fraser and Aureli, 2008). Grooming was used rarely by immature
312 chimpanzees and their preference for play likely reflects their most common form of social interaction with

313 conspecifics at this age (e.g. Bloomsmith et al 1994; Shimada & Sueur 2014), despite the fact that play
314 decreases markedly in late infancy (Lonsdorf et al 2014b). Play has also been reported to function in reducing
315 tension and confrontations during stressful situations in chimpanzees and bonobos (Palagi et al 2005; Paquette
316 1994) which adds to its suitability as a reconciliatory behaviour. Kissing only occurred twice, suggesting that
317 these may be adult forms of reconciliatory behaviour that further develop during juvenility and adolescence.
318 Unfortunately the frequency of embracing could not be determined as it had been combined with sitting in
319 contact, however, sitting in contact occurred at a much lower rate than play.

320 Reconciliation merely requires an ability to recognize individuals and remember past interactions, and a
321 conciliatory disposition (De Waal & Yoshihara 1979). In contrast, consolation is proposed to be cognitively more
322 demanding as it requires some form of sympathetic concern about another's state, including attempts to
323 ameliorate another's state (de Waal & Aureli 1996, 2008; Preston & de Waal 2002; cf Bolhuis 2015 and Puga-
324 Gonzalez et al 2014). Our analysis of third party post-conflict affiliation did not include any measure of stress
325 alleviation in the victim and so we cannot interpret this behaviour as consolation, nonetheless we can compare
326 the occurrence of the operational definition with other studies. The mean triadic conciliatory tendency for
327 immatures in our study was 10%, lower than that reported previously for adults: in the same group (29.4%,
328 Fraser et al 2008); for other captive groups (16.5% and 10.8%, Romero & de Waal 2010; 49.5%, Palagi et al
329 2006); or in the wild (15.1%, Kustukake & Castles 2004). However, we restricted our data collection to conflicts
330 involving an immature and did not collect conflicts between adults. This may have biased our analysis to lower
331 values of triadic conciliatory tendency and restricted to whom immatures offered affiliation. Unlike previous
332 findings, we did not find that immatures had high rates of third party post-conflict affiliation with both adults and
333 infants/juveniles (Clay & de Waal 2013a), but found that immatures only offered third party post-conflict affiliation
334 to other immatures. In another group of captive chimpanzees (Palagi et al 2006), there was no difference in adult-
335 adult, adult-juvenile, or juvenile-juvenile triadic conciliatory tendencies (juveniles were aged between 6-8years)
336 suggesting that third party post-conflict affiliation is fully acquired and expressed after 6 years of age. However,
337 they did not include an analysis of the functional aspect of consolation.

338 It is possible that third party post-conflict affiliation in immatures may be functionally different to
339 consolation in adults. The benefits of 'true' consolation are still debated but possible functions include stress
340 reduction (Fraser et al 2008) and distress alleviation, where contact is more likely between friends than non-
341 friends (Fraser et al 2008; Romero & de Waal 2010). There are different levels of empathy (de Waal 2008), from
342 emotional contagion (being affected by another's emotional or arousal state), to sympathetic concern (appraisal
343 of another's situation) and empathic perspective taking. It is possible that consolation in immatures and adults
344 may reflect these different levels. Given that infant chimpanzees (aged 36-54 months) appear to be capable of

345 instrumental helping i.e. knowing something about the goal another individual is attempting to achieve as well as
346 the current obstacles to that goal (Warneken & Tomasello 2006), it seems reasonable that they may be capable
347 of recognizing and responding to another's distress (i.e. sympathetic concern).

348 Future studies should address whether the variation in individual triadic conciliatory tendency (7.7 to
349 11.5%) reflects stable individual variation or underlying cognitive capacity, ideally by combining experimental and
350 social behavioural data. Consistent individual differences in post-conflict behaviour have been reported for adult
351 and adolescent chimpanzees, where an individual's conciliatory tendency was associated with social switching
352 behaviour that was indexed by changes or switches in social behavioural state or partner (Webb et al 2014).
353 Further, individual emotion regulation is an important component of social competence (Clay & de Waal 2013b).
354 Juvenile bonobos that were better able to manage their own emotions (faster recovery from self-distress and
355 baseline levels of anxiety-related behaviour) showed greater social competence (number of friendships, amount
356 of sustained play and a composite index of sociality) and were more likely to offer consolation.

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

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

370

371 Acknowledgements

372 We thank Chester Zoo for permission to conduct this study and the chimpanzee keepers and Clare Caws for their
373 help. We are grateful to three anonymous reviewers and the Editor for their useful comments that improved the
374 manuscript.

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