

Social Play in Bonobos (*Pan paniscus*) and Chimpanzees (*Pan troglodytes*): Implications for Natural Social Systems and Interindividual Relationships

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KEY WORDS adult play; play signals; social assessment; phylogenetic closeness; egalitarian societies

ABSTRACT This study compares adult play behavior in the two *Pan* species in order to test the effects of phylogenetic closeness and the nature of social systems on play distribution. The social play (both with fertile and immature subjects) performed by adults did not differ between the two species. In contrast, in bonobos, play levels among fertile subjects were higher than in chimpanzees. Findings regarding levels of undecided conflicts (more frequent in bonobos) and formal submission displays (lacking in bonobos) confirm, in the two colonies under study, that bonobos exhibit “egalitarianism” more than chimpanzees. Some authors emphasized the importance of play-fighting for social assessment when relationships among individuals are not codified and structured according to rank-rules. Indeed, adult bonobos

played more roughly than chimpanzees. Moreover, adult bonobos displayed the full play-face at a high frequency especially during rough play sessions, whereas in chimpanzees, the frequency of play signals was not affected by roughness of play. The frequency of social play among bonobo females was higher than in any other sex combinations, whereas no difference was found for chimpanzees. As a matter of fact, social play can be viewed as a balance between cooperation and competition. Among bonobo females, characterized by social competence and affiliation, social play might enhance their behavioral flexibility and increase their socially symmetrical relationships which, after all, are the basis for their egalitarian society. *Am J Phys Anthropol* 129:418–426, 2006.

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The biological functions and evolutionary origins of animal play are issues of considerable debate. Play, like any other biological trait, must have evolved for some reason (Lewis, 1982). Due to the high costs of play, many authors agree that this trait must be functional, because otherwise, animals showing a high level of play would be disadvantaged compared to nonplaying animals (Symons, 1978; Fagen, 1993). Play seems to assume different functions depending on the species, age, and sex of 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 often concentrated on long-term rather than immediate benefits (Bekoff and Byers, 1981; Martin and Caro, 1985). Play behavior is a mechanism for developing motor and cognitive skills and for promoting behavioral flexibility (Poirier et al., 1978; Fagen, 1981, 1993; Byers and Walker, 1995; Špinka et al., 2001). Moreover, playful activity might have an important role in social assessment, especially in solitary species or between individuals with a low degree of familiarity (Pellis and Iwaniuk, 1999, 2000).

Developmental research shows that play behavior begins in infancy, reaches its peak in juvenility, and decreases at puberty (Enomoto, 1990; Fagen, 1981, 1993; Mendoza-Granados and Sommer, 1995; Dolhinow, 1999; Palagi et al., 2002). The possible ultimate explanation for the decrease in play levels with increasing age might be that play is differentially risky at different ages, and that the nutritive demands of immature animals for maintenance increase as they grow (Fagen, 1993). Given

that in many primate species social play (the most pervasive form of play) continues during adulthood (Pellis and Pellis, 1991; Pellis and Iwaniuk, 1999), the occurrence of play during this phase of life needs to be investigated for a full understanding of its adaptive role. Social play in adults suggests that this behavior may also provide immediate benefits (Pellis and Iwaniuk, 2000; Palagi et al., 2004). Adult play sessions most often involve immature partners who are generally responsible for the initiation of the interactions (Brueggeman, 1978). Adult-adult play, while less frequent, was found in some primate species and may occur in both sexual and nonsexual contexts. Courtship play was found to be especially prevalent in solitary species where males and females are unfamiliar with one another (e.g., *Mirza*, *Daubentonia*, *Perodicticus*, and *Pongo*). Nonsexual play is more prevalent in species with a high degree of social aggregation (Pellis and Iwaniuk, 2000). However, the size of social

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groups does not seem to be sufficient to increase the frequency of play (Spijkerman et al., 1996). In fact, in many species of cercopithecids, such as *Papio*, characterized by large troops and highly cohesive subgroups with structured relationships (Kummer, 1995), play among adults has not been reported. On the contrary, adult-adult play was reported in species such as *Ateles*, *Cacajao*, and *Pan*, whose social organizations are based on a more fluid composition, with many combinations of associations that frequently change (Pellis and Iwaniuk, 2000). In many primate and nonprimate mammals, play among mature subjects appears to be used in promoting the establishment and maintenance of social bonds and in testing relationships so as to gain social advantage (Pellis and Iwaniuk, 2000).

There is also evidence for differences in frequency of play between sexes for many primate species. Juvenile males tend to play more than juvenile females in many cercopithecines (Kummer, 1968; Owens, 1975; Symons, 1978; Eaton et al., 1985, 1986; Glick et al., 1986; Pereira, 1984), squirrel monkeys (Biben, 1986, 1998), gorillas (Watts and Pusey, 1993; Maestripieri and Ross, 2004), chimpanzees (Nadler et al., 1987; Mendoza-Granados and Sommer, 1995; Spijkerman et al., 1996), and orangutans (Rijksen, 1978; 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 were found in ring-tailed lemurs (Gould, 1990) and marmosets (Cleveland and Snowdon, 1984). Many authors suggest that sex differences in play are expected whenever males and females differ in their physical, behavioral, and social features (Fagen, 1981; Smith, 1982; Byers and Walker, 1995; Spinka et al., 2001). In this perspective, sex differences in play could represent valuable tools to test some hypotheses on primate sociobiology. In chimpanzees, sex differences in play were reported in captive studies (Nadler et al., 1987; Mendoza-Granados and Sommer, 1995; Spijkerman et al., 1996). Unfortunately, there are very few studies on play in bonobos, and to my knowledge, no data on sex differences (e.g., Enomoto, 1990; Kano, 1980, 1992).

Despite the obvious similarities in their morphology, social system, and behavioral repertoire, chimpanzees and bonobos differ in some striking ways. Bonobos show greater female sociality (greater female-female association, reduced tendency for females to travel alone, and less disparity in male and female ranging behavior), an absence of male dominance, and a stronger tendency for females to have feeding priority and also different mechanisms by which female immigrants transfer into and become established in a new community. In contrast, chimpanzees show strong male-male bonds (male-male associations and coalitions for establishing and maintaining rank, for defending territories, and for engaging in infanticide), male dominance over females, and decreased female sociality (reviewed in Doran et al., 2002).

The present study focuses on comparing adult play behavior in the two *Pan* species in order to test the effects of phylogenetic closeness and the nature of social systems on the occurrence and distribution of play. To achieve this goal, I tested the following predictions.

PREDICTION 1

According to phylogenetic closeness, no differences between the two *Pan* species are expected for overall play frequency in fertile individuals.

PREDICTION 2

According to the hypothesis of Pellis and Iwaniuk (2000) suggesting that adult play is used for social assessment in species whose social relationships are relatively fluid, no differences are expected for play frequency among fertile subjects in the two species.

PREDICTION 2bis

According to the definition given by de Waal (1995, 2001) of bonobos being a more egalitarian species than chimpanzees, and characterized by a high degree of social flexibility and by the possibility of circumvention of rank-ruled interactions, I expect a higher frequency of play invitation and play sessions among fertile bonobos compared to chimpanzees, and a higher frequency of rough rather than gentle play in mature bonobos compared to chimpanzees, and consequently, a higher frequency of play facial displays in the former.

PREDICTION 3

If play has a role in social assessment among bonded individuals, differences in the distribution of adult-adult play are expected according to the sex of the playmates.

METHODS

Subjects and housing

Bonobos. Behavioral data were collected during 3.5 months of observation (July–October 2000) on a group of *Pan paniscus* housed in the Apenheul Primate Park (Apeldoorn, The Netherlands), first established in 1998. During data collection, the colony (the largest captive group of bonobos at that time) was composed of 8 unrelated adults (3 males and 5 females, with the wild-born being rescued from different sites in Zaire) and 3 immature subjects (Table 1). The animals were housed in an enclosure with both an indoor and outdoor facility (about 230 m² and 5,000 m², respectively). Since the animals were not always visible in the indoor facilities, observations were stopped when more than one animal was out of sight. The animals were able to move freely from the indoor to the outdoor enclosure after the first feeding session (at 8:45 AM), and received abundant food three times a day at 8:45 AM, 12:45 PM, and 4:30 PM. Observations were made over a 6-hr period, encompassing both morning and afternoon.

Chimpanzees. Behavioral data were collected during a period of 3.5 months (October 2000–January 2001) on a group of *Pan troglodytes* housed in the ZooParc de Beauval (St. Aignan sur Cher, France). The colony, the largest captive group of chimpanzees in France at that time, was composed of 19 animals (10 adults, 4 juveniles, and 5 infants) (Table 2). The animals were housed in an enclosure with both an indoor and outdoor facility (about 200 m² and 2,000 m², respectively). The indoor facility was composed of two large enclosures (totally visible) equipped with everything necessary to allow the animals to move freely in three dimensions. Since the two enclosures were placed in a glass house, the animals were able to follow the natural 24-hr day/night cycle. The group received abundant food at 9.00 AM, 2.00 PM, and 4.30 PM. The observations were made over a 6-hr period, encompassing both morning and afternoon.

TABLE 1. *Bonobo colony in Apenheul Primate Park (Apeldoorn, The Netherlands)*

Subject	Sex	Class	Date of birth	Origin, arrival date
Hani (H)	M	Adult	1989, wild	Zaire, 1998
Mobikisi (MB)	M	Adult	1981, wild	Antwerpn, 1996
Mwindu (MW)	M	Adult	1985, wild	Zaire, 1998
Jill (J)	F	Adult	1985, captivity	San Diego, 1997
Rosie (R)	F	Adult	1989, wild	Zaire, 1998
Molaso (M)	F	Adult	1985, wild	Zaire, 1998
Zuani (Z)	F	Adult	1990, wild	Zaire, 1998
Lomela (LO)	F	Adult	1992, captivity	Frankfurt, 1998
Liboso (LI)	F	Juvenile	1997, captivity, Zuani's daughter	Zaire, 1998
Tarishi (T)	M	Infant	1998, captivity, Jill's son	Apenheul
Kumbuka (K)	F	Infant	1999, captivity, Molaso's daughter	Apenheul

TABLE 2. *Chimpanzee colony hosted at ZooParc de Beauval (St. Aignan sur Cher, Central France)*

Subject	Sex	Class	Date of birth	Original, arrival date
Joseph (JO)	M	Adult	1983, unknown birth	Cabosse, 1992
Gamin (GA)	M	Adult	1989, wild	Private, 1992
La Vieille (LA) ¹	F	Adult	1959, captivity	Paris, 1992
Charlotte (CH) ¹	F	Adult	1973, captivity	Paris, 1992
Micheline (MI)	F	Adult	1978, unknown 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	1988, captivity	Le Pal, 1993
Domi (DO)	F	Adult	1990, 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

¹ Two oldest adult females, not followed as focal animals.

Procedure

Age-class definition of the subjects under study.

Infants: Prepubertal animals that cannot survive the death of adult caretakers (Pereira, 1993).

Juveniles: Prepubertal animals that would be likely to survive the death of their caretakers or loss of parental provisions, but not yet sexually mature (Pereira, 1993).

Adults: Fertile animals. Menarche indicates the onset of fertility in females (Watts and Pusey, 1993). Males were considered mature when they were >10 years old.

I labeled infants and juveniles as *immature individuals* and all fertile animals as *mature individuals* or *adults*.

Data collection. Three observers (one of whom was the author) followed the chimpanzee group, and two observers (one of whom was the author) followed the bonobo group using scan animal sampling, focal animal sampling, and all-occurrences sampling methods (Altmann, 1974). As play behavior varies according to age (Fagen, 1981, 1993; Caine, 1986; Pusey, 1990; Mendoza-Granados and Sommer, 1995; Dolhinow, 1999; Palagi et al., 2002), in collecting data on this issue, the eight youngest subjects of the 10 adult chimpanzees were selected as

focal individuals, in order to have adult chimpanzees and bonobos of comparable ages. The ages of selected subjects of the two groups did not differ (randomization test for two independent samples: $t = 1.380$, $n_1 = 8$, $n_2 = 8$, n.s.).

For definitions of play patterns, see Table 3.

Data on the apes were collected by speaking into a tape recorder, and these records were later computer-transcribed. Before commencing systematic data collection, the observers underwent a training period (60 hr for chimpanzees, and 80 hr for bonobos). The same focal animals were followed by the observers simultaneously, and the data were then compared and discussed. Training was over when the observations matched in 95% of cases (Martin and Bateson, 1986).

Using scan animal sampling (Altmann, 1974), we recorded the frequency of play using a 5-min interval between subsequent scans. For each scan, the observers recorded date, time, actor, behavior, and possible receiver. Both groups were followed by scan sampling, yielding 344 hr (4,128 scans) for chimpanzees and 380 hr (4,224 scans) for bonobos.

By focal animal sampling (each focal sample lasted 30 min), we collected 824 hr (44 hr per subject) for chimpanzees and 452 hr of data (41 hr per subject) for bonobos. Each animal was followed every day and at different times of day in order to obtain data covering the entire day in balanced proportions as much as possible.

TABLE 3. *Play behavioral patterns recorded during observation sessions*

Gentle play patterns	Initials	Definition
Airplane	AIR	Adult lies on its back and raises infant up with its hands and feet
Grab gentle	GRG	Animal gently massages another
Play bush	PPS	Animal pushes playmate either with its hands or feet
Play bite	PBIT	Animal gently bites playmate
Play recovering a thing	PRCO	Animal chases playmate and attempts to grab object carried by it
Play slap	PSL	Animal slaps any part of playmate's body
Tickle	TK	Partner's body is contacted either with mouth or with hands
Rough play patterns		
Pirouetting	PIRO	One or more animals together turn, somersault, or roll over either on ground or on vertical supports
Acrobatic play	ACP	One (solitary play) or more animals (social play) climb, jump, and dangle from supports in environment (e.g., branches)
Play run	PRUN	Animal runs alone (solitary play) or chases play partner (social play)
Play stamping	PST	Animal jumps on play partner with its feet
Rough and tumble	RT	Two animals (or more) grasp, slap, and bite each other; this pattern is typical of immature individuals
Play brusque rush	PBR	Animal jumps with its four limbs on playmate
Play retrieve	PRE	Animal holds playmate to prevent its flight
Other patterns		
Play invitation	PI	Animal approaches possible play partner, pats it, and then goes away; this display is used to start play session
Play face	PF	Playful facial display: mouth is opened with only lower teeth exposed
Full play face	FPF	Playful facial display: mouth is opened with upper and lower teeth exposed

Under some conditions, it is possible to record all occurrences of certain classes of behaviors in all members of a group during every observation period. Such records are generally possible when 1) observational conditions are excellent, 2) the behaviors are sufficiently "attention-attracting," and 3) the behavioral events never occur too frequently. As in our cases all these conditions were met, we were able to use the all-occurrences sampling technique to collect any agonistic contact among all members of the two groups. We recorded date of aggression, identities of opponents (aggressor and victim, respectively), aggression intensity, context, and kind of conflict (decided or undecided). By means of the all-occurrences sampling technique, we collected 450 hr for bonobos and 412 hr for chimpanzees.

Data analysis

Hierarchical rank-order analysis was carried out with the aid of MatMan 1.0 software by Noldus[®] (De Vries et al., 1993). I analyzed the outcomes of all conflicts that occurred. Since there were tied or unknown relationships, the improved index of linearity (h') rather than Landau's index was calculated and tested by means of a randomization test with the aid of MatMan (Appleby, 1983; De Vries, 1995). The directional consistency (DC) index (Van Hooff and Wensing, 1987) gives the frequency with which the behavior occurred in its more frequent direction relative to the total number of times the behavior occurred. This index varies between 0 (completely bidirectional) and 1 (completely unidirectional). As another descriptive measure, I counted the number of one-way relationships (i.e., number of dyads in which a behavior is shown in one direction only), irrespective of the frequency of interactions within the dyads.

I carried out all analyses via randomization procedures with 10,000 shuffles (Manly, 1997). A one-sample

chi-square test (Zar, 1999) was employed to examine the percent deviation from expected in choice of play partners (immature and adult subjects) in the two species.

All analyses were two-tailed, and the level of significance was set at 5%. Probabilities between 5–6% are reported as trends. Conventional P -values are marked with an asterisk when significant ($P < 0.05$), a double asterisk ($P < 0.01$) when more significant, and a triple asterisk ($P < 0.001$) when highly significant. Statistical analyses were performed using Microsoft Excel, SPSS 9.05, and Resampling Procedures 1.3 by David C. Howell (freeware).

RESULTS

Kind of hierarchy, conflict outcomes, and formal submission

In order to evaluate whether the Apenheul bonobos actually showed a high degree of social flexibility and less structured relationships compared to the Beauval chimpanzees, the kind of hierarchy, conflict outcomes, and formal submission were analyzed. A linear hierarchy was not found among the adults of either species (chimpanzee $h' = 0.49$; bonobo $h' = 0.46$). However, there were some differences in their patterns of hierarchy. The directional consistency index was higher in chimpanzees (0.91) than in bonobos (0.66). Moreover, chimpanzees showed a lower frequency of two-way relationships (4.4%) than bonobos (25.0%). Bonobos showed significantly higher levels of undecided conflicts than chimpanzees (randomization test for two independent samples: $t = 4.006$, $n_1 = 8$, $n_2 = 10$, $P < 0.001$). In order to determine the level of formal submission, I analyzed the frequency of bobbing (BB) and pant grunting (PG). BB and PG were performed only by chimpanzees (mean hourly frequency: BB, 0.37 ± 0.14 SD; PG, 0.40 ± 0.15 SD). Moreover, chimpanzees showed a significantly higher

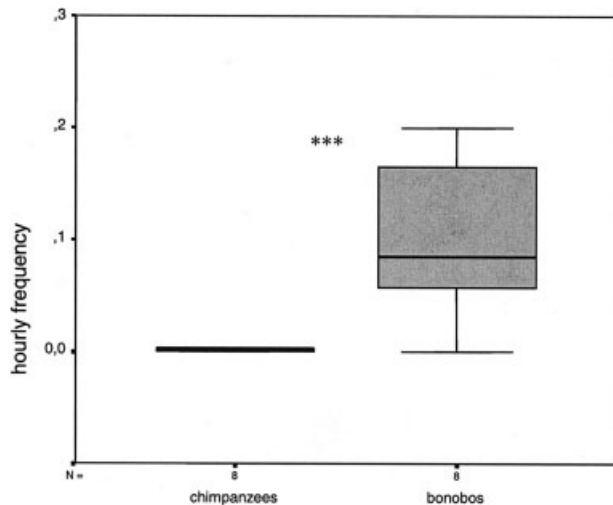


Fig. 1. Social play sessions among fertile individuals of two species (scan data). Solid horizontal lines indicate medians; length of gray boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values. *** $P < 0.001$.

frequency of bared teeth (a fear signal) than bonobos (randomization test for two independent samples: $t = -2.44$, $n_1 = 8$, $n_2 = 10$, $P < 0.05$).

Play in fertile subjects and play partner preference according to age

Overall social play (both with fertile and immature subjects) performed by adults did not differ between the two species (randomization test for two independent samples, focal data: $t = -0.793$, $n_1 = 8$, $n_2 = 8$, n.s.; scan data: $t = -0.139$, $n_1 = 8$, $n_2 = 8$, n.s.). In contrast, in bonobos the frequency of play interactions among adults was significantly higher than in chimpanzees (randomization test for two independent samples, focal data: $t = -2.587$, $n_1 = 8$, $n_2 = 8$, $P < 0.01$; scan data: $t = -4.229$, $n_1 = 8$, $n_2 = 8$, $P < 0.001$; Fig. 1).

The frequency of play invitation (PINV) performed and received by adults also differed significantly in the two species, with adult bonobos showing higher frequencies (randomization test for two independent samples: $t = 4.725$, $n_1 = 8$, $n_2 = 8$, $P < 0.001$). Mature bonobos directed PINV significantly more frequently to each other than to immature subjects (randomization test for two paired samples: $t = -2.486$, $n_1 = 8$, $n_2 = 8$, $P < 0.001$) (Fig. 2a), but there was no significant difference in the PINV distribution for chimpanzees ($t = -1.029$, $n_1 = 8$, $n_2 = 8$, n.s.) (Fig. 2b). However, the degree of deviation from expected revealed that mature bonobos invited other adults to play more frequently than immature individuals (Adult-Adult [AA], chi-square = 5.83, $df = 1$, $P < 0.02$; AI, chi-square = 13.6, $df = 1$, $P < 0.001$). It was not possible to test the preference of adult chimpanzees because of the extremely low frequency of PINVs recorded.

Play patterns used

During mature-immature play sessions, chimpanzees performed Play Slap (PSL) and Tickle, Grab Gentle, Airplane (TK/GRG/AIR) with a higher frequency than the bonobos (randomization test for two independent samples: PSL, $t = 4.491$, $n_1 = 8$, $n_2 = 8$, $P < 0.001$; TK/GRG/AIR, $t = 3.219$, $n_1 = 8$, $n_2 = 8$, $P < 0.01$). All other pat-

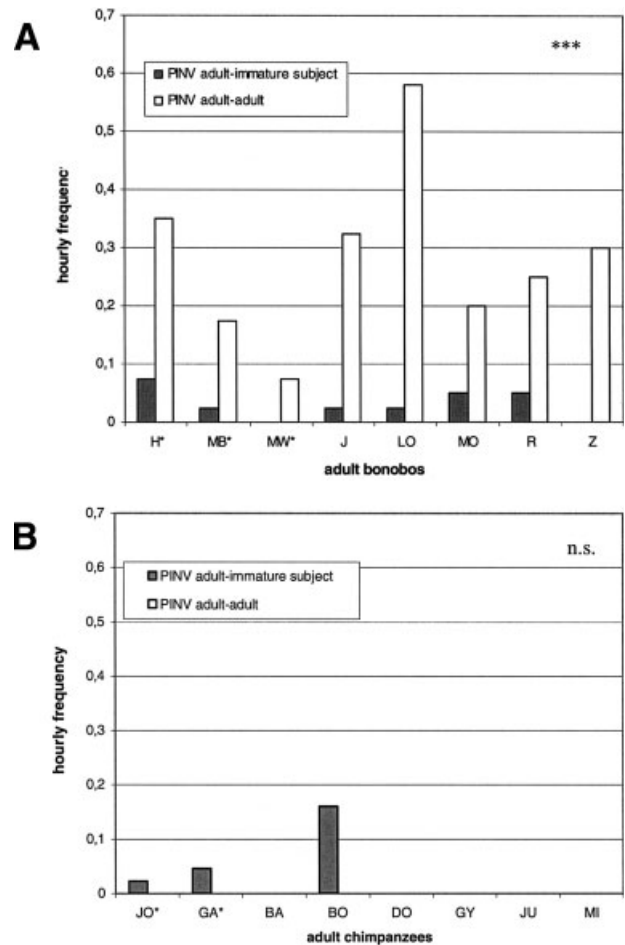


Fig. 2. Hourly frequency of PINV performed by each adult bonobo (A) and by each adult chimpanzee (*** $P < 0.001$). (B) toward immature subjects (shaded bars) and other adults (open bars). Asterisks indicate males.

terns did not differ between the two species (Acrobatic Play, Pirouetting [ACP/PIRO], $t = -2.051$, $n_1 = 8$, $n_2 = 8$, n.s.; Play Bite [PBIT], $t = 0.995$, $n_1 = 8$, $n_2 = 8$, n.s.; Play Brusque Rush, Play Stamping [PBR/PST], $t = 0.972$, $n_1 = 8$, $n_2 = 8$, n.s.; Play Push [PPS], $t = -0.741$, $n_1 = 8$, $n_2 = 8$, n.s.; Play Recovering a Thing [PRCO], $t = -1.000$, $n_1 = 8$, $n_2 = 8$, n.s.; Play Retrieve [PRE], $t = -1.017$, $n_1 = 8$, $n_2 = 8$, n.s.; Play Run [PRUN], $t = -0.433$, $n_1 = 8$, $n_2 = 8$, n.s.; Rough and Tumble [RT], $t = -0.488$, $n_1 = 8$, $n_2 = 8$, n.s.). In adult-adult play, bonobos used rough patterns more frequently than did chimpanzees: PBR/PST, $t = -2.046$, $n_1 = 8$, $n_2 = 8$, $P < 0.05$; ACP/PIRO, $t = -3.148$, $n_1 = 8$, $n_2 = 8$, $P < 0.05$; PRE, $t = -2.717$, $n_1 = 8$, $n_2 = 8$, $P < 0.01$; PRUN, $t = -2.312$, $n_1 = 8$, $n_2 = 8$, $P < 0.01$; RT, $t = -1.745$, $n_1 = 8$, $n_2 = 8$, $P < 0.05$. None of the other patterns differed between the two species (PBIT, $t = -1.944$, $n_1 = 8$, $n_2 = 8$, n.s.; PPS, $t = -1.500$, $n_1 = 8$, $n_2 = 8$, n.s.; PRCO, $t = -1.615$, $n_1 = 8$, $n_2 = 8$, n.s.; PSL, $t = -1.467$, $n_1 = 8$, $n_2 = 8$, n.s.; Tickle, Grab Gentle [TK/GRG], $t = -1.359$, $n_1 = 8$, $n_2 = 8$, n.s.) (Fig. 3).

Play signals

Immature chimpanzees and bonobos performed the play face with comparable frequency (randomization test for

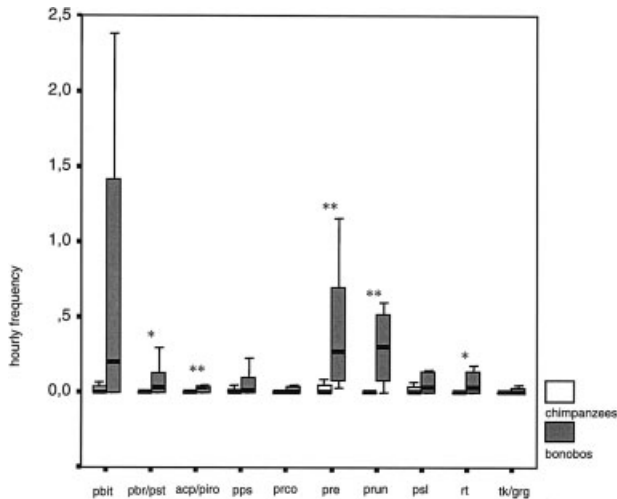


Fig. 3. Distribution of social play patterns among fertile individuals of two species. For abbreviations, see Table 3. Only significant differences are shown. * $P < 0.05$; ** $P < 0.01$.

two independent samples: $t = 1.1184$, $n_1 = 9$, $n_2 = 3$, n.s.), whereas the latter performed the full play face more frequently ($t = 1.1184$, $n_1 = 9$, $n_2 = 3$, $P < 0.01$). However, there was no difference in overall rate of performance of play signals between the immatures of the two species ($t = -1.218$, $n_1 = 9$, $n_2 = 3$, n.s.). For adults, there were no differences in the use of the play face ($t = 0$, $n_1 = 8$, $n_2 = 8$, n.s.), but adult bonobos showed a significantly higher frequency of the full play face ($t = -3.140$, $n_1 = 8$, $n_2 = 8$, $P < 0.01$). Moreover, adult bonobos performed play facial displays significantly more often than did adult chimpanzees (play face + full play face: $t = -3.001$, $n_1 = 8$, $n_2 = 8$, $P < 0.05$) (Fig. 4).

In chimpanzees, the frequency of facial displays per play session did not differ significantly during rough and gentle play sessions (randomization test for two paired samples: $t = 0.018$, $n = 17$, n.s., but note that two individuals were excluded from the analysis because they did not perform any rough play). On the other hand, in bonobos, play signals were performed significantly more frequently during rough play compared to gentle play ($t = -4.377$, $n = 11$, $P < 0.01$).

Distribution of play frequency according to different pairings of the sexes

Among fertile bonobos, play frequency did not follow a random distribution with regard to the partners' sex (randomization ANOVA, one-way: $F = 8.837$, $P < 0.01$). The randomization test for two independent samples revealed a significant difference between female-female (FF) and male-female (MF) combinations ($t = 3.501$, $n_1 = 10$, $n_2 = 15$, $P < 0.001$), and a strong trend between FF and male-male (MM) combinations ($t = 2.334$, $n_1 = 3$, $n_2 = 10$, trend) (Fig. 5). In chimpanzees, there were no significant differences with regard to sex of playmates (randomization ANOVA, one-way: $F = 0.124$, n.s.). Among fertile bonobos, the female/female combination was significantly overrepresented (FF: chi-square = 79.1, $P < 0.001$), whereas male/male and male/female were significantly underrepresented (MM: chi-square = 13.4, $P < 0.001$; MF: chi-square = 31.6, $P < 0.001$). In mature chimpanzees, it was not possible to test for the deviation

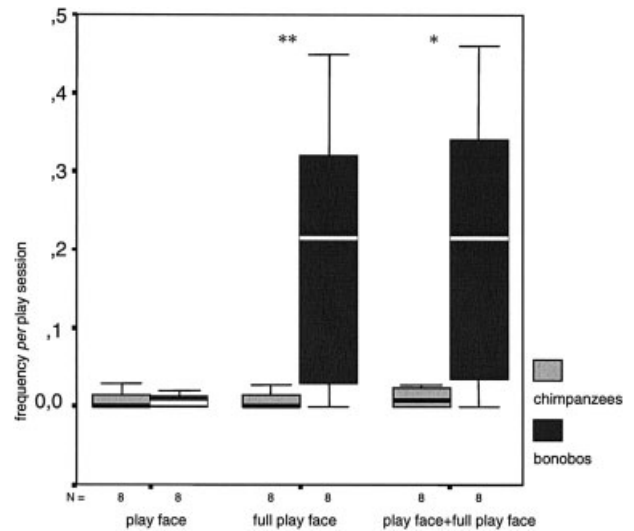


Fig. 4. Frequency of two play facial displays per play session in adults of two species. Solid horizontal lines indicate medians; length of gray boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values. Only significant differences are shown. * $P < 0.05$; ** $P < 0.01$.

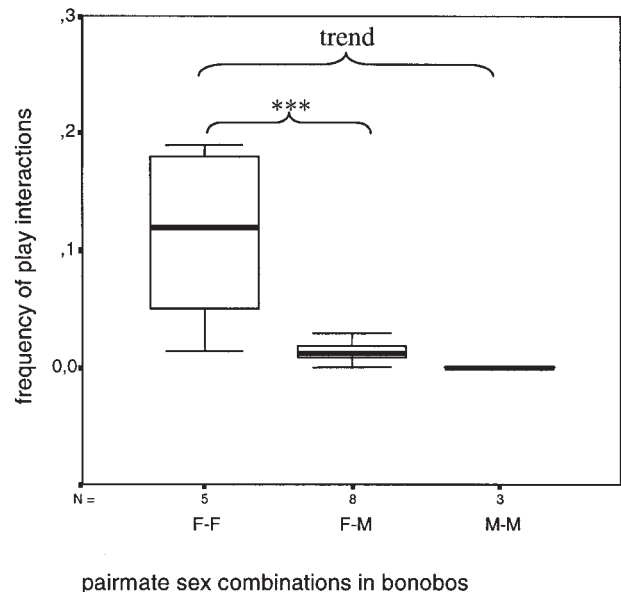


Fig. 5. Distribution of adult-adult play frequency according to pair-mate sex combinations in bonobos. F, female; M, male. Solid horizontal lines indicate medians; length of gray boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values. *** $P < 0.0001$.

from expectation due to the low frequency of play sessions recorded.

DISCUSSION

Primates are notably social and have complex developmental pathways (Fagen, 1981). Play has an essential role not only for developing skills per se, but also for enlarging the behavioral repertoire and refining motor, cognitive, and social abilities (Brown, 1988; Dolhinow, 1999). Although play is typical of juvenile primates, in

some species it is also present during adulthood (Pellis and Iwaniuk, 2000). A possible mechanism for the retention of play in adulthood is neoteny (Enomoto, 1990). However, several variables, such as age, sex, demography, sociobiology, and habitat, can affect the expression of playful behavior in both juveniles and adults (Poirier et al., 1978; Dolhinow, 1999).

To determine whether the two *Pan* species differed in playful behavior, overall play levels in mature subjects were analyzed; I found no difference in overall play levels. This finding supports prediction 1. However, play between fertile individuals was more frequent in bonobos than in chimpanzees (Figs. 1, 2a,b). These findings are 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 involved 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 (Loizos, 1967; van Lawick-Goodall, 1968; Merrick, 1977) suggested that play appears to give way to other forms of social behavior as adulthood is reached (e.g., adult chimpanzees increasingly spend more time engaged in social grooming). In describing playful behavior in wild bonobos, Enomoto (1990) provided some examples of adult-adult play.

Pellis and Iwaniuk (2000) stated that adult social play is present to a higher extent in species with infrequent social aggregation. In such fluid societies, where individuals encounter one another periodically, play among mature individuals may be used for social assessment purposes. Based on a detailed study of play in rhesus monkeys, Brueggeman (1978) argued that social manipulation is a potentially important function of play, particularly when it occurs among adults. Since bonobo society is based on a fission-fusion system, comparable levels of adult-adult play in the two *Pan* species were expected (prediction 2), but the striking difference in play frequency between the adults of the two species would not seem to support prediction 2. The data on the species' difference in mature play seems to support prediction 2bis, i.e., that mature play should be more frequent in the more egalitarian bonobos.

The use of play for social assessment seems to be most important when relationships among individuals are not codified and structured according to rank-rules. The findings regarding the level of undecided conflicts (more frequent in bonobos than in chimpanzees) and formal submission displays (lacking in bonobos) agree with previous work in suggesting that bonobos exhibit egalitarianism (de Waal, 1995, 2001; Fruth et al., 1999; Fortunato, 2003). Some authors emphasized that play patterns reflect the social organization of a species (Cheney, 1978; Miller and Nadler, 1981; Zucker et al., 1986; Watts and Pusey, 1993; Maestripieri and Ross, 2004). If adult-adult play has a fundamental role in social assessment, then such play should be retained in egalitarian societies rather than in despotic ones. Moreover, Pellis and Iwaniuk (2000) suggested that play-fighting may be used both to maintain social bonds and to test for weakness of play partners and therefore gain social advantage (Pellis et al., 1993; Paquette, 1994). Consistent with this view is the finding that the Apenheul adult bonobos frequently play using rougher patterns of behavior (Fig. 4), a tendency already present in the adult-immature play ses-

sions. Among fertile subjects, rough play is probably more effective for assessing social bonds than more gentle forms of play. In this view, play-fighting might be a sort of competitive interaction that serves both to test a partner's willingness to invest in a relationship, and simultaneously to demonstrate willingness to accept vulnerability.

Differences were also present in the performance of play facial displays. Immature individuals of the two species performed play signals with comparable frequency, but they differed with regard to which of the two different configurations of play face they performed more often. Immature chimpanzees performed the play face more frequently, whereas bonobos mainly performed the full play face more often. Furthermore, adult chimpanzees ceased performing play signals altogether, whereas adult bonobos continued to perform the full play face at a high frequency. Moreover, in chimpanzees, the frequency of play signals was not affected by the roughness of play, while bonobos showed significantly higher levels of play signals during rough play than during gentle play (the second part of prediction 2bis confirmed). Van Lawick-Goodall (1968) stated that the play face in the chimpanzees of the Gombe Stream Reserve sometimes involved the showing of both rows of teeth. She interpreted this greater tooth exposure as signifying a higher intensity of play. It is also possible that in socially ambiguous situations, the baring of the upper tooth row (full play face) might represent the introduction of an element of appeasement, since the facial expression now bears more resemblance to the bared-teeth display, which can have an appeasing function (Loizos, 1967).

The high level of full play face found both in immature and, particularly, in adult bonobos (Fig. 4) might be explained by their strong tendency to perform rough play more frequently than chimpanzees (Fig. 3). The full play face is probably performed whenever a clear statement of purpose (e.g., "I am playing") is necessary, especially when play becomes rougher. In fact, play-fighting can be a risky affair (Bekoff, 1995; Bekoff and Allen, 1998), and an "amicable" play signal could be particularly useful in de-escalating such an encounter (Pellis and Pellis, 1996). The selective use of play signals by bonobos in rough vs. gentle play sessions might also corroborate the hypothesis proposed by Pellis and Pellis (1996) that 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 playmate shows weakness, then their dominance relationship may be reversed. In contrast, if the playmate responds by also escalating the encounter, then the partner may signal its play intention to diffuse the situation (retroactive function).

The frequency of social play among bonobo females was higher than in any other sex combinations, thus confirming prediction 3 (Fig. 5). This finding runs counter to the commonly held view that intrasexual play among fertile animals is rare in nonhuman primates (Fagen, 1981). In bonobos, females cope with a male philopatric society by achieving a dominant position, and they do this by cooperating and supporting each other (Kano, 1980; Kuroda, 1980; Furuichi, 1989; Parish, 1994, 1996). Social play among female bonobos may help to facilitate the development of the necessary social bonds to make such cooperation possible.

Another nonprimate mammal species where adult play among females is commonly observed is the spotted hyena (*Crocuta crocuta*) (Fagen, 1981; Burghardt, 1999). This species is characterized by a fission-fusion society, with female dominance and male dispersal. Female spotted hyenas engage in more social play than males (Burghardt, 1999). If social play is a biological adaptation, the occurrence of play behavior to such a high extent both in bonobo and in spotted hyena females may have arisen from evolutionary convergence. Females of both species might use play to test the quality of their relationships. Konner (1975) noted that social play may 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. Other authors (Fagen, 1993; Bekoff, 2001) stressed that if two or more individuals play together for long periods of time, then *cooperation* has to occur much more frequently than conflicts of interest. In fact, failure to negotiate and cooperate prevents animals from continuing to play together and can lead to a decline in honest interaction and cooperation in other behavioral contexts (Dugatkin and Bekoff, 2003).

As a matter of fact, social play can be viewed as a balance between *cooperation* and *competition*. Among bonobo females, characterized by social competence and affiliation, social play might enhance their behavioral flexibility and so further increase their socially symmetrical relationships which, after all, are the basis for their egalitarian society.

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