

## Immediate and Delayed Benefits of Play Behaviour: New Evidence from Chimpanzees (*Pan troglodytes*)

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### Abstract

Evidence for the anticipation of competition at feeding time has been previously documented in both *Pan* species. Chimpanzees seem to cope with competitive tendency through behavioural mechanisms of tension reduction, and grooming is certainly one of these. Social play and grooming are often matched because they bring animals into close physical contact for long periods, and they have an important role in social cohesion. Our goal was to investigate the occurrence of play behaviour during the pre-feeding period, before a basic maintenance activity is about to take place, in the chimpanzee colony housed in the ZooParc de Beauval (St Aignan sur Cher, France). The group was composed of 10 adults and nine immature individuals. By scan animal sampling (344 h of observation), we recorded play and grooming interactions in all age-class combinations during four different periods (pre-feeding, feeding, post-feeding, control). We found peak levels of grooming interactions among adults during the pre-feeding time. A peak frequency at the pre-feeding time was also found in social play between adults and unrelated immature subjects. This finding suggests that during high tension periods, grooming and play might share similar functions in conflict management. Like grooming, play might have an important role to limit aggression and increase tolerance around food (immediate benefits). Immature animals showed a higher frequency of play in the pre-feeding than in any other condition (feeding, post-feeding, and control). During high excitement periods social play probably represents a safe mechanism for immature subjects to test their personal abilities (self-assessment), the strength/weakness of playmates, and the degree of cooperation/competition with them (social-assessment). In the light of this new evidence, we can assert that play behaviour is far from being a purposeless activity, at least in the chimpanzee colony under study.

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## Introduction

...it's hard to define, but I know it (play) when I see it.... (Dolhinow 1999, p. 234)

The subject of play, probably more than any other aspect of animal behaviour, is open to misinterpretation (Loizos 1967; Hayaki 1985; Enomoto 1990). Many young mammals play, but also some birds and a few reptile species do (i.e. *Varanus komodoensis*, *Alligator mississippiensis*) (Fagen 1981), although we still do not really understand why (Fagen 1981; Smith 1982; Martin & Caro 1985; Thompson 1998). The literature on play abounds with hypotheses and speculations, but the theories proposed are often vaguely defined (Byers & Walker 1995; Thompson 1998). The most generally accepted theory is to consider play behaviour as a mechanism for providing 'physical training' (Smith 1982; Byers & Walker 1995), developing motor and cognitive skills (Loizos 1967; Poirier et al. 1978; Fagen 1981; Martin & Caro 1985; Dolhinow 1999), improving individual fighting abilities, achieving 'social assessment' (Thompson 1998; Pellis & Iwaniuk 1999, 2000), and training for the unexpected (Špinka et al. 2001). However, the function of play is not the same in all the species; furthermore, within a given species play behaviour can be influenced by variables such as age, sex, dominance relationships, context, and habitat (Breuggeman 1978; Poirier et al. 1978; Dolhinow 1999). The theories on play function have often focused on delayed rather than immediate benefits, and this is probably the reason why some aspects of its adaptive significance remain unknown (Fagen 1981; Paquette 1994; Bekoff 2001). For example, although play reaches its highest frequency during the juvenile phase, in many species (like chimpanzees and bonobos) it may continue to be present in adulthood (Loizos 1967; Fagen 1981; Pellis & Iwaniuk 1999, 2000). Therefore, a complete understanding of play needs to take into account the multi-functional aspects of this behaviour and, particularly, its immediate benefits (Breuggeman 1978; Poirier et al. 1978; Martin & Caro 1985).

Play seems to occur only when an animal is free from environmental (heat, cold, presence of predators), physiological (need for food, drink, sleep, or sexual activity), and social stressors (Loizos 1967; Rensch 1973; Fagen 1981; Martin & Caro 1985).

Social play and grooming are often matched because they bring animals into close physical contact for long periods, and they have an important role in social cohesion (Loizos 1967; Van Lawick-Goodall 1968; Merrick 1977; Henzi & Barrett 1999). Grooming seems to maintain social stability because of its functions of tension reduction and appeasement (Merrick 1977; Schino et al. 1988; Aureli et al. 2002). In this paper, tension refers to an animal's internal state deriving from a conflict situation. In the lives of animals, limited resources such as food or mating partners often induce conflict of interest (De Waal 1992; Aureli et al. 2002). However, primate and non-primate species living in stable social units use strategies of conflict management such as communicative displays, dominance relationships, and 'greeting' gestures to

mitigate tension and prevent aggressive escalation (De Waal 1992, 2000; Preuschoft & van Schaik 2000; Aureli et al. 2002; Whitham & Maestripieri 2003).

Koyama & Dunbar (1996) provided evidence for the anticipation of competition at feeding time in *Pan troglodytes*. Chimpanzees seem to cope with competitive tendencies through grooming which appears to serve the function of alleviating the tension that builds up before feeding time (pre-feeding) when competition for food may occur.

As mentioned above, play and grooming share some features. If we assume that they also share the function of tension regulation and prevention of conflicts, we expect to find a higher frequency of play during the pre-feeding period (the context of maximal conflict of interest for captive animals) than during both the post-feeding and control conditions. Moreover, we expect that those dyads playing together and/or grooming during the pre-feeding period will show a high level of co-feeding as well.

## Methods

### The Study Group

We collected behavioural data during a period of 3.5 mo (from Oct. 2000 to Jan. 2001) on the group of *P. troglodytes* housed in the ZooParc de Beauval (St Aignan sur Cher, France). The colony, the largest captive group of chimpanzees in France, was composed of 19 animals (10 adults and nine immature subjects = four juveniles + five infants) (Table 1).

The animals were housed in an enclosure with both an indoor and outdoor facility (about 200 m<sup>2</sup> and 2000 m<sup>2</sup>, respectively). Although the animals spent the whole day in the indoor halls because of low temperatures, the observations took place during the winter to limit the interference of visitors. The indoor facility was composed of two large enclosures (totally visible) equipped with everything necessary for allowing the animals to move freely in all three dimensions. As the two enclosures were placed in a glasshouse, the animals were able to follow the natural day/night 24-h cycle. The group received food at 9.00 AM, 2.00 PM, and 4.30 PM.

### Data Collection

Using scan sampling (Altmann 1974), we recorded the frequency of play (Table 2) and grooming interactions and noted the individual identity of interactants using a 5-min interval between consecutive scans. We scored a total of 4128 scans (corresponding to 344 h). Data were collected 6 d/wk over 14 wk between 8.35 AM and 5.20 PM; the observation sessions lasted 5–6 h/d. In order to investigate whether or not the presence of food affected play and grooming behaviour, we distinguished four different periods by preliminary observations:

Table 1: The *Pan troglodytes* colony in the ZooParc de Beauval (St Aignan sur Cher, France)

Subject	Sex	Class	Date of birth	Original, arrival date
Joseph (JO)	M	Adult	1983, unk birth	Cabosse, 1992
Gamin (GA)	M	Adult	1989, wild	Private, 1992
La Vieille (LA)	F	Adult	1959, captivity	Paris, 1992
Charlotte (CH)	F	Adult	1973, captivity	Paris, 1992
Micheline (MI)	F	Adult	1978, unk birth	Cabosse, 1992
Baraka (BA)	F	Adult	1979, captivity	Copenhagen, 1992
Bonobo (BO)	F	Adult	1982, wild	Private, 1992
Julie (JU)	F	Adult	1982, captivity	Circus, 1992
Gypso (GY)	F	Adult	1987, captivity	Le Pal, 1993
Domi (DO)	F	Adult	1989, captivity, CH's daughter	Paris, 1992
Tsavo (TS)	M	Juvenile	1993, captivity, BA's son	Beauval
Christmas (CR)	F	Juvenile	1993, captivity, JU's daughter	Beauval
Isabelle (IS)	F	Juvenile	1994, captivity, CH's daughter	Beauval
Benji (BE)	M	Juvenile	1994, captivity, BO's son	Beauval
Melie (ME)	F	Infant	1997, captivity, GY's daughter	Beauval
Leo (LE)	M	Infant	1997, captivity, JU's son	Beauval
Makury (MA)	M	Infant	1999, captivity, BO's son	Beauval
Bazou (BZ)	M	Infant	2000, captivity, BA's son	Beauval
Rachel (RA)	F	Infant	2000, captivity, DO's daughter	Beauval

unk birth = the place of birth is unknown.

1. Pre-feeding time (Pre): the last 25 min block before food provisioning;
2. Feeding-time (Feed): the 25 min block starting from food provisioning;
3. Post-feeding time (Post): the 25 min block following feeding time as defined above;
4. Control (C): the time block from 10.00 AM to 12.25 PM, the farthest from feeding-times, when animals showed high activity levels, and a sufficiently long time-span to represent a baseline condition.

The parameter for delimiting the three periods linked to feeding activity was the usual time span necessary for complete food consumption (i.e. 25 min). We were able to monitor two feeding times per day (2.00 PM and 4.30 PM), collecting data on 150 feeding sessions. We also defined co-feeding as the frequency with which a certain dyad sits in contact (i.e. contact sitting) during feeding time, in order to establish if a correlation exists between grooming/play level in the pre-feeding time and co-feeding level in feeding time.

### Statistical Analyses

Friedman's two-way analysis of variance was used to test for differences among the four conditions (pre-feeding, feeding, post-feeding, and control) across each age-class combination. When relatedness was the independent variable, the two males were not included in the analysis as paternity is not known in this

Table 2: Play behavioural patterns recorded during the observation sessions

Play patterns	Definition
Acrobatic play	One (solitary play) or more animals (social play) climb, jump and dangle from supports of the environment (i.e. branches)
Airplane	An adult lies on its back and rises an infant up with its hands and feet
Full play face	Playful facial display: the mouth is opened with the upper and lower teeth exposed
Grab gentle	An animal massages another gently
Play manipulation	An animal manipulates and investigates objects found in the environment
Play bite	An animal gently bites a playmate
Play brusque rush	An animal jumps with its four limbs on a playmate
Play face	Playful facial display: the mouth is opened with only the lower teeth exposed
Play invitation	An animal approaches a possible play partner, pats it and then goes away. This display is used to start a play session
Pirouetting	An animal performs turn somersaults and rolling over either on the ground or on vertical supports
Play	Social or solitary play session that lasts more than 10 s
Play push	An animal pushes a playmate either with its hands or feet
Play recovering a thing	An animal chases a playmate and attempts to grab an object carried by it
Play retrieve	An animal holds a playmate to avoid its flight
Play run	An animal runs alone (solitary play) or chases a play partner (social play)
Play slap	An animal slaps any part of a playmate's body
Play stamping	An animal jumps on a play partner with its feet
Rough and tumble	Two animals (or more) keep grasping, slapping and biting each other. This pattern is typical of immature individuals
Tickle	This display is performed either with the mouth or with the hands

colony. In case of significant difference among the four conditions, we employed the Dunnett multiple comparison test (post-hoc test) to determine what pairs of conditions (Pre vs. Feed, Pre vs. Post, Pre vs. C, Feed vs. Post, Feed vs. C, Post vs. C) were significantly different (Zar 1999).

To analyse the correlation between the frequency of grooming and/or play during the pre-feeding period and the frequency of co-feeding (contact sitting levels during feeding time) we employed Spearman test (Zar 1999). The level of significance was set at 5%, and the probabilities between 5 and 10% were reported as trends. All the analyses were two-tailed. We made use of exact tests according to the threshold values suggested by Mundry & Fischer (1998). Conventional p-values were marked with an asterisk when significant ( $p < 0.05$ ), a double asterisk ( $p < 0.01$ ) and a triple asterisk ( $p < 0.001$ ) when highly significant. Statistical analyses were performed by SPSS 9.05 (SPSS Inc., Chicago, IL, USA).

## Results

### Grooming Interactions

We analysed the distribution of grooming in the four conditions (Pre, Feed, Post, and C) for every possible age/class combination except among immature individuals because of the extremely low frequencies recorded. In the adult/adult combination, we found a significant difference across the four periods (Friedman  $\chi_r^2 = 22.44$ ,  $df = 3$ ,  $p < 0.001$ ). For determining what pairs of conditions differed significantly, we used the post-hoc test obtaining the following results: Pre vs. Feed,  $q = 5.14$ ,  $p < 0.01$ ,  $N = 10$ ; Pre vs. Post,  $q = 4.11$ ,  $p < 0.01$ ,  $N = 10$ ; Pre vs. C,  $q = 4.16$ ,  $p < 0.01$ ,  $N = 10$ ; Feed vs. Post,  $q = 3.16$ ,  $p < 0.01$ ,  $N = 10$ ; Feed vs. C,  $q = 0.32$ , n.s.,  $N = 10$ ; Post vs. C,  $q = 2.46$ ,  $p < 0.05$ ,  $N = 10$  (Fig. 1). There was a positive significant correlation between the frequency of grooming performed by the adult dyads during the pre-feeding period and the frequency of contact sitting during the feeding period (co-feeding) (Spearman correlation:  $r_s = 0.402$ ,  $N = 45$ ,  $p < 0.01$ ).

In the adult/immature individual combination, we did not find any significant difference in the distribution of grooming across the four conditions ( $\chi_r^2 = 5.45$ ,  $df = 3$ , n.s.) (Fig. 2).

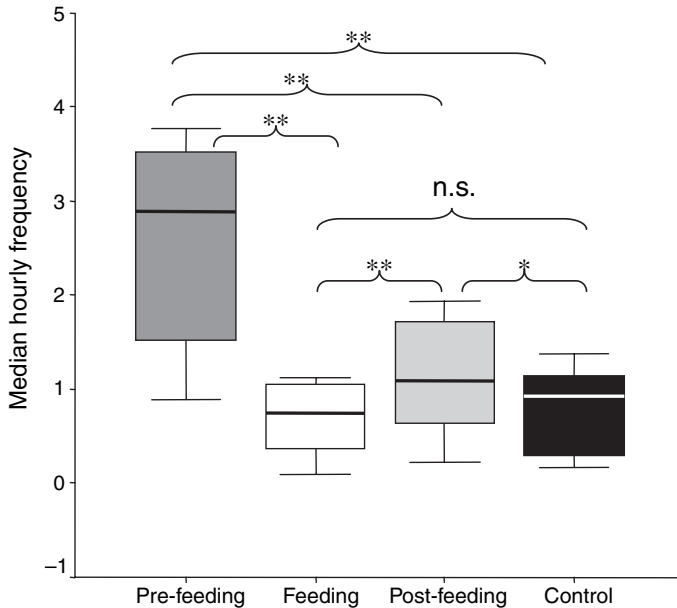


Fig. 1: Grooming distribution in pre-feeding, feeding, post-feeding, and control conditions among the 10 adults. Solid horizontal lines indicate medians; length of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values

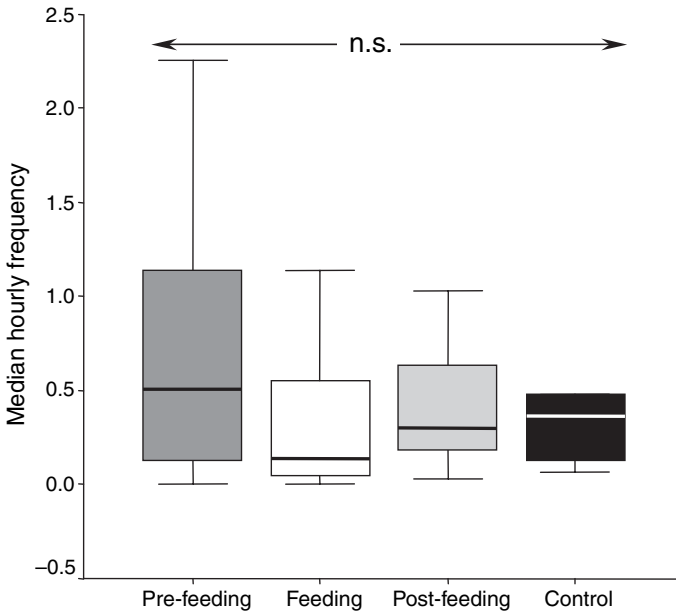


Fig. 2: Grooming distribution across the four conditions between adults and immature individuals. Solid horizontal lines indicate medians; length of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values

### Play Interactions

We analysed play frequencies in pre-feeding, feeding, post-feeding, and control periods for every possible age-class combination except among adults because of the extremely low frequencies recorded.

The overall play frequency that each adult female performed with her own offspring did not differ significantly in the four periods ( $\chi_r^2 = 5.17$ ,  $df = 3$ , n.s., one tailed) (Fig. 3a), whereas that between adult females and unrelated immature individuals did ( $\chi_r^2 = 10.14$ ,  $df = 3$ ,  $p < 0.02$ ). Pairwise comparisons revealed several significant differences: Pre vs. Feed,  $q = 3.01$ ,  $p < 0.05$ ,  $N = 8$ ; Pre vs. Post,  $q = 1.97$ ,  $p < 0.05$ ,  $N = 8$ ; Pre vs. C,  $q = 2.3$ ,  $p < 0.05$ ,  $N = 8$ ; Feed vs. Post,  $q = 2.5$ ,  $p < 0.05$ ,  $N = 8$ ; Feed vs. C,  $q = 2.29$ ,  $p < 0.05$ ,  $N = 8$ ; Post vs. C,  $q = 1.24$ , n.s.,  $N = 8$  (Fig. 3b). There was a significant positive correlation between the frequency of play between adults and unrelated immature individuals during the pre-feeding period and the frequency of contact sitting (co-feeding) during the feeding period by these adults and other adults related to the immature playmates of the pre-feeding period ( $r_s = 0.518$ ,  $N = 34$ ,  $p < 0.01$ ).

Among related immature individuals, there were no significant differences across the four periods with regard to play ( $\chi_r^2 = 4.4$ ,  $df = 3$ , n.s.) (Fig. 4a), but there was a significant difference in play distribution among unrelated immature animals ( $\chi_r^2 = 12.3$ ,  $df = 3$ ,  $p < 0.01$ ). Post-hoc analysis revealed two significant

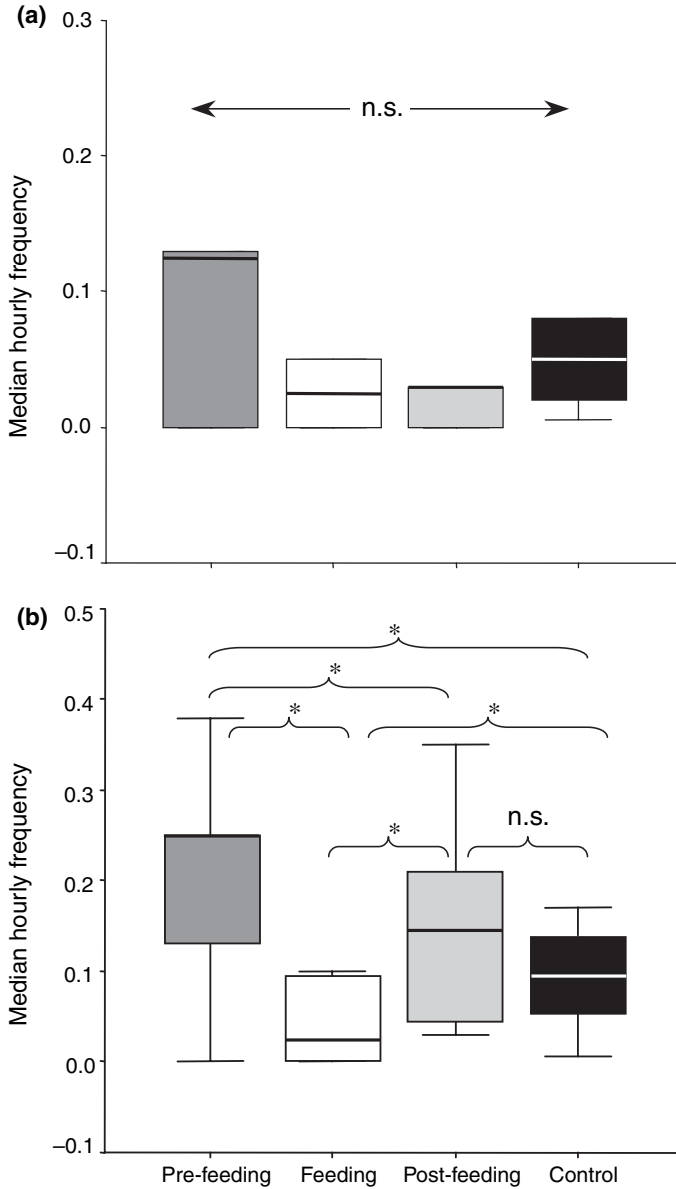


Fig. 3: Play distribution across the four conditions between adults and their immature relatives (a) and between adults and unrelated immature individuals (b). Solid horizontal lines indicate medians; length of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values

differences: Pre vs. Feed,  $q = 4.24$ ,  $p < 0.01$ ,  $N = 9$ ; Pre vs. Post,  $q = 1.89$ , n.s.,  $N = 9$ ; Pre vs. C,  $q = 2.36$ ,  $p < 0.05$ ,  $N = 9$ ; Feed vs. Post,  $q = 1.89$ , n.s.,  $N = 9$ ; Feed vs. C,  $q = 1.89$ , n.s.,  $N = 9$ ; Post vs. C,  $q = 0.45$ , n.s.,  $N = 9$  (Fig. 4b). For



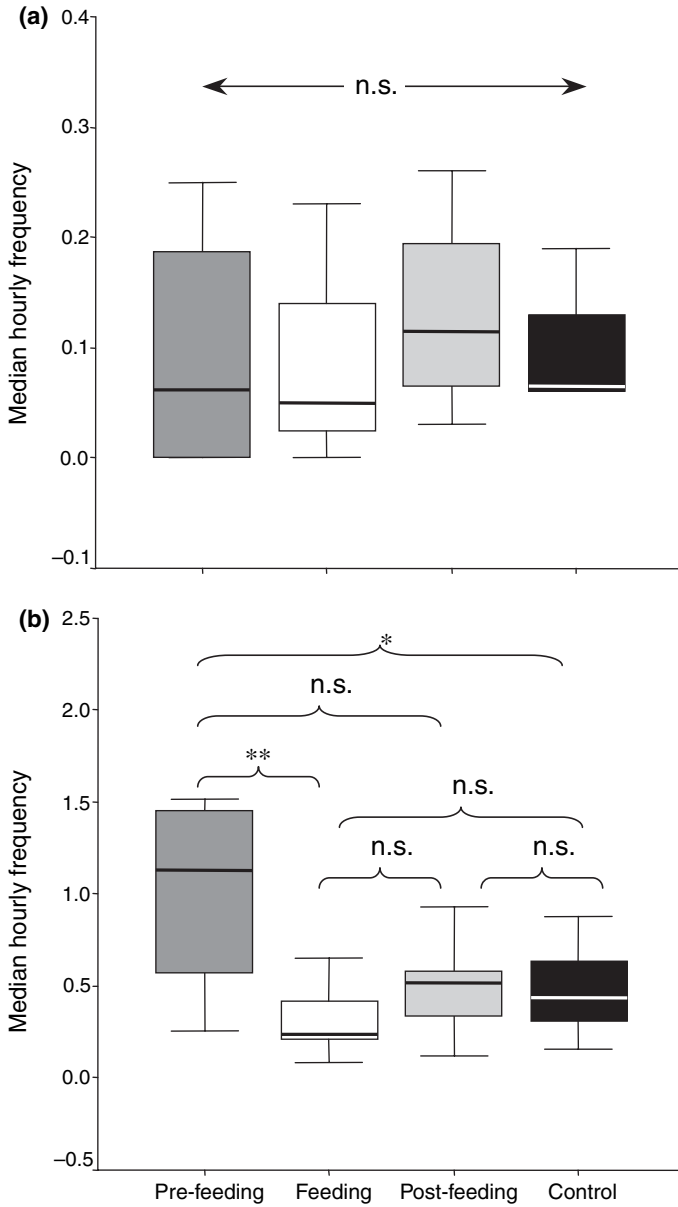


Fig. 4: Play distribution across the four conditions among related immature individuals (a) and among unrelated immature individuals (b). Solid horizontal lines indicate medians; length of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values

immature dyads, there was no significant correlation between the frequency of play performed during the pre-feeding period and the frequency of co-feeding ( $r_s = 0.199$ ,  $N = 23$ , n.s.).

## Discussion

Grooming provides an immediate benefit as it removes ecto-parasites and stimulates the release of  $\beta$ -endorphins (Henzi & Barrett 1999). In many non-human primates, allogrooming may also help animals to establish and reinforce familiarity among the members of a group (Henzi & Barrett 1999; Watts 2000a,b). Grooming is the social activity most frequently used to evaluate the level of affiliation between pairs of individuals, and the time spent on this activity by social partners is used to gauge the strength of the relationship and assess the likelihood of coalitionary support (Walters & Seyfarth 1987; Muroyama & Sugiyama 1994). Many authors have defined grooming as an 'interchange currency' when it is used to increase the level of tolerance among dominant and subordinate animals (e.g. reducing aggression level or increasing access to limited resources) (Seyfarth 1976, 1977; De Waal 1982; Dunbar 1984, 1988; Goodall 1986). Primate social groups might be considered as 'biological markets', in which individuals trade 'commodities' (Henzi & Barrett 1999). Grooming might play an important role in tension reduction and might help conspecifics to maintain social stability during period of high excitement (Merrick 1977; Schino et al. 1988; Aureli et al. 2002).

In our study, we found that the frequency of grooming among adults increased significantly in the pre-feeding period (Fig. 1), a context in which 'conflict of interest' reaches peak levels (De Waal 1992; Aureli et al. 2002). This result agrees with findings by Koyama & Dunbar (1996). These authors found that captive chimpanzees seem to anticipate the occurrence of conflicts during feeding by grooming more beforehand. Moreover, the effect was more marked when food was clumped than when it was dispersed. The positive correlation we found between grooming (pre-feeding) and contact sitting (feeding) by adult dyads might indicate that this anticipatory grooming increases the level of tolerance around the food, even if it is also plausible that this correlation is an independent consequence of other variable(s) that favour friendly social relationships, so that dyads that groom together a lot also feed together in contact a lot. Animals seem to cope with competitive tendencies through mechanisms of tension reduction, and grooming is certainly one of these, at least in chimpanzees. It may be used to prevent aggressive escalation of conflicts (Loizos 1967; De Waal 1997; Aureli et al. 2002). Among adult chimpanzees, grooming seems to be one of the main strategies used in 'conflict management'; they probably use this behaviour to preserve or to set good or valuable social relationships with a particular member of the group (Preuschoft et al. 2002).

The extremely low frequency of grooming recorded among immature animals suggests that grooming is probably not used to reduce tension at this stage of life. Between adults and immature animals, grooming distribution did not differ significantly across all the four conditions indicating that it does not have a role in regulating pre-feeding tension (Fig. 2). However, the risk of aggression during high excitement periods (i.e. pre-feeding) involves all the members of the group. For instance, if a conflict occurs between a juvenile and an adult female, the

consequences might be harmful to both of them. Our findings show that if an adult chimpanzee interacts with an immature subject, a different behavioural strategy in 'conflict management' may be used as a substitute for grooming. As play is the main activity during the immature phase and '...may be a unique category of behaviour in that asymmetries are tolerated...' (Bekoff 2001, p. 88), adults might employ this behaviour as a tension-reduction mechanism when they interact with immature individuals during high tension situations.

Many authors have suggested that play is often suppressed by stress (Loizos 1967; Rensch 1973; Fagen 1981; Martin & Caro 1985). For example, De Oliveira et al. (2003) found that both in wild and in food supplemented troops of golden lion tamarins, social play usually occurs after foraging. This is the opposite to our findings whereby between unrelated chimpanzees, play peaks during the pre-feeding periods. In wild bonobos, Enomoto (1990) observed a play bout between an adult male and an older female occurring when the two animals were aggressively competing over food. A possible function for play might be to protect the members of a social group from escalating such competitive interactions.

Between adults and unrelated immature subjects play occurred significantly more frequently in pre-feeding than in control condition. Based on this finding, we may suggest that play represents a good indirect 'contact point' between adults. The positive correlation found between the frequency of adult-unrelated immature play (pre-feeding) and contact sitting rates (feeding) between the adult involved in these play sessions and adults related to the immature playmate (i.e. co-feeding) might support this hypothesis. However, as for the grooming/co-feeding correlation, a long-term influence of other variables on both play and co-feeding can not be excluded.

The benefits of this adult play strategy in the pre-feeding condition might be found both at immediate and delayed levels. At an immediate level such play could reduce tension around food resources, thus permitting more relaxed feeding or discouraging possible attacks by adult relatives of the immature playmates (Savage & Malick 1977; Kuester & Paul 2000). At a more delayed level, such play could assess the strength of social bonds between adult players and adults related to immature playmates. Bekoff (2001, p. 82) stated that 'animals often have social expectations when they engage in various sorts of social encounters the violation of which constitutes being treated unfairly because of a lapse in social etiquette'. In the light of this statement, 'playing fairly' (Dugatkin & Bekoff 2003) with an unrelated immature subject could be a means to exchange information about the degree of fairness and cooperation in relationships between an adult player and a relative of that immature individual (honest communication).

In chimpanzees, the juvenile phase is a period of rapid and profound changes involving physical, hormonal, and behavioural processes, and play has certainly a particular function during this crucial transitional stage (Kraemer et al. 1982; Paquette 1994). In our research, among related immature animals play distribution did not show any significant variation across conditions (Fig. 4a) whereas among unrelated playmates playful behaviour occurred more frequently in the pre-feeding than in two of the other three conditions (Fig. 4b). In this perspective,

we can hypothesize that play might also be used by unrelated youngsters to reduce tension and prevent the escalation of conflict in high excitement contexts (immediate benefits), even if it does not promote co-feeding.

Moreover, as mentioned above, the juvenile period is crucial for acquiring social role and hierarchical *status* as well as developing physical skills. Play is also a safe mechanism for testing personal (self-assessment) and partner's abilities (social assessment) (Loizos 1967; Poirier et al. 1978; Paquette 1994; Thompson 1998). In the light of our findings, this might be most effective during periods of high social tension such as the pre-feeding time (probable delayed benefits).

In conclusion, our data suggest that play could be used in anticipation of the forthcoming stress associated with feeding. This is particularly interesting given the commonly held view that play is suppressed by stress – here it would appear that play is regulating stress.

In this perspective, play might provide immediate and, probably, delayed benefits for playmates by: (i) reducing the risk of aggression and increasing tolerance around food in a context of high conflict of interest; (ii) representing a safe mechanism for testing personal abilities (self-assessment), the strength/weakness of playmates and the degree of cooperation/competition among them (social assessment).

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