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Play at work: revisiting data focusing on chimpanzees (*Pan troglodytes*)

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Summary - *In this article I combine old and new data to provide an up to date contribution on social play in primates and, particularly, in chimpanzees* (Pan troglodytes)*. Play behaviour is an ontogenetic trait in many mammalian species and is widely believed to have an important role in the assembly of adult behaviour. However, play may be at work also during some peculiar situations favouring cohesion and social manipulation. Here, I investigate some topics on social play. Firstly, I investigate the social mechanisms which are at the basis of the play-partner choice by exploring the "play intensity matching" hypothesis. Original data are used to examine how young chimpanzees modulate play sessions by using play signals (meta-communication). Secondly, I present data on the distribution of social play and grooming in the periods around feeding time and in a control condition, showing that play frequencies between adults and unrelated subjects are significantly higher during pre-feeding. I discuss the possibility that play behaviour can be used to prevent conflict escalation and to increase a peaceful co-feeding (pre-conflict management). Finally, in a comparative approach, I contrast data collected on the two Pan species in order to evaluate whether, despite their phylogenetic closeness and similar social structure (fission-fusion society), chimpanzees and bonobos* (Pan paniscus) *show differences in adult play behavior.*

Keywords - *Social play, Play signals, Play functions, Pre-conflict mechanism, Adult play,* Pan troglodytes.

> *"We need more comparative studies of play, both in captivity and in the wild, in order to access rigorously the relative importance of the many possible different functions of play for different species that engage in the activity"*
> (Bekoff, 1982, p. 157, in Smith, 1982).

What we think we know about animal play

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

The difficulty of finding an objective definition of play derives from the fact we can only state that play lacks certain characteristics that are typical of functional behaviors.

Bierens de Haan (1952) defined play as functionless behaviour but the concept that play has no obvious benefits involves a subjective interpretation on the part of the observer (Martin & Caro, 1985). Play has probably several benefits (both at a delayed and at an immediate level) even they are not easily detectable. Play can be defined as all the activity that appears to an observer to have no obvious immediate benefits for the performer, but which involves motor patterns typical of functional contexts (i.e. agonistic, anti-predatory, and mating behaviour) (Martin & Caro, 1985; Pellis & Pellis, 1996; Bekoff, 2001). The difference between playful and functional contexts is not in the actual behavioural patterns performed but in the way they are performed (Pellis & Pellis, 1998). There are many aspects in which playful activity differs from the serious functional contexts from which its motor patterns derive (Loizos, 1967; Fagen, 1981; Martin & Caro, 1985). Firstly, movements show more a variable order compared with those of serious contexts (*fragmentation* or *disordering*), the actions are *exaggerated* and *repeated* more often in play compared to non-play interactions. Play sequences (often relatively brief) may be relatively incomplete (e.g., a movement may be started but not finished) or interrupted by higher-priority behaviours (i.e. anti-predatory behaviour) (Fagen, 1981). In short, we have to consider that many of the things we think we know about play strictly depend on how play is defined.

Play is typical of vertebrates

It may occur in birds and reptiles (Lazell & Spitzer, 1977; Burghardt, 1982; 1998; 2005), but it is especially prevalent in mammals. The latter have large and complex brains that correlate with the size of the behavioural repertoire, particularly with the part of the behavioural repertoire that is learned (Fagen, 1981). Lewis (2000) observed that social play is correlated with the proportion of the brain composed of neocortex in some primates, suggesting that such behaviour might be implicated in the development of the social cognition competence typical of most primate species.

Play is most typical of young animals

In nonhuman primates average rates of play decline consistently from late infancy or early juvenility through adolescence to adulthood. This trend holds both for social play and non-social play (Fagen, 1993).

Lability of play

Play tends to decrease or disappear under stressful conditions. It is generally less prominent in wild than in captive populations. Some authors (Loizos, 1967; Martin & Caro, 1985) argue that since the most costly activities (including the least important ones) might be dropped temporarily during stressful conditions, the lability of play might also point to its possible very large costs.

Play typically involves meta-communication

A play session can occur only if the playmates are capable of some degree of meta-communication (e.g. exchanging the signals that carry the message "this is play"; Hayaki, 1985). An agreement to play rather than to fight, mate, or engage in any pattern, can be negotiated in different ways. Some play markers have evolved to signal the beginning of a play session and/or to maintain a play mood (Bekoff, 2001).

Costs of play

The assertion most commonly found in literature is that play has immediate costs and delayed benefits. These costs are represented by energy and time expenses and by high risks of injury and predation (Fagen, 1981; Burghardt, 2005). For example, young Southern fur seals are much more likely to be killed by sea lions when they are playing than at other times (Harcourt, 1991).

Many authors also agree with the assertion that play has large costs and must have large benefits (Hinde, 1974; Bekoff & Byers, 1981; Fagen, 1981; Smith, 1982). However, the energetic cost of play has never actually been measured in the field. Fagen (1981, p. 311) speculates that a young animal devotes "95 or perhaps even 99% of its daily caloric expenditure to play". For this reason, play generally occurs when the animal is free from environmental (heat, cold, wet, presence of predator) and physiological (food, drink, sleep, sexual partner) constraints. Thus, play is often most typical of young individuals (their needs are taken care of by their parents) and captive animals (their needs are taken care of by keepers) (Loizos, 1967; Fagen, 1981).

Martin (1984) measured empirically the time and energy costs of play behaviour for young domestic cats (*Felis catus*). He found that play occupied 9% of the total time and, approximately, 4% of the total daily energy expenditure. This finding suggests that play is probably not so "costly" in terms of time and energy. Certainly, play has a survivorship cost, due to a variety of factors such as increased risk of injury and predation, separation from the parents or possible attack by playmates (Martin, 1984). However, only anecdotal accounts are reported on the potential risks (Fagen, 1981 see table 5-2, 1993) and the survivorship cost of play is far from being quantitatively defined or measured. In this view, immediate costs of play behaviour remain unknown (Caro, 1995). However, assuming that play does not have large biological costs does not necessarily imply that it has small benefits.

Hypothesized functions of play

Play appears to be multi-functional: it may assume different functions depending on the species, age and sex of the players (Poirier *et al.*, 1978; Paquette, 1994). Since play interactions are characterized by the apparent absence of immediate benefits, theories concerning the function of play have often concentrated on the long-term rather than on the immediate benefits (Bekoff & Byers, 1981).

Play behaviour can be a mechanism for developing motor and cognitive skills (Poirier *et al.*, 1978; Dolhinow, 1999). Byers & Walker (1995) introduced the term *motor training* to refer to juvenile activity that improves motor performance: improvement of endurance and strength, increase of motor skill and energetic economy of movement, development of muscles, bones, connective tissues, nervous and cardiovascular system (Byers & Walker, 1995). But why do animals use such a risky behaviour for developing their skills? Probably because the main benefit of play is learning to cope with extremes. In a recent review, Špinka *et al.* (2001) proposed that play might increase the versatility of movements used to recover from sudden shocks such as a loss of balance and falling over, and to enhance the ability of animals to cope emotionally with unexpected stressful situations. Cognitive and motor skills improve in relation to exposure to environmental and social contingencies during development and this promotes an increase in *behavioural flexibility* (Fagen, 1981). A couple of ways by which such behavioural flexibility can be enhanced by playful experiences have been suggested. Firstly, through social play an individual can estimate the strength, abilities and weakness of fellows (*social assessment*) as well as demonstrate and test its own skills (*self-assessment*) by reducing tension and preventing the rise of conflict, which could result in a serious injury (Pellis & Pellis, 1996; Thompson, 1998; Pellis & Iwaniuk, 1999; Palagi *et al.*, 2006a). Secondly, play may promote *social cohesion* by enhancing continual contact with other group members, learning species-specific (and perhaps group-specific) behavioural and communicative (postures, gestures, vocalizations) elements in the repertoire, and learning one's own social role (Poirier *et al.*, 1978; Fagen, 1981). Therefore, playful activity might have an important role especially in solitary species or between individuals with a low degree of familiarity (Pellis & Iwaniuk, 1999, 2000).

Primate play

Highly structured social play is characteristic of all primates from prosimians to apes, but detailed studies of play are still lacking for most species. In particular, comparative studies on play behaviour are needed to rigorously assess the relative importance of the different possible functions of play for different species (Fagen, 1993; Palagi, 2006).

Both solitary and social play are typical of immature primates, with the highest rates of play occurring in late infancy and early juvenility (Enomoto, 1990; Fagen, 1993; Mendoza-Granados & Sommer, 1995; Dolhinow, 1999; Palagi *et al.*, 2002). Caine (1986) and Pusey (1990) stated that the age-related decline in play is probably linked to the increase in competition and aggression during the play bouts. For example, adolescent chimpanzees exhibit a general decrease in responsiveness to playful invitations by potential play partners. Nonetheless, it should be noted that youngsters usually continue to invite adolescents to play despite their aggressiveness. In *Macaca mulatta*, Levy (1979) observed that the oldest juvenile males established their rank by playing: they monopolized the opportunities to perform in particular roles and consequently play partners were difficult to attract and play sessions difficult to maintain. Probably, a reduced capacity for role-reversals, expressed as an inability to accept mock attacks from subordinates, diminished the rates of play in the older juvenile males, which showed tension and fear when they were approached by a like-aged play partner. When play between like-aged playmates occurred, it was faster, more forceful, and characterized by asymmetry. A more symmetric play among like-sexed and like-aged dyads tended to persist for longer during development in females.

Pereira (1993) found that in infant ring-tailed lemurs play is quite symmetrical while, during juvenility, play sessions are used by animals to establish their first dominance relationships. Paquette (1994) also found that in adolescent chimpanzees asymmetry in play was strongly linked with ranking position.

The possible ultimate explanation for the decrease of play levels with the increase of age might be that play is differentially risky at different ages and that nutritive demands of immatures for maintenance increase as they grow (Fagen, 1993).

Developmental researches show that play behaviour begins in infancy, reaches its peak in juvenility, and drops at puberty (Fagen, 1981). Given that in many primate species social play (the most pervasive form of play) continues also during adulthood (Pellis & Pellis, 1991; Pellis & Iwaniuk, 1999) a full understanding of its adaptive role can be reached by taking into account the occurrence of play during such phase of life. The presence of social play behaviour in adults suggests that play may provide immediate benefits (Pellis & Iwaniuk, 2000; Palagi, 2004).

Social play during adulthood most often involves immature partners which are also responsible for the initiation of the play sessions (Breuggeman, 1978). Although adult-juvenile play appears to be influenced by demographic factors (e.g. paucity of peers), differences in the propensity of adults to play with immature subjects may exist (Caine & Mitchell, 1979). Adult-adult play, while less frequent, has been found in some primate species and it may occur both in sexual and non-sexual contexts. Courtship play has been found to be especially prevalent in species where males and females are solitary, and so unfamiliar with one another (e.g. in the genus *Mirza*, *Daubentonia*, *Perodicticus,* and *Pongo*; Anderson, 1970; Epps 1974; Hladik & Charles-Dominique, 1974; Pagès, 1978, 1983). Non-sexual play is more prevalent in species with a higher degree of social aggregation (Pellis & Iwaniuk, 2000). However, the size of social groups does not seem to be sufficient to explain the increase of the frequency of play (Spijkerman *et al.*, 1996). In fact, in several genera of cercopithecids, such as *Papio*, characterized by large troops (one hundred or more individuals) and highly cohesive subgroups with structured relationships (Kummer, 1995), play among adults has not been reported. On the contrary, adult-adult play has been reported in genera such as *Ateles*, *Cacajao*, and *Pan* whose social organizations are based on a more fluid composition, with many combinations of associations that change frequently (Pellis & Iwaniuk, 2000).

Brueggeman (1978), investigating adult-adult play in rhesus macaques in detail, found that this trait is used in different contexts (multi-functional behaviour) and that social manipulation is a potential function of play. In many primate and non-primate mammals, play among mature subjects appears to be used for promoting the establishment and maintenance of social bonds and in testing relationships to gain social advantage (Pellis & Iwaniuk, 2000). Some authors suggest that play in courtship may be viewed as a particular kind of social-assessment. Unfamiliarity among individuals, due to a low likelihood of interacting or because they live in a loose social structure, can increase the occurrence of mature play both in sexual (Pellis & Iwaniuk, 1999) and non-sexual contexts (Brueggeman, 1978; Pellis & Iwaniuk, 2000; Palagi, 2006).

There is evidence for differences in frequency of play between sexes for many species of primates.

Juvenile males tend to play more than juvenile females in many cercopithecines (Kummer, 1968; Owens, 1975; Symons, 1978), squirrel monkeys (Biben, 1986, 1998), gorillas (Watts & Pusey, 1993), chimpanzees (Mendoza-Granados & Sommer, 1995) and orangutans (Becker, 1984). In other species such as red colobus (*Colobus badius*) infant and juvenile females play more frequently than males of the same age (Starin, 1990), while no sex differences in juvenile play have been found in *Lemur catta* (Gould, 1990) and in marmosets (Cleveland & Snowdon, 1984).

Fagen (1993) explained sex differences in juvenile play in terms of a much tighter resource budget for females (due to pregnancy and motherhood) than for males. Two studies on *Macaca fuscata* seem to confirm this hypothesis (Koyama, 1985; Imakawa, 1990). These researches showed that the distribution of male and female juvenile play overlaps extensively until females are on the verge of adulthood.

Although studies on sex differences in primate play will require detailed age-specific and sex-specific data (particularly on play in adulthood), sex differences in juvenile play could represent valuable tools to test some hypotheses on primate socio-biology. In this view, it is important to take into account that play behaviour can be affected by several factors, such as individual variability, demography, nutrition, age, and intra-group social relationships.

Konner (1975) stated that social play can be viewed as a conflict of interest since each animal might have its own preferred play manner as a result of age, sex, dominance, and individuality. If play behaviour coincides with a situation of conflict of interest how do strangers or animals belonging to different species play together? Other authors (Fagen, 1993; Bekoff, 1995) suggest that if two or more individuals play for long periods, *cooperation* has to occur much more frequently than conflict of interest, especially when playmates are unfamiliar. In fact, failure to negotiate and cooperate prevents animals from playing well together and can lead to a decline in play frequencies. In this view, social play can be viewed as a balance between *cooperation* and *competition*. Individuals characterized by competence and successful social affiliation would benefit further from refining these skills and so increase their behavioural flexibility. In contrast, in individuals lacking social competence, play likely reinforces social and physical asymmetries. In the first case, "benefits of play will result distributed very widely among individuals, reinforcing symmetries and equality of future opportunities" (Fagen, 1993 p. 193). In the latter, play benefits will be limited to a small number of high-quality subjects.

Play is one of the most sophisticated types of social communication (Fagen, 1981, 1993; Bekoff, 1995; Pellis & Pellis, 1996). The function of play in the ontogeny of primate social cognition may be to recognize stimuli that might appear ambiguous (e. g., intentions of other animals). The ability to interpret such ambiguous features of social signalling could represent a central issue in the evolution of behavioural flexibility and intelligence in primates. By playing, primates develop individual creativity, interpretation, and improvisation (Dolhinow, 1999). Moreover, novel behaviours can be culturally transmitted to the new generations by playing (Goodall, 1973, 1989).

Social play in chimpanzees

Up to date, only naturalistic observations on mother-offspring play have been provided in chimpanzees (Loizos, 1967; van Lawick-Goodall, 1968; Savage & Malick, 1977). The first play sessions between mother and offspring occur when the infants are about 12 weeks old. The most common play pattern used by mothers is gently tickling and four-five month old infants begin to respond to such stimulation by grabbing and patting at their mother's hands. Afterwards, infants try to trigger play sessions with the mothers by pulling their hands (van Lawick-Goodall, 1968). Play between mothers and one year old infants is more vigorous, including behavioural patterns such as rolling, biting, gently sparring, and pushing (Loizos, 1967).

As immature animals grew, the mothers spend less time playing with their offspring, which generally become more inclined to play with siblings, peers (Fig. 1) and other adults (Horvat & Kraemer, 1981).

In chimpanzees, as in many primate species, play reaches its peak frequency during the juvenile phase (Fagen, 1981; Palagi *et al.*, 2002). However, play has an important role at any stage of the behavioural development (Burghardt, 2005), even though play modality varies as a function of age. For example, social play among infants is characterized by a mild intensity, whereas juvenile and/or adolescent play is rougher (Hayaki, 1985; Palagi *et al.*, 2002b).

Generally, play is most frequent among individuals that are age- and size-matched (Loizos, 1967; Mendoza-Granados & Sommer, 1995). Probably, during a play fight it is useful to practice against a well-matched partner, because symmetry characterizing the session gives play-mates the possibility to compete, practice, and strategize in a safer context (Dolhinow, 1999). However, in the chimpanzee colony hosted at the Zoo Parc de Beauval (France, Table I) I did not find any significant difference in the play distribution according to the age of immature play-mates (randomization ANOVA, one-way: F=0.802, ns; Fig. 2). This result can be explained by the fact that the older or larger subjects may reduce their strength and roughness when playing with younger or smaller individuals. In other words, the animals may use role reversal and self-handicapping when the players strikingly differ in size, age and ranking position. The "play intensity matching" can function for both promoting and prolonging the session and, at the same time, for communicating to the playmate that "this is only play" (Hayaki, 1985; Biben, 1986; Pellis, 1993; Bekoff & Allen, 1998; Pereira & Preisser, 1998). Obviously, the occurrence of such fine regulation of the play bouts indicates that chimpanzees are able to assess each other's skills.

Partner choice in juvenile primates often means also a partner of the appropriate gender (Fagen, 1981). Mendoza-Granados & Sommer (1995)

Fig. 1 - Two young chimpanzees playing.

showed that chimpanzee juvenile males played significantly more than females, which spent more time playing solitarily. Markus & Croft (1995) showed that males engaged in play sessions characterized by rough-and-tumble and chasing behaviours; whereas, chimpanzee females performed selectively play-mothering and tickling. These findings fit perfectly with the *Social Skill Hypothesis*, which predicts that play may help to establish social relationships among individuals likely to interact to each other in the future (Baldwin & Baldwin, 1974; Bekoff, 1974; Fagen, 1981; Holmes, 1994, 1995; Maestripieri & Ross, 2004; Palagi, 2006).

Chimpanzees live in a fission-fusion society characterized by male philopatry, female dispersal and strong alliances among the resident males (male bonded society) (for an extensive

Tab. 1 - Play behavioural patterns recorded during the observations of the Beauval chimpanzee colony (St. Aignan sur Cher, France) (Palagi, 2006).

GENTLE PLAY PATTERNS	**DEFINITION**
Airplane	An adult lies on its back and raises an infant up with its hands and feet
Grab Gentle	An animal massages gently another
Play Push	An animal pushes a playmate either with its hands or feet
Play Bite	An animal gently bites a playmate
Play Recovering a Thing	An animal chases a playmate and attempts to grab an object carried by it
Play Slap	An animal slaps any part of a playmate's body
Tickle	The partner's body is contacted either with the mouth or with the hands
ROUGH PLAY PATTERNS	
Pirouetting	One or more animals together turn, somersault or roll over either on the ground or on vertical supports
Acrobatic Play	One (solitary play) or more animals (social play) climb, jump and dangle from supports of the environment (e.g. branches)
Play Run	An animal runs alone (solitary play) or chases a play partner (social play)
Play Stamping	An animal jumps on a play partner with its feet
Rough and Tumble	Two animals (or more) grasp, slap, and bite each other. This pattern is typical of immature individuals
Play Brusque Rush	An animal jumps with its four limbs on a playmate
Play Retrieve	An animal holds a playmate to avoid its flight
OTHER	
Play Invitation	An animal approaches a possible play partner, pats it and then goes away. This display is used to start a play session
Play Face	Playful facial display: the mouth is opened with only the lower teeth exposed
Full Play Face	Playful facial display: the mouth is opened with the upper and lower teeth exposed

review see Doran *et al.*, 2002). On the contrary, females spend a lot of time travelling with their offspring; thus, social relationships among adult females are not frequent. In this view, if social play has an important role in social assessment, in chimpanzees the potential benefits of this activity are expected to be lower for females than for males. This hypothesis is supported by some of my recent findings on play distribution in bonobos (Palagi, 2006). I found that in the Apenheul bonobo group (The Netherlands) social play was significantly more frequent among females than any other sex combination. I interpreted this result in the light of the peculiar inter-individual relationships existing in *Pan paniscus*. In this species, females migrate from their natal groups as chimpanzees do (female exogamy) but, unlike chimpanzees, they form strong coalitions and alliances with other unrelated females, thus acquiring dominance advantage over males (Kano, 1982; Furuichi, 1989; Parish, 1994, 1996; Paoli & Palagi, in press). In this view, play may be a means by which bonobo females obtain their cohesiveness and social dominance (Palagi, 2006).

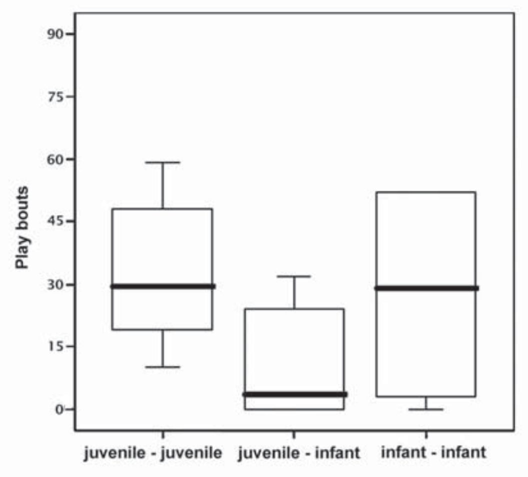

Fig. 2 - *Number of play sessions performed by juvenile-juvenile (J-J), juvenile-infant (J-I) and infant-infant dyads (I-I). Solid horizontal lines indicate medians; length of the grey boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.*

Spijkerman *et al.* (1996) compared social play performed by adolescent chimpanzees (7-10 years) raised in peer-only groups and in a socially complex semi-natural zoo situation. Sex differences in play behaviour were found in the subjects living in a more natural condition only, indicating an earlier sex-differentiation in the zoo than in the peer group. Particularly, sex differences were evident in the wrestle duration (longer in males than in females), in the relative frequencies of tickle, chase and wrestle, and in the partner preference with adolescent females playing more with infants and juveniles. It appears that the rearing condition of animals may affect the correct time-schedule of the behavioural development of play in chimpanzees.

Modulating a play session: play signalling in juvenile chimpanzees

How do both playmates "know" if the fighting behaviour is playful or not? A further important issue on animal play implies meta-communication, by which playmates negotiate and agree during the session (Pellis & Pellis, 1996). One of the most familiar and well-documented examples of a play signal is the bow, which is associated with the readiness to engage in play activity in canids (Bekoff, 1972; 1974). Bekoff found that coyotes (*Canis latrans*), which are less social and more aggressive to one another than wolves and dogs, punctuate their play sessions with more play bows than the more social canids (Bekoff, 1972).

Van Lawick-Goodall (1968) stated that the play face in the chimpanzees of the Gombe Stream Reserve sometimes involved showing both rows of teeth. She interpreted such greater teeth exposure as signifying a higher intensity of play. It is also possible that in socially ambiguous situations the baring of upper tooth row (full play face) represents the introduction of an element of appeasement since the facial expression bears more resemblance to the bared-teeth display, which can have an appeasing function (Loizos, 1967; Palagi, 2004).

To test such hypothesis, I provide additional data on the use of play signals according to the intensity of the play session (for the definition of the two play modalities see Tab.1). I found that the 4-7 years old chimpanzees of the Beauval group performed more frequently play signals during the rough play sessions than during the gentle ones (Exact Wilcoxon test T=0, ties=0, n=6, p=0.031; Fig. 3). Moreover, I found that infant, juvenile and adult chimpanzees performed play facial displays more frequently to maintain rather than to initiate play sessions (Exact Wilcoxon test T=0, ties=6, n=19, p=0.001; Fig. 4).

When play becomes rough an "amicable" play signal is useful in de-escalating such an encounter. My findings corroborate the hypothesis proposed by Pellis & Pellis (1996): if rough play in mature animals has the function of assessing social relationships, then play signals may be useful in manipulating the situation to the best advantage of the performer. For instance, if an animal begins to escalate the roughness of a playful interaction and the play-mate shows weakness, then their dominance relationship may be reversed. In contrast, if the play-mate responds by also escalating the encounter, then the partner may signal its play intention to diffuse the situation. In this way, such signals could have a retroactive function. Moreover, there is evidence that play bouts between two participants are significantly longer when both individuals exhibit play face; this facial display can be explained as an honest reflection of the sender's motivation to play and therefore a signal of play (Waller & Dunbar, 2005).

In an elegant study, Flack *et al.* (2004) took a further step by demonstrating that older and younger chimpanzees increase their play signals in the presence of mothers of the younger playmates, especially when the roughness of play is high. The authors suggested that juveniles use play signals to prevent the interference by mothers of younger playmates. Therefore, play signals can be useful for play-mates to manipulate not only the play session but also the social context in which the play session occurs. Consequently, the signals provided by the sender, even if targeted to play partners, can be optimized also for third-parties (e.g. the mother of the younger play-mates).

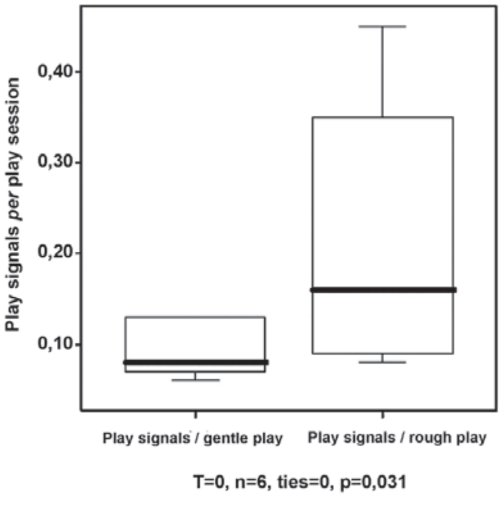

Fig. 3 - Frequency of play signals per play session performed by immature chimpanzees (4-7 years old) during gentle and rough sessions. Solid horizontal lines indicate medians; length of the grey boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.

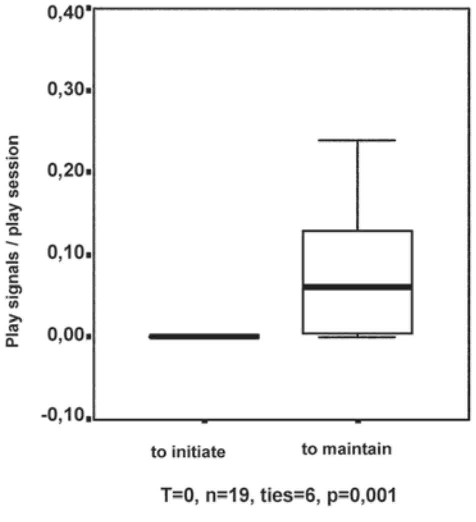

Fig. 4 - Frequency of play signals per play session performed by immature chimpanzees (4-7 years old) for initiating and maintaining the sessions. Solid horizontal lines indicate medians; length of the grey boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.

In conclusion, all the findings reported here show that the ability of an animal to maintain play sessions may give information on the cognitive skills necessary to negotiate cooperative agreements, to ask for permission to engage in a specific activity, to encapsulate one's own behaviour within a pretended context, and perhaps even to make mental attributions to others (Bekoff & Allen, 1998). For this reason, clarifying how animals are able to cope with a play bout may permit us to shed light on animal cognitive abilities.

Social play: an important tool in conflict management

Most of conflict management research has focused on the modalities used by animals to deal with either existing aggression or the consequences of such aggression. Here, I provide and discuss data on tactics used by primates to keep in check the potential risk of conflicts before they occur. Some observations (i.e. transport of tools, Boesch & Boesch, 1983) and experimental evidence strongly indicate that apes have the skills of planning and foresight (see for an extensive review Tomasello & Call, 1997). The ability to anticipate forthcoming events could confer a selective gain to those subjects capable of planning.

A kind of conflict of interest that can be anticipated is the one occurring over food, especially in captive animals. Among primates, diverse tactics have evolved to mitigate tension and prevent conflict escalation. Communicative displays, dominance relationships, and greeting gestures are common mechanisms employed in order to avoid potential conflicts (Preuschoft & van Schaik 2000, Whitham & Maestripieri 2003; Koyama & Palagi, 2006). One of the most famous examples is the use of socio-sexuality among bonobos during food consumption. This finding was interpreted by the researchers as an appeasement mechanism of tension regulation (de Waal 1987, 1992; Paoli *et al.*, 2007).

Social play and grooming involve a close physical contact for long periods and have an important role in the cohesion of social animals (Loizos, 1967, Merrick, 1977, van Lawick-Goodall 1968). During the predictable situations characterized by conflict of interest, grooming may function to maintain social stability by reducing tension and providing appeasement within groups (Aureli *et al.* 2002, Merrick 1977, Schino *et al.* 1988).

Adult 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. Evidence for the anticipation of competition at feeding time in *Pan troglodytes* was provided by Koyama & Dunbar (1996) and Palagi *et al.* (2004), which found an increase of grooming rates between adult dyads just before food distribution; such increase was more striking when food was clumped then when it was dispersed. Moreover, Palagi *et al.* (2004) found a positive correlation between grooming (during pre-feeding) and contact sitting (during feeding) by adult dyads. This finding seems to indicate that anticipatory grooming increases the level of tolerance around food.

Between adult and immature chimpanzees, grooming did not increase during the pre-feeding period, indicating that probably grooming does not function in regulating pre-feeding tension within this age-class combination. However, the risk of aggression during such period may involve all the members of the group. Aggressive events between juvenile males and adult females are not uncommon during the pre-feeding periods and the consequences of such agonistic episodes are potentially harmful for both of them (Palagi *et al.*, 2006b). In the pre-feeding period social play between adults and juveniles occurred more frequently compared to the control condition, thus suggesting that adult chimpanzees interact with immature subjects via a different behavioural strategy (play), which may be used as a substitute for grooming to increase the likelihood of cooperative behaviour at feeding time. Since play is the main activity during juvenility and "…may be a unique category of behaviour in that asymmetries are tolerated…" (Bekoff 2001, p. 88), adults might choose this activity when they interact with immatures during strong tense situations.

The positive correlation found between the frequency of adult-unrelated immature play (pre-feeding) and contact sitting rates (feeding) between the adult involved in play sessions and adults related to the immature playmate (i.e. co-feeding) suggests that play behaviour represents a good indirect "contact point" between the adults (Palagi *et al.*, 2004). 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, play could reduce tension around food resources, thus permitting more relaxed feeding sessions or discouraging possible attacks by adult relatives of the immature playmates (Savage & Malick 1977; Kuester & Paul 2000). At a more delayed level, play could assess the strength of social bonds between adult players and adults related to immature playmates.

In many primate species, females interact regularly with other females' infants, making attempts to greet, sniff, inspect, and tickle them (Altmann, 1980; Silk, 1980; Silk *et al.*, 2003; Maestripieri, 1994; Paul & Kuester, 1996; Bentley-Condit & Smith, 1999). These kinds of interactions, labelled "infant handling", are often performed by experienced mothers who have successfully raised their own infants. Loizos (1967) claimed that adult chimpanzees maintain high levels of play with immature partners, and do so by initiating playful interactions. Infants, in particular, are attracted to unrelated older individuals (probably due to their more diverse ways of playing) and seem to interact more often with their mothers' preferred social partners. 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 this view, playing fairly 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) (Dugatkin & Bekoff, 2003). Moreover, the active engagement in alloparental behaviour by adult females may also facilitate infants' acquisition of social rules and species-specific signals (ultimate benefits) (Enomoto, 1990).

Juvenility is a period of rapid and marked changes including both physiological and behavioural processes, and play may function to modulate this transitional stage (Kraemer *et al.* 1982; Paquette 1994). Palagi *et al.* (2004) found that among related immature chimpanzees play frequency did not show any significant increase during the pre-feeding period; whereas, among unrelated immature playmates playful activity showed a peak level just during such period. The same finding was also found in juvenile lowland gorillas (*Gorilla gorilla gorilla*), which may finely use social play to anticipate the forthcoming tension and dissipate the excitement associated with feeding (Palagi *et al.*, 2007). Nunes *et al.* (2004) suggested that social play has immediate adaptive motor benefits for young animals; one possible immediate benefit of play is to increase the versatility of motor responses in individuals, thus preparing them to cope with novel, foreign or tense situations (Špinka *et al.*, 2001). Moreover, as play is also a safe mechanism to test personal (self-assessment) and partner's abilities (social assessment) (Loizos, 1967; Poirier *et al.*, 1978; Paquette, 1994; Thompson, 1998), it could be most effective during periods of high social excitement (probable delayed benefits) (Palagi *et al.*, 2004).

In conclusion, play seems to be an ubiquitous mechanism generally used in anticipation of the forthcoming stress associated with food distribution. This is particularly interesting given the commonly held view that play is suppressed by stress (Martin & Caro, 1985) – here it would appear that play is regulating stress. Play may provide immediate and delayed benefits for playmates by i) reducing the risk of aggression and increasing tolerance around food and ii) representing a safe mechanism for testing the degree of cooperation/competition among the playmates and their relatives (social assessment).

Chimpanzees and bonobos: similar species with dissimilar play modalities

Efforts to study and explain play behaviour have been primarily focused on immature subjects (Pellis & Iwaniuk, 2000; Power, 2000) and, although in many species play can continue into adulthood as well (Fagen, 1981) adults have been often neglected (Pellis & Iwaniuk, 1999; Palagi, 2004). The permanence of play in adults strongly suggests that this peculiar activity may have immediate benefits other than delayed ones (Burghardt, 1998; Pellis & Iwaniuk, 1999). As above mentioned, when adults engage in social play, they most often do so with immature playmates. However, this phenomenon is difficult to interpret as these playful bouts are generally initiated by the juveniles and most often arise as a result of demographic factors (such as few other immature subjects available to play) (Pellis & Iwaniuk, 2000). Therefore, the most convincing data to fully understand the adult propensity to engage in social play are those involving adult-adult dyads (Caine & Mitchell, 1979).

Although less frequent, adult-adult play was found in sexual context (during courtship in some prosimians species and in orangs) and in nonsexual context as in species characterized by a fission-fusion society (e.g. *Ateles* spp, *Cacajao* spp, and *Pan* spp). In these species play seems to be particularly frequent among the animals which meet together after periods of separation (Pellis & Iwaniuk, 2000). This evidence led the authors to hypothesize that in many primate and non-primate mammals, play among mature subjects can be used for promoting the establishment and maintenance of social bonds.

Following such hypothesis, in 2004 I began to search for a way of testing this assumption. A comparative approach would have permitted to address such topic empirically. I focussed on comparing adult play behaviour in the two *Pan* species in order to control for the effects of phylogenetic relations and the nature of social systems on the occurrence and distribution of play (Palagi, 2006). Over the last three decades research has shown that, despite their phylogenetic closeness, bonobos (*Pan paniscus*) differ from chimpanzees (*Pan troglodytes*) in many aspects of their social behaviour. Bonobos are characterized by a reduced level of aggressions (within and between groups) and by the absence of formalized submissive signals (Kuroda, 1980; Badrian & Badrian, 1984; Wrangham, 1993; White, 1996; de Waal, 2001). In contrast, chimpanzees show high levels of aggressions and formalized relationships associated with ranking (male dominance over females), territorial defence, and infanticide (for an extensive review see Doran *et al.*, 2002).

Many authors suggest that bonobos are a more tolerant species compared to chimpanzees (Kuroda, 1980; Kano, 1992; Furuichi, 1997; Hohmann & Fruth, 2003; Paoli & Palagi, in press). In this view, bonobos and chimpanzees can be considered as model species to test some predictions on adult play behaviour.

In a recent paper (Palagi, 2006), I showed that despite their phylogenetic closeness and similar social structure (fission-fusion society) the two species presented striking differences in adult-adult play frequency, with chimpanzees performing extremely low levels. This finding is supported by observations from free-living chimpanzees and bonobos. For example, van Lawick-Goodall (1968) noted that play among mature individuals is infrequent among the Gombe chimpanzees, and it generally involves idle tickling or soft wrestling, usually in a sitting or reclining position. The same author reported that only on two or three occasions during a 1-year period did mature females play with other adults. Moreover, some authors suggested that play appears to give way to other forms of social behaviour as adulthood is reached (e.g., adult chimpanzees increasingly spend more time engaged in social grooming) (Loizos, 1967; van Lawick-Goodall, 1968; Merrick, 1977; Deschner, personal communication). In describing playful behaviour in wild bonobos, Kuroda (1980) and Enomoto (1990) provided some anecdotic reports of adult-adult play. These reports support the idea that the playful temperament of adult bonobos is not a side-effect of captivity which, however, should have had repercussions also on adult chimpanzees.

In Palagi (2006), I showed that the use of play appears to become most important when relationships among individuals are less codified and structured according to rank-rules. If adult-adult play has a fundamental role in the social assessment, then such type of play is expected to be retained within tolerant societies rather than within despotic ones. Accordingly, Palagi *et al.* (2007) did not find any play interactions among adult lowland gorillas, a strongly despotic species characterized by an extremely low degree of inter-individual affiliation (Harcourt, 1979; Watts, 1995, 1996).

Adult bonobos used play facial displays at high levels during their rough play sessions; whereas, in chimpanzees play signals were almost absent. This result can also be explained with the degree of uncertainty in rank relationships among adult bonobos, which probably need to keep signalling clearly and frequently that "this is only play". The marked use of meta-communication (play signals) may also be due to the obvious lack of role-reversal, which becomes useless when, within a dyad, rank relationships are not clear cut (like in bonobos) but has a fundamental role when within a dyad the ranking position is well-defined (like in chimpanzees) (de Waal, 2003).

Social play and morality

"Play is not just play"
(Burghardt, 2005, p. 398)

Social play in animals seems to have an influence upon other social skills, e.g. by allowing members to learn how to maintain social bonds (Lewis, 2005). Primates, and particularly the great apes, are characterized by an extended juvenile period, which is probably linked to their need to learn (Joffe, 1997). Play is a means of acquiring adult social skills (Smith, 1982) but it is considered by psychologists as a developmental scaffold, which rapidly drops once its job is done (Lewis, 2005). However, play can be retained into adulthood as well (see above) and this evidence contrasts with psychologists' point of view. In fact, if we assume that play has an important role in constructing long-term social relationships (Bekoff, 1974; Brueggeman, 1978; Palagi, 2006), then play may be at work also during adulthood, especially considering that many primates live in cooperative social groups and show division of labour, food sharing, communal care of young, and dominance hierarchies. The question that frequently arises is "are animals able to regulate their behaviour in terms of what is permissible and what is not during their social interactions?".

In an extensive review on the evolution of social morality, Bekoff (2004) tried to answer the question and stated that the social dynamics of play require that players cooperate and agree behaving fairly. This paradigm led the author to suggest that social play may be an essential precursor to the behavioural evolution of cooperation, fairness, and ultimately, social morality. In 2003, Dugatkin & Bekoff proposed a mathematical model, based on the Game Theory, in which they show that failure to negotiate and cooperate prevents animals from continuing to play together and, successively, leads to a decline in honest interaction and cooperation in serious and functional contexts as well.

Social play in animals and, particularly, in the great apes is of significant interest to ethologists, anthropologists, and psychologists. However, in comparison with other behaviours whose functions are more easily identified, play behaviour remains an intriguing challenge. Even though recent research focussed on the importance of social play on developmental, neurological, and socio-biological levels, further empirical studies are needed. Data on different species with different level of sociality, behavioural complexity, and flexibility need to be compared using standardized methods for observations and analyses. In particular, it is crucial to extend such ethological approach also to the research on play behavior in humans. In fact, given the consensus on the complex socio-cognitive abilities of the great apes (Tomasello & Call, 1997; Preston & de Waal, 2002), it would be particularly interesting if future ethological research could compare peculiar aspects of play behaviour between apes and humans.

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Info on the web

http://www.eva.mpg.de/psycho/

The page of the Department of Developmental and Comparative Psychology of the Max Planck Institute for Evolutionary Anthropology.

http://pin.primate.wisc.edu/factsheets/entry/chimpanzee.

Chimpanzee fact sheet of Primate Info Net.

http://www.janegoodall.org.

The site of the Jane Goodall Institute, created by the famous British ethologist for the conservation of chimpanzees.

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