Play behaviour: A functional approach

by focussing on adult-adult social play in the bonobo (*Pan paniscus*)

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Abstract

It is hard to find an appropriate definition of 'play' in animals that encompasses all its forms and varieties. Consequently, the adaptive function of play is a highly debated subject. Here, we review earlier proposed hypotheses about the functionality of play. Specifically, we describe hypotheses for a less common form of play: adult-adult social play. In addition, a case study on social play in adult bonobos (*Pan paniscus*) is provided. We use recordings of social play in European zoos (Apenheul, Frankfurt, Stuttgart and Wuppertal) to test predictions drafted from earlier proposed hypotheses. These entail that adult social play is used to assess and manipulate uncertain social relationships. Our preliminary results seem to confirm that the certainty of inter-individual relations play an important role in the adaptive function of (adult) social play.

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Introduction

Humans and animals share an intrinsic drive to engage in ludic competitive activities with conspecifics. By its very nature, such playful behaviour affects both humans and animals positively (Panksepp, 1984). Usually, three (often overlapping) play forms are distinguished: object play, locomotor-rotational play, and social play. Object play entails the playful exploration and manipulation of objects in the environment. Locomotor-rotational play often resembles behaviours used in normal locomotor activities, but are performed in an exaggerated fashion. Social play involves more than one play participant. It is typically seen as a form of play fighting, including behaviours like slapping or wrestling. However, social play can also involve locomotor-rotational play, for example when individuals chase each other (Bekoff and Byers, 1981; Fagen, 1981; Power, 2000; Palagi and Paoli, 2007; Graham and Burghardt, 2010). Sometimes there is a vague distinction between play and non-play that is difficult to interpret for an observer, but most importantly needs to be discriminated by the individuals that engage in social play (Power, 2000; Bekoff, 2001). To prevent escalation into aggression and to initiate or maintain a playful interaction, animals must communicate their playful intentions (Bekoff, 2001; Palagi, 2008). This makes social play specifically a complicated and sophisticated type of social behaviour (Palagi and Paoli, 2008) and particularly interesting to investigate in animals.

The difficulty of studying play behaviour is that the concept of "play" is difficult, perhaps even impossible, to define accurately and objectively (Tinbergen, 1963; Panksepp, 1984). Burghardt (2005) listed sixteen earlier noted differing views about play behaviour that contrasted greatly with each other, indicating the difficulty of grabbing hold of this phenomenon. Play can take on varying forms within one species but also differs between species (Enomoto, 1990; Špinka et al., 2001). Additionally, it is receptive to anthropomorphism (Tinbergen, 1963), and the benefit of playing is difficult to interpret on a first sight (Enomoto, 1990). Thus, even after years of studying play, it still seems that we can only understand what "play" is by describing what it is not: It lacks certain characteristics, or is a "non-serious variant", of functional behaviour (e.g. aggression) (Burghardt, 2005; Palagi

and Paoli, 2008). From this follows that behaviours used in play often resemble behaviours used in 'serious' contexts. An important difference is that in play animals are more involved with the actual performance of the behaviour, rather than in which it may result (Pellegrini *et al.,* 2007).

Since we are struggling to come up with a satisfactory, all-round definition of play, Burghardt (2005) proposed five criteria to clearly distinct play from other behaviours; Play is 1) not "fully functional in the form or function in which it is expressed" (i.e. does not contribute to current survival), 2) is purposed for oneself (i.e. is rewarding, pleasurable, spontaneous, voluntarily etc.), 3) differs from "serious" behaviour by structure or timing in at least one way (i.e. is incomplete, exaggerated, role reversals are frequent, etc.), 4) is a repeated behaviour, but without characteristics of stereotypical behaviour, and 5) occurs when the animal is in a "relaxed field" (i.e. is without immediate threats) (Burghardt, 2005: pp. 71-78).

Play frequency decreases, or complete ceases, when animals are in presence of stressors (e.g. food limitation). From this it can be taken that there are at least some costs involved with play behaviour (Fagen, 1993, Pellegrini *et al.,* 2007). Indeed, there are direct risks involved. Individuals, most noticeably juveniles, face increased risk of transmitting diseases (Kuehl *et al.,* 2008) and getting injured or predated (Fagen, 1993). However, the cost of play in terms of loss of calories, loss of time and decrease in survivorship have been estimated as 'moderate' (Fagen, 1981 cited in Pellegrini *et al.,* 2007).

The (fast) disappearance of play under the influence of stressors also indicates that the ultimate benefits are not high enough to retain the behaviour when under pressure (Špinka *et al.,* 2001). Therefore, play is sometimes designated as "luxury" behaviour (Lawrence, 1987). Consequently, one could wonder if there are any benefits associated with play. Yet, play is widely present in the animal kingdom. Play is very common among mammals (Špinka *et al.,* 2001), but also in a number of bird species. Complex social play is mainly found in corvids and parrots (Diamond and Bond, 2003). Increasingly more non-mammals such as reptiles are also found to exhibit play behaviour (Burghardt, 1996). This wide array of animals that exhibit play behaviour despite the risks and costs involved, can be seen as proof for beneficial aspects of play (Barber, 1991). If no benefits could be attributed

to a behaviour, natural selection should have selected against it and it should not be present today (Fagen, 1993; Graham and Burghardt, 2010). In other words, costly activities like play must be functional or else playing animals would be disadvantaged compared to animals that do not play or play less (Fagen, 1993).

The importance of play was stated already over a hundred years ago: "Animals cannot be said to play because they are young and frolicsome, but rather they have a period of youth in order to play" (Groos, 1898: pp. 75). Yet, empirical proof remained absent for a long time. Now, some examples exist. Belding's ground squirrels (*Spermophilus beldingi*) show a positive correlation between rate of social play and the successful weaning of a litter in the first year of life (Nunes, 2004). Consequently, we can now quite certainly state that there must be benefits to play. Nonetheless, a general applicable hypothesis for the adaptive function of play has yet to be proposed (Špinka *et al.,* 2001).

In this paper, we study the adaptive function of play. First, we describe three theories that have framed most of the recent hypotheses on play functionality, and we will shortly discuss a few of these more recent hypotheses. We debate what the difficulties are of proposing an accurate hypothesis on play functionality. Then, we describe phylogenetic and ontogenetic aspects of play behaviour needed to understand the adaptive function of play. The focus will then shift to a more ambiguous and less common case of play behaviour; adult social play. We discuss hypotheses proposed specifically for this type of play. Last, we will provide a case study in which we aim to examine predictions drafted from these hypotheses. Primates have the longest juvenile stage of life relative to body size of all mammals (Watts and Pusey, 1993) and are all characterized by high rates of play (Fagen, 1993). A great ape, the bonobo (*Pan paniscus*), has been suggested to be an extremely playful primate species. It displays high levels of social and solitary play continuing into adulthood (Enomoto, 1990; Palagi, 2006; Palagi and Paoli, 2007), but few data are available on adult-adult bonobo play. We therefore designated this as the model of our case study. We examine recordings of bonobo play behaviour in four zoos in Europe (Apenheul (NL), Frankfurt (DE), Stuttgart (DE), Wuppertal (DE)), to provide preliminary results on adult play behaviour in light of earlier proposed hypotheses.

Theories on the adaptive function of play

Statements about play, at least in humans, date back to Plato (360 B.C.) (Livescu, 2003). Consequently, the number of viewpoints on the function of play is overwhelming. Three main historical views can be identified that frame most of the existing theories on animal play, as listed by Burghardt (2005); surplus energy, instinct practice and recapitulation (Burghardt, 2005; Graham and Burghardt, 2010).

1) Surplus energy

One of the earliest views on play behaviour is the *'surplus energy theory'*. Originally, Friedrich von Schiller, an 18th century German poet, put in words that play is a way of releasing excess energy. Yet, this theory is usually attributed to Herbert Spencer (1873), who stated that 'higher' animals (i.e. mammals) have an abundance of energy, which at a certain point may release itself in a simplified imitation of serious behaviours; play (cited in Groos, 1898).

2) Instinct practice

Groos's (1898) theory stated that play is a way of practicing for the future. He pointed out that behaviours only start occurring when they are needed, for example foraging only starts when animals are no longer fed by their parents. If there would be no practice in the form of play behaviour, an animal would have to be born with a perfectly developed instinct. For example, a young tiger that needs to start feeding itself, would have to be perfect in seizing a prey and killing it without any practice once it is no longer fed by its parents. Groos argued that this is unlikely and that play therefore is used to perfect the innate instinct in animals, as a way of practicing skills that are needed during adulthood (Groos, 1898).

3) Recapitulation

Hall (1904) is known for the expression: "ontogeny recapitulates phylogeny", meaning that different stages of life are shortened versions of phylogenetic history that do not necessarily serve a function today. So, play is the 'left-over' of once important behaviour. For example, children that climb trees re-enact our primate phylogenetic history. Although he did see play as a remnant of once important behaviour, he did not state it was not important. He described play as a necessary developmental process in which the organism is perfected and is able to explore the world around it (cited in Burghardt, 2005; Pellegrini and Smith, 2005).

Each of these three historical views have been abundantly criticized. But, although they contrast each other greatly, one could wonder if they exclude each other (Burghardt, 2005). In fact, these theories focus on different areas of Tinbergen's four questions and thus are not mutually exclusive (Graham and Burghardt, 2010). Schiller's and Spencer's original theory can be considered a proximate cause, explaining the mechanism on how play can occur in a species. Hall's theory mainly explains ontogenetic origins of play, and also focusses on phylogenetic aspects of play. Only Groos's theory describes a possible function for play (Graham and Burghardt, 2010). Yet, these three theories can often be traced back in modern views on the functionality of (juvenile) play. We will shortly list some of the best outlined theories on the adaptive function of play;

I)   Surplus energy (modern)

The surplus energy hypothesis goes against the general idea that play is costly because of energy loss. Barber (1991) points out that this idea is true, but only if we assume that energy is in short supply. He states that animals have an abundance of energy supplies. Excess energy is stored as fat reserves and one example where energy loss is beneficial is that lean individuals have an advantage over obese individuals (e.g. ability to escape predators). The little occurrence of obese animals in

nature may be explained by the existence of "BAT", a site in the brain that induces thermogenesis when over-ingestion of energy supplies occurs. Thermogenesis wastes energy, thus regulating energy maintenance. Play triggers thermogenesis in BAT. Besides preventing obesity, play induced thermogenesis has other benefits, such as protection against pathogens and cold exposure. If play occurs repeatedly, it increases the caloric capacity of BAT (Barber, 1991). This theory shows that Spencer's surplus energy theory remains present in modern hypotheses on play. But, the surplus energy hypothesis has yet to be excepted. For example, the hypothesis predicts that play increases when animals have a higher food intake. A study on Belding's ground squirrels (*Spermophilus beldingi)* proved the opposite. Juveniles that had a high food intake played less than ones that had low food intake (Nunes *et al.,* 2004).

II)   Sensitive period hypothesis

The function of play was early on related to the exercise and development of muscles and skills (Brownlee, 1954). Many variants of this 'motor training' theory have been proposed, and consequently a variety of terminology developed. Essentially, they are all concepts related to Groos' *instinct practice* theory. Byers and Walker (1995) refined the motor training hypothesis. Three types of benefits related to motor training were specified and examined as possible functions of play: Greater endurance, increased strength and increased motor skill/energetic economy of movement. All effects related to the first two benefits were not specific to the juvenile phase and thus were likely to promote an immediate benefit that can be gained at any age. However, it is possible that play bouts do not last long enough to truly improve endurance or strength. Furthermore, these effects diminish quickly and so are not permanent (Byers and Walker 1995). Consequently, Byers and Walker (1995) searched for an effect of which the sensitive period for development overlaps with the increased occurrence of play behaviour in early life, and of which effects are permanent. The most likely benefit of play would as a result be the modification of

muscle fibre differentiation and cerebellar synapse distribution. This hypothesis was later termed by Byers (1998) as "*sensitive period hypothesis*".

III)   Self-assessment hypothesis

Thompson (1998) proposed the "*self-assessment hypothesis*". This hypothesis posits that play gives the opportunity to immediately assess an individual its physical ability. This leads to play activities having two possible outcomes: succeeding (winning) or failing (losing). It states that playing has a role in managing development. If an animal succeeds in doing a motor or social task, it will continue into a more difficult task. If not, it will switch to an easier task. Thus, play is a way of self-assessment (Thompson, 1998).

IV)   Training for the unexpected

Špinka *et al.* (2001) defined the "*Training for the unexpected hypothesis*". This hypothesis focuses on play as a way of practicing for situations in which animals lose control over where they are or how they move, such as when fleeing from a predator. The animal wants to escape, but will be interrupted in its own motor patterns by the activities of conspecifics and the opponent, and the presence of objects in the habitat. In order to recover from shocks such as falling, colliding, or being shaken, standard movements are combined with non-typical movements (Špinka *et al.,* 2001). Play can give the practice regarding locomotion patterns to prepare for these types of occurrences. Perhaps animals are able to recover faster in unexpected situations, which can mean the difference between life and death in certain situations (Špinka *et al.,* 2001). In addition, emotional aspects of unexpected situations such as being confronted with a stranger, predator or dominance conflicts, can be practiced in order to prevent emotional overreaction, or panic. Panic will decrease the chance of an animal its survival (Špinka *et al.,* 2001).

The play debate: Why play?

The varying views on the adaptive function of play behaviour makes studies contemplate if there is one 'true' hypothesis. Špinka *et al.* (2001) argued that we should study play as one phenomenon and try to posit a single ultimate explanation for the existence of play. Two reasons were given: The distinction between behaviour that is "play" or "non-play" is clear, suggesting that all play has some shared aspects which would make it not sensible to divide play into separate categories. Second, play is found in nearly all mammal species, making it questionable that it has repeatedly evolved on independent occurrences (Špinka *et al.,* 2001).

Alternatively, it can be wondered whether the proposal of one hypothesis for the function of such a variable phenomenon is possible. We do seem able to differentiate between play and non-play, especially using Burghardt's five criteria (2005), but it is important to notice that 'play is in the eye of the perceiver' (Fagen, 1993). Human observers may be wrong to interpret certain behaviours as play. Sometimes play and non-play can be quite difficult to distinguish (Power, 2000). Furthermore, play varies greatly across species, and within species of different sex or age (Enomoto, 1990; Barber, 1991). Brain mechanisms underlying these varieties probably differ (Graham and Burghardt, 2010). Thus, there are likely varying adaptive functions of play (Barber, 1991; Fagen, 1993; Watts and Pusey, 1993; Power, 2000; Burghardt, 2005), and perhaps we can only state that we have not found the *main* function of play (Burghardt, 2005; Graham and Burghardt, 2010).

As an animal develops from infant to adult, each stage of life may bring upon a different set of behavioural and physiological characteristics (Palagi and Paoli, 2007), which can be traced back in the differential forms of play (Barber, 1991)**.** The graph that represents play frequency throughout life is comparable for human and nonhuman animals. Play begins at a low rate just after birth, then increases quickly during infancy and (early) juvenility up to a peak and then declines again after or during juvenility through adolescence (Byers, 1998), but does often continue into adulthood (Špinka *et al.,* 2001) (figure 1). Mostly, adult play is seen in the form of adult-infant social play, where the infant typically initiates a

play session (Pellis and Iwaniuk, 2000b). But, adult-adult social play does occur, of which humans are the most clear example. For example, many humans are engaged in games (e.g. soccer, chess) long past their juvenile phase. Yet, play in the adult phase does occur at much lower rates than during the juvenile phase (Byers and Walker, 1995). Consequently, until recently studies of play have mostly neglected this behaviour in adults (Palagi, 2006) and focuses on functionality of play during infancy and early juvenility.

The increased occurrence of play during early life, and because it is inherent to play behaviour that we cannot interpret its immediate benefits on first sight (Enomoto, 1990; Bekoff, 2001; Graham and Burghardt, 2010), has led to the 'delayed-function approach'. Groos's instinct practice theory was first to state that play has a delayed function useful during adulthood (Groos, 1898), and is now incorporated into many of the modern views. This approach has been criticised (Burghardt, 2005; Held and Špinka, 2011) for a number of reasons. First, the initial and presumably most effective approach of attributing function to behaviour is to study immediate benefits (Burghardt, 2005). After all, the existence of delayed benefits is difficult to empirically prove (Power, 2000), but the existence of immediate benefits was recently proved. Fagen and Fagen (2004) conducted a field study on brown bears (*Ursus arctos*) and found that juveniles had more chance to survive the end of their second summer if they played more during their first summer, irrespective of salmon availability, condition of the bear and traits of the mother (Fagen and Fagen, 2004).

An additive problem with the delayed-function approach is that survival rates, independent of play behaviour, are relatively low during infancy. It is not sensible that play occurs at high rates during times of life where mortality rates are highest, when it only serves the individual during later stages of life (Burghardt, 1984 in Graham and Burghardt, 2010). Last, if we aim to find a main hypothesis for the function of play, the delayed function approach is not applicable to adult play, since that individual has already successfully survived into adulthood (Barber, 1991; Graham and Burghardt, 2010; Held and Špinka, 2011). Recent research realized the problems with a delayed function approach and there is now a shift of focus back to immediate benefits of play (Burghardt, 2005; Held and Špinka, 2011).

Summarizing, we face a few problems in proposing an adaptive function to play. First, there is discussion about the proposition of one overlapping hypothesis, or if there must be differentiated between different categories of play. Second, must focus be on immediate benefits, or should the possibility be retained that play may have delayed benefits?
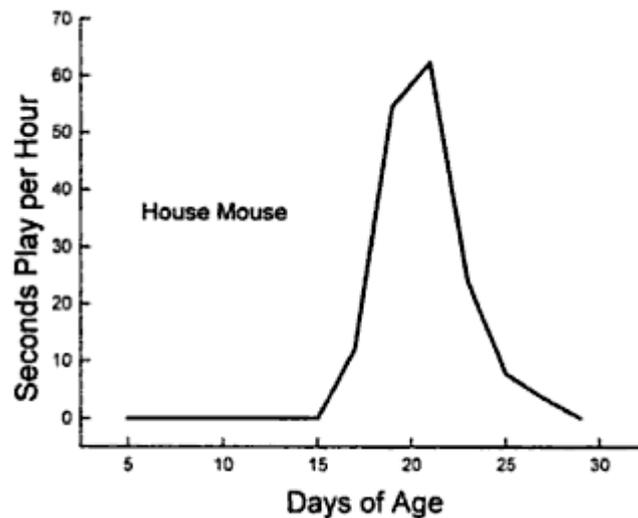
Figure 1: The age distribution of play rate for the house mouse (source: Byers, 1998 as redrawn from Byers and Walker, 1995)

An evolutionary view on adult social play

Before proposed adaptive functions of adult-adult social play will be reviewed, it is important to understand more about the phylogenetic and ontogenetic aspects of play (Tinbergen, 1951; Burghardt, 2005). Pellis and Iwaniuk (2000b) proved through phylogenetic comparative analyses that play is correlated with the degree of postnatal development. This was measured as the percentage of adult weight at birth. Animals with a higher percentage of adult weight at birth, experience less postnatal growth. It was found that animals with a higher degree of postnatal development, generally play more frequently and more complex.

In primates, the frequency and complexity of play was highly dependent on the percentage of adult brain weight at birth (60% of variance) (Pellis and Iwaniuk. 2000b). Thus, play is to a certain degree correlated to the degree of postnatal development of an animal. However, as pointed out by Pellis and Iwaniuk (2000b), this does not clarify the direction of the causality. It could be, as Groos (1898) stated, that animals have a period of youth because they must play, or, animals play because they have a period of youth (Pagel and Harvey, 1993).

More specifically, we can regard three processes of play that apply both in phylogenetic as ontogenetic terms (Burghardt, 2005; Graham and Burghardt, 2010). *Primary process play* is the result of other factors that do not relate to the behaviour itself, like dismissing excess energy or preventing boredom. It is not necessarily adaptive for future behaviour. Note that Spencer's surplus energy theory and Hall's recapitulation theory focus on the existence of such play behaviour. *Secondary process play* develops an importance in maintaining or perfecting the condition of the animal once it is established. This can be regarding physiology or behaviour, like perfecting skills used for predation. Last, *tertiary process play* is important in modifying, improving and innovating behavioural skills. Note that Groos's theory focusses on secondary and tertiary process play, like most modern theories (e.g. Thompson's self-assessment hypothesis) (Burghardt, 2005; Graham and Burghardt, 2010), and that it relates more to adaptive benefits of play.

Last, we will consider a fitness model, composed by Fagen (1993), that can be used to investigate adaptive benefits of play during different phases of life. The model assumes that play has low costs, and that it provides equal benefits across all ages. If these assumptions are correct, the model provides one possible explanation for differential rates of play depending on age; play is differentially risky at varying ages. From this follows that play rates should be highest when risks involved with playing are lowest. But, what actually occurs is opposite to the expectation. Play risks are lower in older juveniles than in infants, while play occurs mostly in infants and decreases in older juveniles (Fagen, 1993). Consequently, Fagen (1993) posed that the assumptions in the model are incorrect. He then proposed that two possible outcomes are possible: 1) Play is more costly than the model assumes, and consequently occurs more when resources are more abundant or nutritious, or, 2) Play is not

equally beneficial across all ages, and thus increasingly occurs when it is most effective, or, a combination of these two statements (Fagen, 1993).

When it is assumed that the first statement is correct, it is expected that play increases when resources are more abundant. Indeed, Sharpe *et al.* (2002) found that when meerkats (*Suricata suricatta*) were experimentally provisioned with food, play rates increased compared to non-provisioned animals, irrespective of changes in time budget due to foraging reduction (Sharpe *et al.,* 2002). From this follows that costs associated with play are possibly higher than expected (Fagen, 1993; Sharpe *et al.,* 2002). The energy cost of play, integrated in Spencer's surplus theory, can either be regarded as the physical requirements in order for play to occur (Burghardt, 2005), or as a beneficial consequence of play (Barber, 1991). We can summarize that play is a "facultative response to nutritional conditions" (Barber, 1991: pp. 133-134) and its frequency is related to the availability of adequate resources and nutritive demands (Fagen, 1993; Sharpe *et al.,* 2002).

On the other hand, the second outcome of the model predicts that benefits differ across life. This may also provide insight in why play is less often seen during adulthood than during early life. Animals play most during that time of life when play is both more risky and when their survivorship possibility, independent of play, is quite low (Fagen, 1993). Benefits of play during this time of life must outweigh both of these factors. Consequently, it could indeed be that benefits are more effective during infancy and early juvenility than during adult life.

Summarizing, it is proposed that the occurrence of play is related to the length of postnatal development. For primates, this specifically goes for development of the brain (Pellis and Iwaniuk, 2000b). Furthermore, play evolves as a primary process, which is likely correlated with the energy cost of play. However, play is able to gain complex adaptive functions both in phylogenetic as in ontogenetic terms. The acquired benefits may vary across different stages of life. Thus, if we focus on the individual, that would mean that play can, for example, in some variances be a way of releasing excess energy, but in other forms it can be used to innovate novel behaviours (Burghardt, 2005).

The innovation of new behaviours have been integrated in some of the earlier mentioned modern theories. For example, Pellegrini *et al.* (2007) proposed that play is a way to form innovative behaviours that are particularly important to survive in a changing environment. The innovation of behaviours can be beneficial because it would increase the resistance against shifts in the environment, increasing developmental plasticity (Pellegrini *et al.,* 2007). Špinka's 'training for the unexpected hypothesis' predicted that adults continue playing if they have to deal with unpredictable conspecifics, and hunting or being hunted (Špinka et al., 2001).

Adaptive functions of adult social play

It is sometimes suggested that adult play is a neotenic trait. The occurrence of adult play would then be a residue of juvenile behaviour retained into adulthood (Enomoto, 1990). This theory can be traced back in Hall's recapitulation theory.

However, there are also theories that suggest an adaptive function to adult-adult social play. Pellis and Iwaniuk (1999b) examined a possible adaptive function of play between adults that states that it can familiarize individuals that potentially will become pair mates. In this scenario, it could decrease the occurrence of aggression caused by the unfamiliarity between the individuals. It could also be used to assess the other individual in mate quality. A comparative analyses among courtship play in 35 primate species revealed that indeed a large percentage of the variance was explained by the level of association between male and female (Pellis and Iwaniuk, 1999b).

Yet, this hypothesis does only explain play that occurs in a courtship related context. Research has shown that play, phylogenetically spoken, first appeared in a context not related to courtship and only later evolved a function in courtship (Pellis and Iwaniuk, 2000a). Furthermore, it does not explain why play occurs between two adult females or two

adult males. Recently, two hypotheses have been proposed as adaptive functions of adult-adult social play in non-sexual contexts: tension reduction and social assessment.

Palagi (*et al.,*2004; 2006) focussed on play as a tension reduction mechanism. They assessed play rates in captive chimpanzees around the stressful event of feeding. Feeding can be stressful because it requires competing over a limited amount of food. It was found that play rates between adults and unrelated juveniles were higher just before the feeding. These individuals spend more time in proximity to each other when feeding commenced. Unrelated juveniles also played more often before feeding, although they did not spent more time co-feeding afterwards. Adults did not show a similar pattern. The authors suggested that the higher play rates before feeding functioned to reduce tension and to anticipate for conflicts with adult relatives of the juveniles, by performing a social behaviour before the stressful event. The higher rates of co-feeding would support this suggestion. Adults that play with unfamiliar juveniles may test the relationship with the adult related to that juvenile. Perhaps playing 'fair' with the juvenile sends an indirect message to the adult related to that juvenile (Palagi *et al.,* 2004).

Later, a similar test was performed with bonobos. Adults played more often with each other and with juveniles during pre-feeding times than when during feeding, post-feeding or control times. Consequently, adults co-fed more often when they had played during pre-feeding times (Palagi *et al*., 2006). This indicates that stress was anticipated by increasing social behaviour. From this it was concluded that play is used to reduce tension on short terms (Palagi *et al.,* 2006).

Recently, the tension reduction hypothesis has been tested in a New World monkey, the common marmoset (*Callithrix jacchus*). Similar to the studies on chimpanzees and bonobos, it was found that social play among adults was highest just before feeding commenced. Furthermore, scratching rates (an indicator for stress) decreased after playing bouts.

However, we must keep in mind that these studies are performed on captive animals that do not need to forage and are being fed at specific times. Thus, the tension reduction

function may be caused by captivity rather than portraying true functionality of play (Graham and Burghardt, 2010).

Although studies on play in wild bonobos are very limited, Enomoto (1990) did show that many of the observed adult-adult play interactions in wild bonobos occurred in a feeding context. Here, bonobos were provided with sugar canes in order to observe them. During those feeding sessions, play was observed between adults. The author proposed that it may function to reduce tension (Enomoto, 1990). However, this is opposite from the general assumption that play decreases in presence of stressors (Fagen, 1993). From this hypothesis, it is suspected that play increases during stressful times. When a group of captive chimpanzees was moved to a new enclosure, supposedly a highly stressful event, play was inhibited for several weeks (Merrick, 1977). Play should therefore be investigated in other stressful events besides feeding competition.

The "*social assessment hypothesis*" (Pellis and Iwaniuk, 2000a) predicts that social play is a way of assessing an (unfamiliar) individual. This may occur in (at least) two important contexts; First, to assess the strength of the individual, estimate its position in a dominance rank and (re-)establish a dominance position without any true aggression (Paquette, 1994). Second, it can serve to establish and/or maintain an affinitive bond between individuals (Pellis and Pellis, 1991).

Three predictions can be drawn from this hypothesis; 1) individuals deprived from social play may show abnormal social skills (Graham and Burghardt, 2010), 2) social play (in particular play fighting) decreases true aggression (Graham and Burghardt, 2010), and 3) play becomes more prevalent in species where relationships are uncertain or not structured through dominance (Palagi, 2006).

The first prediction is partly supported. Indeed, rats that were isolated during times when normally social play occurs in high rates (fourth and fifth week of life), did show an abnormal response to social situations later in life. They did not show the appropriate submissive behaviour when confronted with a territorial dominant rat (van den Berg *et al.,* 1999). However, a study on Squirrel monkeys (*Saimiri*) showed that social play was not a

prerequisite for developing normal social interactions or cohesiveness of the group (Baldwin and Baldwin, 2004).

In coyotes, dominance hierarchies are established through real fighting, before play fighting begins. This is reversed of what would be expected from the social assessment hypothesis (Bekoff, 1974 in Barber, 1991). Similarly, a study on juvenile meerkats (*Suricata suricatta*) did not show that aggression between individuals decreased when play fighting occurred more often between those individuals (Sharpe and Cherry, 2003). A study on wolves (*Canus lupus*) suggested that wolves evaluated each other's strength through social play, although play did not correlate with either affinitive or agonistic interactions (Cordoni, 2009), so a clear effect in reducing aggression cannot be proven. A study on gorilla's (*Gorilla gorilla*), showed that males stop playing when they become mating rivals (Watts and Pusey, 1993), while playing is presumably more useful during that time if it can be used to assess the competitors.

The last prediction stated that play should occur more often in animals where relationships are uncertain or not clearly structured through dominance. From this follows that adult play should be more common in egalitarian species than in despotic species (Palagi, 2006; 2008). Pellis and Iwaniuk (2000a) compared data among 71 primate species. They found that species with more cohesive social relationships were less involved in adult social play. When social relationships were uncommon or uncertain, adult social play increased. This provides some evidence that indeed the certainty of relationships plays an important role in the occurrence of adult-adult play (Pellis and Iwaniuk, 2000a).

The correlation between the certainty of relationships and the occurrence of social play can also be examined within a single species. Consequently, studies focussed on sex and modality differences in adult-adult play. In bonobos, sex differences are found in adult-adult play. Adult female bonobos play more often together than males with females or males with males (Palagi, 2006; Palagi and Paoli, 2007; 2008), while no sex preference is found in chimpanzees (Palagi and Paoli, 2008). Bonobo females play more often together in contact play (e.g. pay fighting) (figure 2) (Palagi and Paoli, 2007), but no such difference was found for locomotor-rotational play (e.g. acrobatic play) (Palagi and Paoli, 2007). Furthermore,

social play in adults was significantly correlated with social behaviours as grooming or contact sitting (Palagi and Paoli, 2007).

The fact that social behaviours are correlated with the occurrence of adult-adult play can be an indication of social bonding through play (Palagi and Paoli, 2007). Bonobos show higher frequencies of adult social play and invitations to play than chimpanzees (Palagi, 2006). From this, it may follow that bonobos should have a more egalitarian society than chimpanzees (Palagi, 2008). Indeed, the structure of bonobo society has often been proposed as an explanation for the adaptive function of adult-adult play. The increased occurrence of female-female play fighting is assigned to presumed strong female bonds and female dominance over males (Palagi and Paoli, 2008). Playing would then be a way of assessing the other individual, without escalation into true aggression (Palagi and Paoli, 2007; 2008).
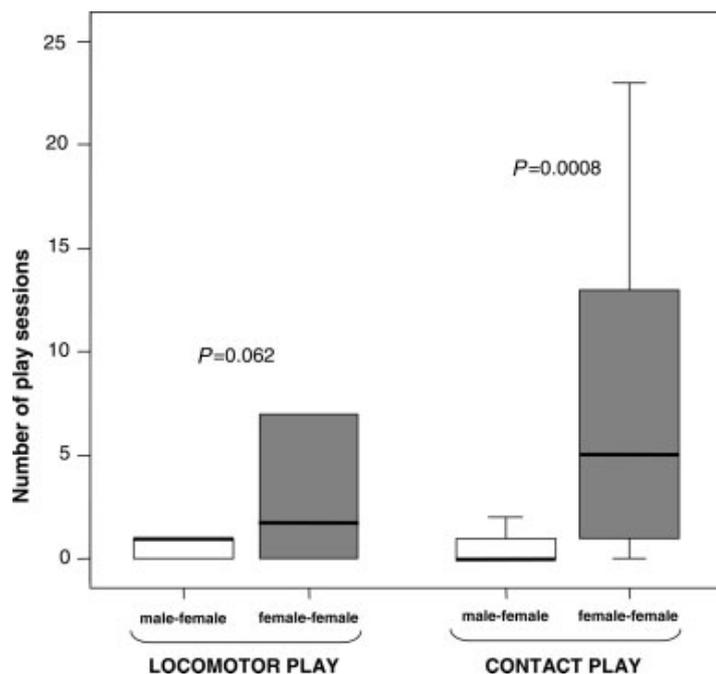
Figure 2: The frequency of locomotor-rotational and contact play in adult male-female and female-female play sessions (source: Palagi and Paoli, 2007).

Social play, especially play fighting, requires cooperation and reciprocation (Palagi and Paoli, 2008). The use of play signals enables the communication of a playful intention. Bonobos elaborately use play signals to communicate and maintain a playful mood (Palagi and Paoli, 2007; 2008; Palagi, 2008). Palagi (2008) discriminated two play faces shown by bonobos: the full play face (both upper en lower teeth are exposed when the mouth is opened) and the relaxed open mouth display (only the lower teeth are exposed). Communication becomes more important as the level of aggression increases between individuals. After all, the line between playing and true aggression becomes thinner and thus fine tuning of play becomes more important (Palagi, 2008). Consequently, the rate of play signals is higher in social play than solitary play, and when there is more than one play partner involved, the use of play signals between each player is higher than in dyadic play sessions (Palagi, 2008). Communicating a playful mood is more important when social play occurs between individuals of matched size or age. Indeed, a play face is used more often between adults playing than when an adult is playing with a juvenile (Palagi, 2008). Yet another way of signalling 'this is only play' is by 'self-handicapping'. Here, the individual purposely restrains itself. This type of signalling is often associated with play with a younger or smaller individual (Allen and Bekoff, 2005). Self-handicapping can be seen as a form of using gestures to communicate. Indeed, during human-bonobo play, bonobos show gestures in order to stimulate their human play partner to continue playing (Pika and Zuberbühler, 2008). Also, gestures can serve as an invitation to play. Drumming on the ground with the palm of the hand may allocate a playful response by conspecifics (Pika *et al.,* 2005).

The complexity of social play and the maintenance of a playful mood and preventing escalation into aggression, borders onto human morality. Why not cheat (Bekoff, 2001)? Two bonobos that were able to communicate with humans through symbols on a keyboard showed they had a concept of "good" and " bad" .They denominated their own behaviour with value judgements, which was influenced by what their human caretakers considered to be good or bad. For example, a bonobo pointed to the lexigram representing 'bad' and shortly after showed the keyboard, a behaviour obviously not appreciated by the researcher. But, in addition, they seemed to negotiate whether their behaviour was good or bad and sometimes asked for clarification. Even though these value judgements are culturally

transmitted, it does seem apes can comprehend value judgements, which is the foundation for morality (Lyn *et al.,* 2008).

We can summarize that hypotheses regarding the adaptive function of adult-adult play all have one thing in common: the uncertainty of relationships plays an important role. In a way, all three above described hypotheses state that social play will be most important in species and within species that are characterized by uncertain relationships, either through a lack of clear dominance hierarchies, or because they live in un-cohesive societies. The problem with applying these hypotheses to the bonobo is that there is still much confusion about bonobo society. We are uncertain how it can best be characterized regarding dominance structures and which individuals form strong bonds. In the next section, we will elaborate on bonobo society and dominance relationships and provide the available opinions on this subject. We can then better evaluate the proposed hypotheses for the adaptive function of adult-adult social play.

Bonobo society and dominance structure

An important feature of bonobo society is the fission-fusion system (Kano, 1980). This means that there are different levels of aggregation within bonobo society (van Elsacker *et al.,* 1995). The community is the largest and most stable aggregation of individuals among which fission and fusion occurs (van Elsacker *et al.,* 1995). The number of individuals in a community observed in the wild ranges from 17 to 120 (reviewed in van Elsacker *et al.,* 1995). Within the community, the smallest and least stable groupings of individuals are called "parties" (Kano, 1980; Kano, 1982; Watts and Pusey, 1993; van Elsacker *et al.,* 1995). Parties are the "functional units" of bonobo society (van Elsacker *et al.,* 1995) that can alter on very short time scales (Kano, 1982; Lacambra *et al.,* 2005) (figure 3). Females form the centre of the parties, with their daughters or sons, while unrelated males stay in the periphery of the party (Furuichi, 1989). In between the community level and the party level,

there is an intermediate level of aggregration; the subgroup (van Elsacker *et al.,* 1995). Subgroups are typically composed of different sexed individuals (Kano, 1980), with equal sex ratios or with slightly more females (Kano, 1982).

Male bonobos stay within their natal community (Lacambra *et al.,* 2005; Kano, 1987a). Females leave and switch between communities before settling down to breed (Lacambra *et al.,* 2005; Kano, 1987c; 1990). This results in females that are unrelated with each other and did not previously know each other within a group, while most males know each other since birth (Kano, 1982; 1987c). Sex plays an important role during such introductions of unfamiliar females. It seems that sex is used as a type of tension-reduction mechanism, to anticipate aggression, or a greeting gesture (Kano, 1980; 1987c; 1989). Female bonobos have their first sexual swelling at seven (Kano, 1989). These swellings are important because over 75% of the copulations will occur when females exhibit maximum swelling (Kano, 1989).
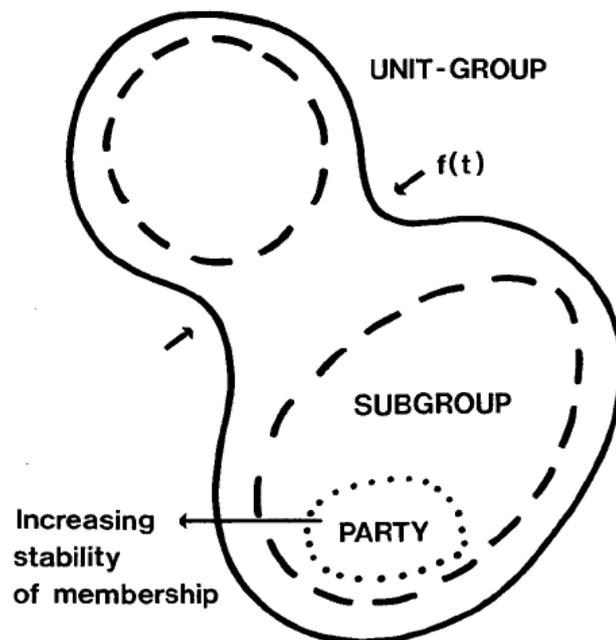
Figure 3: Levels of aggregation in a fission-fusion society (source: van Elsacker *et al.,* 1995).

Females are receptive for a relatively long time, irrelevant of their ability to conceive (Kano, 1980; 1982). This leads to a multitude of receptive females present during most of the time, un-limiting mating opportunities for males (Kano, 1982; Furuichi, 2011). The prolonged receptivity of females has strong effects on the bonobo society (Kano, 1980). Males usually compete over a high dominance status because it gives the advantage of monopolizing mating opportunities or prioritized access to food (Kano, 1987b). The existence of dominance relationships is an important characteristic of primate societies (Newton-Fisher, 2004). Primate societies range from egalitarian to despotic species (Vehrencamp, 1983). In egalitarian species, positions in the dominance hierarchy differ little, with all individuals being relatively equal and tolerant of each other (Vehrencamp, 1983). Despotic species show a high steepness in relative dominance positions which generally do not reverse, i.e. are linear (de Vries *et al.,* 1995). An example of a highly despotic species is the Rhesus macaque (*Macaca mulatta*) (Dubuc *et al.,* 2002). An example of a species where relationships lack a dominance hierarchy is the Muriqui monkey (*Brachyteles arachnoides hypoxanthus*) (Strier *et al.,* 2002). Where bonobo society would fit in regarding dominance style is still subject to discussion.

From a male perspective, it would not be sensible to compete with other males to obtain a high status when there is an abundance of mating opportunities (Kano, 1990; Furuichi, 2011). After all, it would not be possible to monopolize mating opportunities in any case (Furuichi, 2011). Wild male bonobos do indeed not seem to have steep linear dominance relationships, as dominance dyads are dependent on the context (Kano, 1987b; Furuichi, 1997). Status of males depend on the status of their mothers and their age (Furuichi, 1989). However, a study on captive bonobos found a steeper dominance hierarchy than females among male bonobos (Stevens *et al.,*2008). Being more dominant over other males may have a benefit because they can stay in the centre of the party, which may lead to higher copulation frequencies (Furuichi, 1997).

Furthermore, in contrast to chimpanzees that are receptive for much shorter periods of time (approximately 5% vs. 50% of adult life) (Parish *et al.*, 2000), studies seem to indicate that clear male dominance over females lacks in the bonobo society. Males often leave an area with food when a female, or group of females approaches. Almost all males, at least

lower ranked among males, are subordinate to females (Kano, 1987b). Kuroda (1980), however, states from a field study that males were dominant over females, because no agonistic interactions were seen and only sub-adult males avoided a female approach.

However, the alternative option, female dominance over males, is debated (Vervaecke *et al.,* 2000; Stevens *et al.,* 2007). This mainly follows from the suggestion that females form strong bonds and use this to construct alliances used to compensate for size differences with males (Lacambra *et al.,* 2005; de Waal, 1995; Parish, 1996a). The point of discussion is that it would make the bonobo a rare exception to the rule that the philopatric sex forms strong bonds (de Waal, 1995; Parish, 1996a).

Nonetheless, in bonobo society, female bonds are claimed to be apparent and important (Parish, 1996a). Studies on wild bonobos show that female-female and female-male bonds are stronger than male-male bonds (Kano, 1980; 1982; 1983). Affinitive behaviour between male-female and female-female occurred more often than male-male, and vice versa for agonistic interactions (Kano, 1980; 1983). This was also found by Kuroda (1980), but here the author adds that differences are little. Some data on captive bonobos show similar results. Parish (1996) found that in a captive group in San Diego, females formed and maintained social relationships much more often with other females than they did with males. However, Stevens *et al.,* (2006) found contrasting results. Captive groups in Europe were examined and it was found that female bonding was not characteristic of all groups. So, female bonding may be overemphasized in captive studies and influenced by sex ratio or timing of observations (Stevens *et al.,* 2006). This is supported by a different study performed on wild bonobos. Here, it was found that it males and females formed the closest association and not females with other females (Hohmann *et al.,* 1999).

It can be wondered why females would bond in bonobos but not in chimpanzees. A possible explanation might be found in the food distribution. It seems that the large food patch distribution allows female aggregation (Wrangham, 1986), and females may benefit from bonding because they can then defend it against males (Kano, 1987b; Parish, 1994; Furuichi, 2011). Indeed, wild bonobo females seem to share food among each other much more often than they do with males and group together to gain access to food (Kano, 1980; 1987b).

If females form strong bonds, and are centralized in the temporary parties, it is a logical assumption that females are the dominant sex (Furuichi, 2011). Females would benefit by gaining prioritized access to food (Kano, 1980; Kano, 1987b; Parish, 1996a; Furuichi, 2011), which directly affects their reproductive success (Parish, 1996). However, the assumption that females dominate males is only partially supported in the literature.

For example, Stevens et al (2008) examined four different captive bonobo groups in Europe, and did not find exclusive female dominance. In all captive groups, there was always one male that could at least outrank one female. Furthermore, male dominance hierarchies were steeper than female dominance hierarchies and with exception of one captive group (Planckendael), rank was not correlated with age. Although this suggest no total female dominance, all highest ranked individuals were females, and all lowest ranked individuals were males, suggesting at least partly domination by females (Furuichi, 2011). However, Paoli *et al.* (2006) examined bonobos in captivity (Apenheul) and did not find a linear dominance hierarchy, and also no effects of sex. They suggested that dominance hierarchies may be flexible in bonobo society. Indeed, we must be careful with drawing conclusions from small captive groups of bonobos.

Different results may be explained by different measures for "dominance". Vervaecke *et al.* (2000) proposed that the best measure for dominance is the actual agonistic interactions between two individuals in which one individual submits and flees. Other interactions such as bared teeth or shielding must not be considered when assessing the dominance hierarchy.

Furthermore, bonobos are often compared to chimpanzees. This is a logical effect of their shared visual features and/or small phylogenetic distance to each other and to humans (Prüfer *et al.,* 2012). But, the present comparison between chimpanzees and bonobos may have led to stereotyping of the two apes. Traditionally, data was available on chimpanzees more abundantly and more than a decade earlier than bonobos (de Waal, 1995). Observations of chimpanzees included descriptions of warfare between communities, infanticide, male domination over females, hunting and cannibalism (Stanford, 1998). Then, when data on bonobos became more apparent, it was described as a female-centred, egalitarian species that replaces agonistic behaviour for elaborate sexual behaviour (de

Waal, 1995). Consequently, the bonobo got stereotyped as "make-love-not-war ape", "peace-loving ape", "sciences gift to feminism", while the chimpanzee became its "evil" relative (de Waal, 1997; 2001). Stanford (1998) pointed out that we must not exaggerate differences between these species but rather focus on similarities. Rightfully so, he pointed out that data in the wild will give differing results than data of captive apes. Indeed, a wide array of bonobo characterizing has passed over the years. Depending on which group is studied and how dominance is defined, it still remains unclear if bonobo society is leaning towards egalitarian or despotism, and how dominance is structured.

The uncertainty of the bonobo dominance hierarchy, and the ambiguous adaptive function of adult-adult social play requires more attention in research. In the next section, we present a case study that focusses on adult social play in bonobos.

Case study: Adult-adult social play in bonobos (*Pan paniscus*)

Introduction (recapitulated)

The adaptive function of play behaviour remains unknown. A variety of hypotheses have been proposed on this subject, of which most apply to play occurring early in life. Many of these hypotheses propose a delayed benefit of play behaviour. However, this cannot be applied to play during adulthood. After all, the participants already reached adulthood successfully (Barber, 1991; Graham and Burghardt, 2010; Held and Špinka, 2011). Social play between adults specifically requires a hypothesis that suggests an immediate adaptive function for play (Norscia and Palagi, 2011).

Social play between adults is not uncommon in the animal kingdom (Špinka *et al.,* 2001). It can occur in sexual contexts but also in non-sexual contexts. Social play in a sexual context is hypothesized to familiarize individuals that possibly become pair mates in the

future (Pellis and Iwaniuk, 1999b). Two hypotheses are proposed for adult social play in a non-sexual context: play as a tension reduction mechanism (Palagi *et al.,* 2006) and play as a mechanism to assess and manipulate social relationships (Pellis and Iwaniuk, 2000a).

From all three hypotheses follow that social play in adults will be prevalent in species, and in individuals in which relationships are uncertain (i.e. individuals are unrelated or do not acquaint with each other often) (Pellis and Iwaniuk, 2000a) and/or unclear (i.e. lack a clear dominance structure) (Palagi, 2006; 2008) . For example, the need to reduce tension (e.g. during feeding competition) will be most needed in species that live in large cohesive societies. Within that species, it will be most necessary between those individuals that have not acquainted with each other often, or between those in which the dominance relationship is uncertain. Therefore, we bundle these hypotheses as the 'uncertainty of relationships' hypotheses. It follows that the type of society and dominance structure predicts the degree of adult social play both between as within species (Pellis and Iwaniuk, 2000a; Palagi, 2006; 2008).

The bonobo is often used as a model species for adult social play, since it is a species in which play is common in adulthood (Enomoto, 1990; Palagi, 2006; Palagi and Paoli, 2007). Furthermore, the dominance structure characterizing bonobo society remains subject to discussion. We will use adult social play within this species to explore the adaptive function of play regarding the uncertainty of relationships. We do not have the data available to differentiate between the separate hypotheses. First, we will shortly summarize the main statements on the bonds and dominance relationships occurring in bonobos.

Females presumably form strong bonds (Kano, 1980; 1982; 1983). This is unusual because they are not philopatric and thus females living in a group do not tend to be related, while males do tend to be related but do not form strong bonds (Kano, 1987c). The female dominance structure is unclear, but is thought to be less steep than the dominance hierarchy found in males (Stevens *et al.,* 2007). Females dominate, at least partly, over males (Furuichi, 2011). Overall, dominance hierarchies are probably flexible (Paoli *et al.,* 2006).

In order to formulate predictions, we assume the above is true. In that case, it seems that the above stated hypotheses mainly apply to females. After all, female relationships are

uncertain because they are not clearly structured through a dominance hierarchy. Males do seem to have a steep dominance hierarchy, so perhaps adult social play will be less important in that sex. If females dominate over males, this also applies to male-female relationships.

We include the effect of kinship on the occurrence of social play. We suspect that kinship is important in the certainty of social relationships and therefore do not wish to deny this in exploring the adaptive function of play. Indeed, a study on wild bonobos found that related individuals formed close associations and groomed each other more often than would be expected based on the number of relatives living in a group. The strongest bonds were found between males and females, and a genetic analyses showed that these were partly explained by a kinship bond. The associations between mothers and sons and adult half siblings were the most consistent. Furthermore, it was expected that reciprocity would be most apparent in unrelated individuals, but the opposite was found. Related individuals portrayed a higher degree of reciprocity regarding grooming (Hohmann, 1999).

From the above, we predict to see adult female-female play more often than female-male or male-male play (Palagi, 2006) (1). Furthermore, females should engage in relatively more contact play (i.e. play fighting) with other females, since in that modality relationships and the other individual can be better assessed than when engaging in locomotor-rotational play (i.e. acrobatic play) (Palagi and Paoli, 2007) (2). Similarly, rough (i.e. intense play with behaviours resembling serious fighting) play would provide better information about the strength of the other individual than gentle play, and should therefore occur more between females than in other sex combinations (Palagi and Paoli, 2007) (3). Play should occur most between unrelated individuals, since then there is no pre-existing bond and the relationship is presumably less certain than when there is a kinship bond (4).

The use of play faces are important during social play. Play sessions can be fine-tuned and escalation into aggression is prevented (Pellis and Pellis, 1996). It is expected that the use of the play face is most important between individuals of which the relationship is uncertain (Pellis and Pellis, 1996). Therefore, we predict that it is most often seen between females (5). This effect may be most noticeably between adults, since there it is specifically important that play sessions do not escalate into true aggression because the risk of injuries

or affecting an affiliative bond is more prevalent (Burghardt, 2005; Pellis and Pellis, 1996; Palagi *et al.,* 2007; Palagi, 2008) (6). Likewise, the need to state a playful intention is presumably more necessary during rough play sessions, and is therefore expected to be seen more often in those occasions (Palagi, 2006) (7). We also predict that there is less need for a play face between individuals that have a kinship bond, since there is a higher level of familiarity (8).

Furthermore, we predict that the use of play invitations should differ between sexes. Females likely invite other females to play more often (9). Since play is especially apparent during early stage of life, non-adults are expected to have a higher motivation to play and consequently invite adults to play more often than vice versa (Fagen, 1981). Adults presumably have a different motivation to play and are expected to invite other adults more often (Palagi, 2006) (10). Additionally, individuals are expected to invite unrelated individuals more often than related individuals to play because of the presumed uncertainty of those relationships (11).

Methods

From February until June 2012, *ad libitum* preliminary recordings of social play behaviour in four captive groups (Apenheul (NL), Frankfurt, Stuttgart, and Wuppertal (DE)) were collected. These recordings include interactions between adults, non-adults and between adults and non-adults. An individual was considered 'adult' if it had reached seven years of age. It was not discriminated between infants or juveniles if an individual was less than seven years old. We included non-adults in our analyses in order to better compare results and because adults may play with non-adults to assess the relationship of a related adult through the non-adult (Pellis and iwaniuk, 2000a). Recordings also entailed all sex combinations; between females (F/F), males (M/M) and females and males (F/M). In total, 35 (Apenheul 6; Frankfurt 7; Stuttgart 12; Wuppertal 10) different combinations of individuals engaging in play behaviour were observed. These combinations include 27 bonobos, of which six male adults, nine female adults, seven male non-adults and five

female non-adults. This means that 59% of the bonobos living in the four captive groups was recorded playing (Appendix 1). We do not have recordings of M/M adult play in any of the captive groups. Social play between adults and non-adults was recorded in all groups but Apenheul. In Apenheul, only recordings of non-adults playing with each other were available, while social play between non-adults was not recorded in Wuppertal. It was also very rarely recorded in Frankfurt, with only one play session.

Social play between two certain individuals ('dyad') was often recorded on more than one recording, or even within one recording. Therefore, a specific dyad could occur in multiple play sequences. We only discriminated between sequences of the same dyad within one recording if the modality of the play behaviour changed or if there was a clear intermission (i.e. individual(s) engaged in a different behaviour, moved away from the other individual, and/or interacted with another individual). It also occurred that one recording involved play behaviour between more than two individuals. In that case, the recording was observed multiple times. Each time, no more than one dyad was focussed on and only behaviours occurring in that dyad were scored. Thus, we analysed each play sequence between two individuals separately. This means that a play sequence must be regarded as a fragment of a recording of social play. The recordings were analysed by scoring play behaviours in JWatcher software (downloaded from: http://www.jwatcher.ucla.edu/).

For each observed play sequence the modality was scored. This entailed the notion if it was contact (C) play (i.e. play fighting) or locomotor-rotational (LR) play (i.e. acrobatic play, often involving an object). We also noted if the play occurred in a rough or gentle fashion. If applicable, we noted the occurrence of play invitations and play faces. We followed Palagi and Paoli (2007) in their descriptions of these behaviours, although we did not note the individual behaviours that are included in these categories (Table 1). For each play sequence we documented the sex and age of the participants. In addition, we noted if a kinship bond existed. Half siblings were noted as kin (Hohmann, 1999). For the play faces and play invitations, it was specifically documented in which direction the behaviour was performed (e.g. female non-adult gives play face towards related male adult).

Since data was not recorded systematically, we could only provide information on the proportion of sequences in which a certain behaviour was found. We could not provide

numerical data because not all individuals were observed the same amount of time. The direction of play faces and play invitations was calculated as the average number of times it was observed per play sequence. However, in F/F or M/M social play this would result in duplicated data. After all, both possible directions would result in a value for the same sex. In order to be able to compare between same sex and mixed sex interactions, values for mixed sex interactions are presented as the average value for half of the total play sequences in which they occur. The limited sample size led to the decision to not perform statistical analyses on this data, to prevent ungrounded results.

Table 1: Description of play signals and play behaviours recorded in rough or gentle locomotor-rotational play and contact play (source: after Palagi and Paoli, 2007).

| Locomotor-rotational play	
Rough	
Acrobatic play	Individuals follow each other in using objects in the enclosure to fastly move in an acrobatic way
Pirouetting	Rotational movements such as somersaults or pirouettes are made together
Play run	An individual chases another individual by running after it, but not necessarily uses objects
Gentle	
Play recovering a thing	An animal tries to steal an object carried by another individual
Contact play	
Rough	
Play brusque rush	An individual uses both feet as hands to jump on other individual
Play retrieve	An individual holds another play individual to prevent it from leaving
Play stamping	An individual uses feet to stamp on another individual
Rough and tumble	Two individuals play fight by holding each other and bite or slap the other individual
Gentle	
Airplane	An adult lies on its back and balances an infant on its hands or feet
Grab gentle	An individual gently touches another individual
Play bite	An individual uses its teeth to gently bite another individual
Play push	An individual uses hands or feet to push another individual
Play slap	An individual uses its hands to gently slap another individual
Tickle	An individual uses hands or mouth to tickle another individual
Play signals	
(Full) play face	The mouth is opened with lower (and upper) teeth exposed and directed at another individual
Play invitation	An individual pats another individual in order to invite the start of a play session

Results

      The 35 recorded dyads resulted in 231 play sequences in total. Adult-adult play was mainly observed in Wuppertal, with 43 sequences divided over five dyads. Just one

adult/adult play dyad was recorded in Frankfurt (in one sequence) and in Stuttgart (in five sequences) and none in Apenheul. Most of the total recorded play sequences entailed interactions between adults and non-adults (45%) or non-adults and non-adults (34%). Adult/adult play was observed rarely, with only 49 sequences (21%). Of these sequences, we noted 25 F/F and 24 F/M sequences. Adult M/M play was not recorded.

Play modality

In adults, F/F social play behold half of the total amount of adult social play sequences (51%). As no male adults were recorded playing with other males, the other half was represented by F/M adult social play. We also included other age combinations to investigate the overall effect of sex. More than half of all play sequences encompassed a F/F interaction (52%). M/M play was least often recorded (12%), and F/M play intermediately (36%). In all age combinations, F/F was recorded most often. In non-adult social play, F/F social play entailed 68% of the interactions (Figure 4).
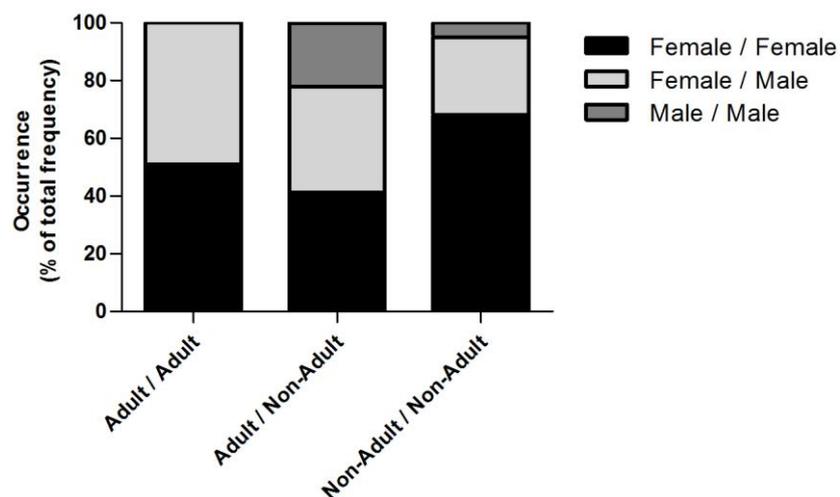
Figure 4: The relative proportion of female/female, female/male and male/male social play found in play sequences with different age combinations.

We discriminated 84 sequences as locomotor-rotational (LR) play, and 147 sequences as contact (C) play. In adults, we did not observe a noticeable effect of sex on the occurrence of C or LR play. F/F play did not seem to entail a larger proportion of contact play than F/M play (F/F: C 48%, LR 52%; F/M: C 54%, LR 46%) (Figure 5). If no age discrimination was made, all sex combinations engaged more often in C play than in LR play (F/F: C 63%, LR 37%; F/M: C 68%, LR 33%; MM: C 56% LR 44%), this was not specific to females.

Adults were recorded to engage in C play with other adults 25 out of 49 interactions (51%). Between adults and non-adults this was 32% and in between non-adults 35%. Related individuals were not recorded to engage in relatively more contact play with each other (68%) than unrelated individuals (63%).
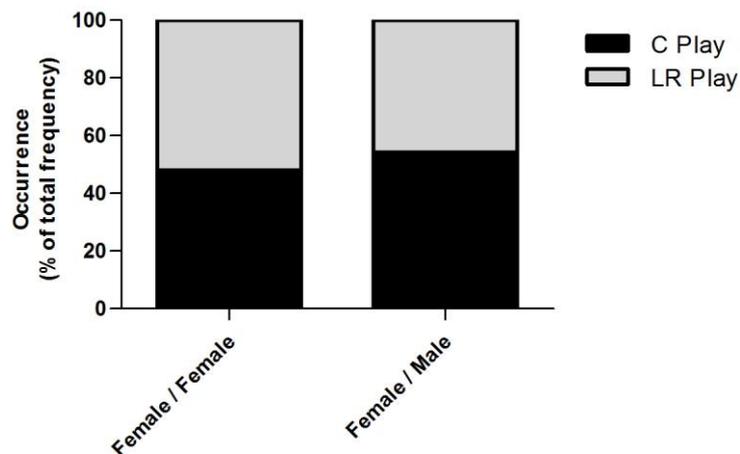

Figure 5: The relative proportion of contact (C) play or locomotor-rotational (LR) play found in adult female/female or female/male social play sequences.

In all sex and age combinations, rough play was noted more often than gentle play. Of all F/F interactions, 95% occurred in a rough way. This trend was also found with F/M play, with rough sequences entailing 80% of the total interactions. In M/M play, this was 74% of the interactions. Of the 25 adult F/F social play sequences, 24 were recorded as rough play. In F/M adult play, 20 out of 24 interactions were rough play.

Last, over 75% of the interactions recorded occurred between individuals that were unrelated to each other. Play with unrelated individuals was common F/F play (play with kin: 3%, no kin: 97%), while for M/M play the effect was reversed (play with kin: 78%, no kin: 22%) (Figure 6). This effect was noticeable in adult social play. Recorded adult females played with unrelated females in all but one sequence. On the other hand, females were unrelated with males that they played with in 14 out of 24 interactions.
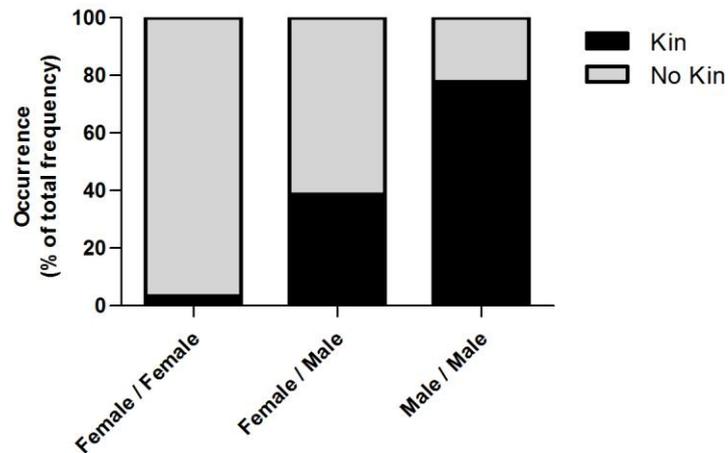
Figure 6: The relative proportion of social play between individuals that are related (kin) or unrelated (no kin), as found in female/female, female/male and male/male social play sequences.

Play faces

Play faces were observed on 115 occasions in total. We did observe differences in the corrected values for the direction of play faces given per play sequence (F>F: 0.4, F>M: 0.8, M>F: 0.5,M>M: 0.4). There were also no large differences found in the relative occurrence of play faces in adults. The corrected relative frequencies of play face per play sequence were: F>F: 0.7, F>M: 0.5 and M>F: 0.3 (Figure 7).

Furthermore, the relative frequency of play faces did not seem to alternate in different age combinations. In adult-adult play, each play sequence included a play face on

average 0.6 times. In adult play with non-adults, this value was 0.8. Last, non-adults showed on average 0.6 times a play face per play sequence when they played together.

Rough and gentle play sessions did not show an apparent difference in the use of a play face. In rough play sessions, the relative frequency of a play faces was 0.5, while in gentle play sessions this was 0.4.

In adult social play, the average frequency of a play face was 0.6 in interactions between non kin. On the other hand, in play with kin the average frequency was 0.3 (Figure 8). This effect was limited to adult social play. If we included all age combinations, we did not find a noticeable difference.
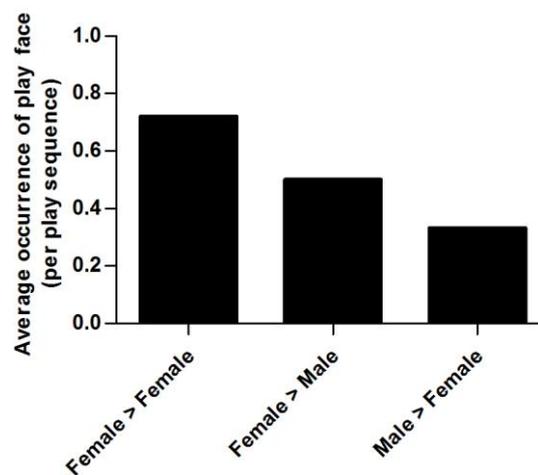
Figure 7: The average occurrence of a play face in adult social play sequences, directed (>) from a female towards another female, from a female towards a male, and from a male towards a female.

Play invitations

Adult females were observed to invite other adult females on average 0.7 times per recorded play sequence, while they invited males 0.5 times per play sequence. Males seemed to invite females about equally often, on average 0.4 times per play sequence (corrected data). These differences are very small. Including all ages, also no large differences were found. Females invited other females and other males on average 0.5 times

per play sequence. Males invited females 0.7 times and other males 0.5 times on average per play sequence.

Adults seemed to invite non-adults to play about equally often as the other way around (17/104 and 22/104, respectively). Adults invited other adults on average 0.6 times per play sequence. If we include all age combinations, we seem to find that younger individuals (so not necessarily a different age group) tended to invite older individuals more often (in 68% of the play sequences) than the other way around.

Play invitations were observed 38 times in 57 interactions (0.7 times per play sequence) between individuals that were related. Non-related individuals were observed to invite each other 86 times in 174 interactions (0.5 times per play sequence).
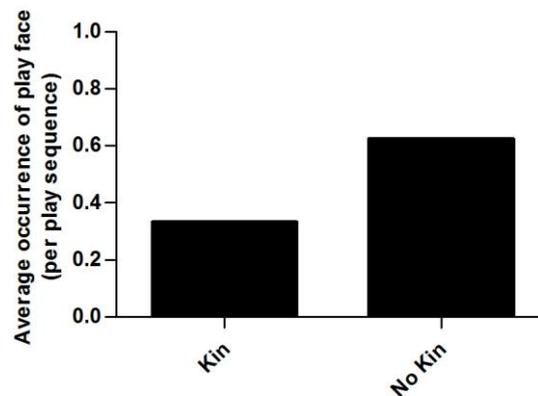
Figure 8: The average occurrence of a play face in adult social play sequences directed towards related individuals (kin) or unrelated individuals (no kin).

Discussion

In our study, adults were recorded playing together approximately equal in male-female as in female-female combination. On the other hand, adult male-male social play was not recorded altogether. Females of all ages were recorded often playing with other females. The modality of adult social play did not seem to differ between sexes. Adult female-female social play did not involve more contact play than in male-female social play.

Play modality did seem to differ between ages; adults engaged in contact play more often when playing with other adults than when playing with non-adults, or when non-adults played together. Rough play was more often recorded in all sex or age combinations. Furthermore, play faces were observed mostly from adult females towards other females in the available recordings, although differences were small compared to play faces directed from males to females or vice versa. Generally, adults tended to portray a play face towards related individuals in a smaller proportion of the play sequences than they did towards unrelated individuals. Most recorded interactions between females entailed unrelated individuals, while males seemed to play often with related individuals. We did not find any noticeable differences in the direction of play invitations between different sex or age categories. If we did not differentiate between age categories, we did note a trend in which younger individuals invited older individuals more often to play.

From the main three proposed adaptive functions of adult social play (courtship familiarization (Pellis and Iwaniuk, 1999b), tension reduction (Palagi *et al.,* 2006), and social assessment (Pellis and IWaniuk, 2000a)) follows that social play is most important for individuals of which the relationship is uncertain or unclear (Pellis and Iwaniuk, 2000a; Palagi, 2006; 2008). From the (presumed) structure of dominance in bonobo society was predicted that adult social play modality, the use of play faces and the frequency of play invitations should especially be important in female-female relationships (Palagi, 2006) and/or in unrelated individuals.

Play modality

Indeed, our preliminary results suggest that females generally seemed to play more often and the lack of male-male adult play recordings affirms some of these predictions. Similarly, Palagi (2006; & Paoli,2007) observed in a former study that bonobo adult females played more often together than they did with males, and did not observe any male-male adult play. However, a study on wild bonobos did record adult male-male play, but no adult female-female play (Enomoto, 1990). We therefore must be careful drawing conclusions from these results, as it may not correspond with what occurs in wild bonobo society.

Other predictions were not affirmed. We followed Palagi and Paoli (2007) in their expectation that play modality would be a good way to inspect the relative importance of social play in different sex combinations. They found that females played more often using contact play compared to when females played with males. We did not find that female-female adult play differed with female-male play in modality, both the difference in contact or locomotor-rotational play as in rough or gentle play. Thus, from our data on play modality we cannot affirm that female-female relationships are more uncertain than male-female or male-male relationships.

What we did notice, is that contact play seemed to occur more between adults than in other age combinations. This does seem to support the relationship-uncertainty hypotheses for adult-adult social play. It was also found that most of the recorded play sequences involved unrelated individuals. This additionally affirms that play may be most important in those individuals that do not share a kinship bond, and perhaps have a less certain relationship than related individuals. This was overall most noticeable in females, which would explain why females were often recorded playing. However, we also did not find a difference in play modality between related or unrelated individuals.

Play faces

Play faces are important to communicate a playful intention and maintain that mood throughout a play session. This is especially important in play sessions between individuals of which the relationship is unclear (Pellis and Pellis, 1996).

A logical expectation is that play faces are more often used during rough play sessions, in which the risk of escalation into aggression is higher (Pellis and Pellis, 1996). Indeed, Palagi (2006) showed that adult bonobos showed a play face more often during rough play sessions than during gentle play sessions. We only observed a small difference and cannot affirm that there was a true effect. Similarly, one would expect to see more play faces in adult-adult play than in other age combinations, since the risk of injuries caused by aggression may be increased. Palagi (2008) did find this effect. We, however, cannot affirm this with our data.

The finding that adult females seemed to show play faces most often when playing with other females supports that the relationships among females are uncertain and thus playful intentions need to be reaffirmed regularly. The fine-tuning of play according to context and play partner by using play signals has been shown in gorillas (*Gorilla gorilla gorilla*). Males displayed play faces in a higher frequency when they were involved in rough play, resembling serious fighting, with other males. Also, when confined in small spaces, where escape possibilities were limited, the frequency of play faces was also increased (Palagi *et al.,* 2007).

In a similar way does the relatively less often displayed play face by adults in interactions with kin than with non-kin seem to support the uncertainty of relationships hypotheses. A kin ship bond brings about a level of familiarity and possible trust regarding issues as reciprocity (Hohmann, 1999), and does therefore maybe require less fine-tuning than with an unrelated play partner.

Play invitations

Inviting another individual to play may reflect the motivation to play with a specific individual. It is therefore unexpected that we did not note any large differences in the direction of these invitations in age, sex or kinship bonds. We only found that younger individuals, not necessarily a different age group, did tend to invite older individuals more often than the other way around. This is likely due to the fact that play occurs in much higher frequencies in juveniles and infants, and thus their motivation to play is likely higher. The general assumption is that young individuals often invite adults, and is less common to be seen the other way around (Fagen, 1981).

We must note that our data set did not always record the beginning of a play session, and so these relative frequencies of play invitations may not be representative of true frequencies. Also, when we investigate the occurrence of play faces, we must take into consideration that play faces occur more often in polyadic sessions than in dyadic sessions (Palagi, 2008). In this study, we disentangled polyadic play sessions in order to focus on play dyads. In these dyads, a play face was only recorded if it was clearly directed towards the

other participant of the dyad. However, a small part of differences in play face frequency can be caused by the effect of polyadic play sessions.

Our results must be interpreted carefully due to differences in the captive groups. Most of the total amount of play sequences was recorded in Stuttgart, where only three males compared to ten females live. The chance of observing two females play is therefore higher. Our data may consequently be skewed. However, Wuppertal produced a slightly smaller proportion of the total play sequences and here three females lived compared with six males. We therefore can only state that there may be an indication of females playing more often, but we cannot verify this result in absolute quantities.

Similarly, effects in kinship may be reflected by group compositions. Indeed, most or all adult females were unrelated in all captive groups. Nonetheless, it was not uncommon that mothers and daughters, or sisters (half or full) lived in the same group. The very skewed proportion towards play with non-kin in all females can therefore not be fully attributed to the lack of related individuals. Consequently, we interpret results on kinship with caution, but do suggest it is an interesting factor to investigate in further research.

Our data was retrieved from *ad libitum* observations, that were not recorded systematically. Therefore, we cannot conclude from our data that certain behaviours occurred more often than others. We can only state that those behaviours were recorded more often. Our data can be used as an indication of actual frequencies, but further studies are necessary to truly quantify and statistically test these data.

A problem with using captive groups is that individuals are not able to display their natural fission-fusion social system to the same degree as in the wild. In the wild, a fission-fusion society would be described as a 'loose' society (Pellis and Iwaniuk, 2000a). From the uncertainty of relationships hypotheses may be suspected that play would be prevalent when unfamiliar individuals are fused. Unfortunately, we did not find data on the occurrence of social play during fusion events in the wild. In captivity, we cannot describe bonobo society as a loose one. All bonobos live in the same enclosures. What we did not take into account is how long ago individuals had been introduced in the group. The introduction of a new, unfamiliar individual in captivity would be a good opportunity to observe the

importance of play behaviour during these events, and investigate if play is used to assess and manipulate social relationships. After all, that individual has yet to obtain a position in the dominance hierarchy and establish relationships with the already present individuals.

This would also be a useful event to further investigate the tension reduction hypothesis. Most of the tension reduction studies in primates have been performed regarding the event of feeding and anticipated feeding competition (Palagi *et al.,* 2004; 2006; 2007; Norscia and Palagi, 2011). A different stressful event, like an introduction, would make a good comparison to these studies. A former study on chimpanzees found that stressful events, such as the death of a group member, movement to a new enclosure, and reintroduction of a former high-ranked member, was followed by a decrease in play (Merrick, 1977).

The difficulty with examining the uncertainty of relationships hypotheses in bonobos is that there is still much discussion about the dominance structure in this species. In order to examine the adaptive function of play, perhaps we should compare results in bonobos with studies that examine these hypotheses in species where there is no or little discussion about its dominance structure.

Conclusion

We conclude that former studies and our preliminary study show promising results affirming uncertainty of relationships hypotheses. It does seem that social play in adults is related to the degree of familiarity between individuals. We do not fully support that this is necessarily restricted to female-female relationships in the bonobo and suspect that dominance in bonobos is still not fully understood. We were unable with the available data to differentiate between the separate uncertainty of relationships hypotheses; tension reduction, courtship familiarization and social assessment. Future studies are advised to investigate the effects of familiarity between individuals into more detail and include effects of kinship when investigating the adaptive function of social play.

Appendix 1: Animals used in the case study. Individuals recorded playing are marked grey.

ZOO	Individual	Date of Birth	Sex	Studbook No	Mother	Father
Apenheul	HORTENSE	1-1-1978	F	91	N/A	N/A
Apenheul	JILL	15-7-1985	F	134	40	64
Apenheul	ZUANI	1-1-1990	F	1009	N/A	N/A
Apenheul	ZAMBA	16-4-1998	M	243	91	113
Apenheul	KUMBUKA	9-7-1999	F	260	1006	1004
Apenheul	HONGO	25-2-2006	M	370	91	197
Apenheul	YAHIMBA	7-8-2009	F	390	260	243
Apenheul	MAKASI 2	11-8-2009	M	391	1009	243
Apenheul	MONYAMA	17-7-2010	F	424	134	N/A
Apenheul	BOLOMBO	7-11-1997	M	225	166	111
Frankfurt	MARGRIT	1-1-1951	F	31	N/A	N/A
Frankfurt	NATALIE	1-1-1964	F	46	N/A	N/A
Frankfurt	LUDWIG	26-8-1984	M	126	67	57
Frankfurt	KAMITI	21-1-1987	F	138	56	54
Frankfurt	ZOMI	28-1-1998	F	240	88	113
Frankfurt	KUTU	29-5-1998	F	246	56	54
Frankfurt	HERI	23-1-2001	M	274	46	126
Frankfurt	NYOTA II	24-2-2007	M	376	46	126
Frankfurt	OMANGA	18-12-2008	F	387	138	126
Frankfurt	BILI II	8-10-2008	M	386	245	194
Frankfurt	PANGI	16-7-2009	F	389	246	126
Frankfurt	PANISCO	15-12-2009	M	394	240	126
Frankfurt	MIXI	18-12-2001	F	282	220	177
Frankfurt	BONDO	17-9-1991	M	164	106	38
Stuttgart	KOMBOTE	1-1-1966	F	56	N/A	N/A
Stuttgart	HERMIEN	1-1-1978	F	88	N/A	N/A
Stuttgart	ZORBA	1-1-1980	M	168	N/A	N/A
Stuttgart	MOBIKISI	1-1-1980	M	167	N/A	N/A
Stuttgart	CHIPITA	1-1-1993	F	220	N/A	N/A
Stuttgart	CHIMBA	1-1-1995	F	313	N/A	N/A
Stuttgart	LIBOSO	17-12-1997	F	227	1006	1009
Stuttgart	HAIBA	16-11-2001	F	281	132	126
Stuttgart	BANBO	3-9-2002	F	293	155	194
Stuttgart	KASAI	27-12-2004	M	341	220	215
Stuttgart	KIANGA	17-7-2005	F	349	56	215
Stuttgart	NAYEMBI	26-4-2006	F	373	227	1003
Stuttgart	HUENDA	6-7-2006	F	374	88	161
Wuppertal	BUSIRA	16-2-2004	F	332	158	38
Wuppertal	EJA	14-7-1990	F	158	42	102
Wuppertal	LUSAMBO	21-7-1980	M	107	56	54
Wuppertal	BIROGU	11-8-1989	M	151	55	38
Wuppertal	LISALA I	24-4-1980	F	106	55	54
Wuppertal	MATO	22-12-1963	M	38	31	15
Wuppertal	LUEBO	18-3-2006	M	371	106	151
Wuppertal	AZIBO	2011	M	N/A	158	N/A
Wuppertal	AYUBU	2011	M	N/A	158	N/A

References

Allen, C. and Bekoff, M. (2005) Animal Play and the Evolution ofMorality: An Ethological Approach. *TOPOI, 24(2), pp. 125-135*

Barber, N. (1991) Play and energy regulation in mammals. *The Quarterly Review of Biology, 66(2), pp. 129-147*

Bekoff, M. (1974) Social play in coyotes, wolves, and dogs. *Bioscience, 24(4), pp. 225-230*

Bekoff, M. (2001) Social Play Behaviour. Cooperation, Fairness, Trust, and the Evolution of Morality. *Journal of Consciousness Studies, 8(2), pp. 81-90*

Bekoff, M. and Byers, J.A. (1998) (editors) *Animal play: Evolutionary, Comparative, and Ecological perspectives.* Cambridge University Press, Cambridge

van den Berg, C.L., Hol, T., van Ree, J.M., Spruijt, B.M., Everts, H., Koolhaas, J.M. (1999) Play is Indispensable for an Adequate Development of Coping with Social Challenges in the Rat. *Social Psychobiology, 34(2), pp. 129-138*

Brownlee, A. (1954) Play in domestic cattle in Britain: an analysis of its nature. *British Veterinary Journal, 110, pp. 48–68.*

Burghardt, G.M. (1984) On the origins of play. Pp. 5-41 in *Play in Animals and Humans.* Edited by Smith, P.K. Basil Blackwell, Oxford

Burghardt, G.M. (2005) *The Genesis of Animal Play. Testing the limits.* MIT Press, Cambridge

Byers, J.A. (1998) Biological effects of locomotor play: getting into shape, or something more specific? Pp. 205-220 in *Animal play: Evolutionary, Comparative, and Ecological perspectives.* Edited by Bekoff, B. and Byers, J.A. Cambridge University Press, Cambridge

Byers, J.A. and Walker, C. (1995) Refining the motor training hypothesis for the evolution of play. *The American Naturalist, 146(1), pp. 25-40*

Cordoni, G. (2009) Social play in captive wolves (*Canis lupus*): not only an immature affair. *Behaviour, 146(10), 1363-1385*

Cordoni, G. and Palagi, E. (2011) Ontogenetic Trajectories of Chimpanzee Social Play: Similarities with Humans. *PLoS ONE, 6(11), art. no. e27344.*

Diamond, J. and Bond, A.B. (2003) A Comparative Analysis of Social Play in Birds. *Behaviour, 140(8-9), pp. 1091-1115*

Dubuc, C., Hughes, K.D., Cascio, J., Santos, L.R. (2012) Social Tolerance in a Despotic Primate: Co-Feeding Between Consortship Partners in Rhesus Macaques. *American Journal of Physical Anthropology, 148(1), pp.73-80*

van Elsacker, L., Vervaecke, H., Verheyen, R.F. (1995) A Review of Terminology on Aggregation Patterns in Bonobos (*Pan paniscus*). *International Journal of Primatology, 16(1), pp.37-52*

Enomoto, T. (1990) Social Play and Sexual Behavior of the Bonobo (*Pan paniscus*) with Special Reference to Flexibility. *Primates, 31(4), pp. 469-480*

Fagen (1981) *Animal Play Behavior.* Oxford University Press, Oxford

Fagen, R. (1993) Primate Juveniles and Primate Play. Pp. 182-196 in *Juveniles Primates: Life History, Development, and Behavior.* Edited by Pereira, M.A. and Fairbanks, L.A. Oxford University Press, New York

Fagen R, Fagen F (2004) Juvenile survival and benefits of play behaviour in brown bears, *Ursus arctos. Evolutionary Ecology Research, 6, pp. 89–102*

Fruth, B. and Hohmann, G. (2006) Social grease for females? Same-sex genital contact in wild bonobos. Pp. 294-315 in *Homosexual Behaviour in Animals, an Evolutionary Perspective.* Edited by Sommer, V. and Vasey, P.L. Cambridge University Press, Cambridge

Furuichi, T. (1987) Sexual Swelling, Receptivity, and Grouping of Wild Pygmy Chimpanzee Females at Wamba, Zaire. *PRIMATES, 28(3), pp. 309-318*

Furuichi, T. (1989) Social Interactions and the Life History of Female *Pan paniscus* in Wamba, Zaire. *International Journal of Primatology, 10(3), pp. 173-197*

Furuichi, T. (1997) Agonistic Interactions and Matrifocal Dominance Rank of Wilde Bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology, 18(6), pp. 855-875*

Furuichi, T. (2011) Female Contributions to the Peaceful Nature of Bonobo Society. *Evolutionary Anthropology, 20(4), pp. 131-142*

Furuichi, T. and Thompson, J. *The Bonobos Behavior, Ecology and Conservation.* Springer, New York

Graham, K.L. and Burghardt, G.M. (2010) Current perspectives on the biological study of play: signs of progress. *The Quarterly Review of Biology, 85(4), pp. 393-418*

Groos, K. (1898) *The Play of Animals*. D. Appleton, New York

Hall, G. S. (1904) *Adolescence: Its Psychology and its Relations to Physiology, Anthropology, Sociology, Sex, Crime, Religion, and Education.* Appleton, New York

Held, S.D.E. and Špinka, M. (2011) Animal play and animal welfare. *Animal Behaviour, 81(5), pp. 891-899*

Hohmann, G., Gerloff, U., Tauts, D., Fruth, B. (1999) Social bonds and genetic ties: Kinship, association and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour, 136(9), pp. 1219-1235*

Ito, Y., Brown, J.L. and Kikkawa, J. (1987) *Animal Societies: Theories and Facts.* Japan. Sci. Soc. Press, Tokyo

Kano, T. (1980) Social Behavior of Wild Pygmy Chimpanzees (*Pan paniscus*) of Wamba: A Preliminary Report. *Journal of Human Evolution, 9(4),pp. 243-260*

Kano, T. (1982) The Social Group of Pygmy Chimpanzees (*Pan paniscus*) of Wamba. *Primates, 23(2), 171-188*

Kano, T. (1983) An Ecological Study of the Pygmy Chimpanzees (*Pan paniscus*) of Yalosidi, Republic of Zaire. *International Journal of Primatology, 4(1), 1-31*

Kano, T. (1987a) A Population Study of a Unit Group of Pygmy Chimpanzees of Wamba – with a Special Reference to the Possibly Lack of Intraspecific Killing. Pp. 159-172 in *Animal Societies: Theories and Facts.* Edited by Ito, Y., Brown, J.L. and Kikkawa, J. Japan. Sci. Soc. Press, Tokyo

Kano, T. (1987b) Commentary: Social Regulation for Individual Coexistence in Pygmy Chimpanzees (*Pan paniscus*). Pp. 105-118 in *Dominance, Aggression and War.* Edited by McGuinnes, D. Paragon House Press, New York

Kano, T. (1987c) Social Organisation of the Pygmy Chimpanzee and the Common Chimpanzee: Similarities and Differences. Pp. 53-64 in *Evolution and coadaptation in biotic communities.* Edited by Kawano, S., Connel, J.H., Hidaka, T. Tokyo University Press

Kano, T. (1989) The sexual behaviour of pygmy chimpanzees. Pp. 176-183 in *Understanding Chimpanzees,* edited by Heltne, P.G. and Marquardt, L.A. Harvard University Press, Cambridge, USA

Kano, T. (1990) The Bonobos'Peaceable Kingdom. Zaire's pygmy chimpanzees may be the most pacific of primates. *Natural History, 11, pp. 62-72*

Kawano, S., Connel, J.H., Hidaka, T. (1987) *Evolution and coadaptation in biotic communities.* Tokyo University Press

Kuehl, H.S., Elzner, C., Moebius, Y., Boesch, C., Walsh, P.D.(2008) The Price of Play: Self-Organized Infant Mortality Cycles in Chimpanzees. *PLoS ONE, 3(6), art. no. e2440*

Kuroda, S. (1980) Social Behavior of the Pygmy Chimpanzees. *Primates, 21(2), pp. 181-197*

Lacambra, C., Thompson, J., Furuichi, T., Vervaecke, H., Stevens, J. (2005) Bonobo (*Pan paniscus*). Pp. 83-96 in *WORLD ATLAS OF GREAT APES AND THEIR CONSERVATION.* Edited by Caldecott, J. and Miles, L. Prepared at the UNEP World Conservation Monitoring Centre. University of California Press, Berkeley, USA

Lawrence, A. (1987) Consumer Demand Theory and the Assessment of Animal Welfare. *Animal Behaviour, 35(1,) pp. 293-295*

Livescu, S. (2003) From Plato to Derrida and Theories on Play. *CLCWeb: Comparative Literature and Culture (http://docs.lib.purdue.edu/clcweb/vol5/iss4/5), 5(4), pp. 1-7*

Lyn, H., Greenfield, P., Savage-Rumbaugh, S. (2006) The development of representational play in chimpanzees and bonobos: Evolutionary implications, pretense, and the role of interspecies communication. *Cognitive Development, 21(3), pp.199-213*

Lyn, H., Franks, B., Savage-Rumbaugh, E. (2008) Precursors of morality in the use of the symbols "good" and "bad" in two bonobos (*Pan paniscus*) and a chimpanzee (*Pan troglodytes*). *Language & Communication, 28(3), pp. 213-224*

Merrick, N.J. (1977) Social Grooming and Play Behavior of a Captive Group of Chimpanzees. *Primates, 18(1), pp. 215-224*

Newton-Fisher, N.E. (2004) Hierarchy and social status in Budongo chimpanzees. *Primates, 45(2), pp. 81-87*

Norscia, I., Palagi, E. (2011) When play is a family business: adult play, hierarchy, and possible stress reduction in common marmosets. *Primates, 52(2), pp. 101-104*

Nunes, S., Muecke, E., Lancaster, L.T., Miller, N.A., Mueller, M.A., Muelhaus, J., Castro, L. (2004) Functions and Consequences of Play Behaviour in Juvenile Belding's ground squirrels. *Animal Behaviour, 68(1), pp.27-37*

Pagel, M. D., & Harvey, P. H. (1993). Evolution of the juvenile period in mammals. Pp. 28-37 in *Juvenile primates: Life history, development, and behaviour.* Edited by Pereira, M.E. and Fairbanks, L.A. Oxford University Press, Oxford

Palagi, E. (2006) Social Play in Bonobos (*Pan paniscus*) and Chimpanzees (*Pan troglodytes*): Implications for Natural Social Systems and Interindividual Relationships. *American Journal of Physical Anthropology, 129(3), pp. 418-426*

Palagi, E. (2008) Sharing the motivation to play: the use of signals in adult bonobos. *Animal Behaviour, 75(3), pp. 887-896*

Palagi, E., Cordoni, G., Borgognini Tarli, S.M. (2004) Immediate and Delayed Benefits of Play Behaviour: New Evidence from Chimpanzees (*Pan troglodytes*). *Ethology, 110(12), pp. 949-962*

Palagi, E., Paoli, T., Borgognini Tarli, S. (2006) Short-Term Benefits of Play Behavior and Conflict Prevention in *Pan paniscus. International Journal of Primatology, 27(5), pp. 1257-1270*

Palagi, E., Antonacci, D., Cordoni, G. (2007) Fine-Tuning of Social Play in Juvenile Lowland Gorillas (*Gorilla gorilla gorilla*). *Developmental Psychobiology, 49(4), pp. 433-445*

Palagi, E. and Paoli, T. (2007) Play in Adult Bonobos (*Pan paniscus*): Modality and Potential Meaning. *American Journal of Physical Anthropology, 134(2), pp. 219-225*

Palagi, E. and Paoli, T. (2008) Social Play in Bonobos: Not Only an Immature Matter. Pp. 55-74 in *The Bonobos: Behavior, Ecology and Conservation.* Edited by Furuichi, T. and Thompson, J. Springer, New York

Panksepp, J., Siviy, S., Normansell, L. (1984) The Psychobiology of Play: Theoretical and Methodological Perspectives. *Neuroscience & BioBehavioral Reviews, 8(4), pp. 465-492*

Paoli, T., Palagi, E., Borgognini Tarli, S.M. (2006) Reevaluation of Dominance Hierarchy in Bonobos (*Pan paniscus*). *American Journal of Physical Anthropology, 130(1), pp. 116-122*

Paquette, D. (1994) Fighting and playfighting in captive adolescent chimpanzees. *Aggressive Behavior, 20(1), pp. 49-65*

Parish, A.R. (1994) Sex and Food Control in the "Uncommon Chimpanzee": How Bonobo Females Overcome a Phylogenetic Legacy of Male Dominance. *Ethology and Sociobiology, 15(3), pp. 157-179*

Parish, A.R. (1996) Female Relationships in Bonobos (*Pan paniscus*). Evidence for Bonding, Cooperation, and Female Dominance in a Male-Philopatric Species. *Human Nature, 7(1), pp. 61-96*

Parish, A.R., de Waal, F.B.M., Haig, D. (2000) The Other "Closest Living Relative" How Bonobos (*Pan paniscus*) Challenge Traditional Assumptions about Females, Dominance, Intra- and Intersexual Interactions, and Hominid Evolution. *Annals of the New York Academy of Sciences, 907, pp. 97-113*

Pellegrini, A.D. Smith, P.K. (2005) *The Nature of Play: Great Apes and Humans*. The Guilford Press, New York

Pellegrini, A.D., Dupuis, D., Smith, P.K.(2007) Play in evolution and development. *Developmental Review, 27(2), pp. 261-276*

Pellis, S. M. and Pellis, V. C. (1991) Role reversal changes during the ontogeny of play fighting in male rats: Attack versus defense. *Aggressive Behavior, 17, pp. 179-189.*

Pellis, S.M. and Pellis, V.C. (1996) On knowing it's only play: The role of play signals during play fighting. *Aggression and Violent Behavior, 1(3), pp.249-268*

Pellis, S.M. and Iwaniuk, A.N (1999a) The roles of phylogeny and sociality in the evolution of social play in muroid rodents. *Animal Behaviour, 58(2), pp. 361-373*

Pellis, S.M. and Iwaniuk, A.N. (1999b) The Problem of Adult Play Fighting: A Comparative Analysis of Play and Coursthip in Primates. *Ethology, 105(9), pp. 783-806*

Pellis, S.M. and Iwaniuk, A.N. (2000a) Adult-Adult Play in Primates: Comparative Analyses of its Origin, Distribution and Evolution. *Ethology, 106(12), pp.1083-1104*

Pellis, S.M. and Iwaniuk, A.N. (2000b) Comparative Analyses of the Role of Postnatal Development on the Expression of Play Fighting. *Developmental Psychobiology, 36(2), pp. 136-147*

Pereira, M.E. and Fairbanks, L.A. (1993) *Juvenile Primates: Life History, Development, and Behavior.*Oxford University Press, New York

Pika, S., Liebal, K., Tomasello, M. (2005) Gestural Communication in Subadult Bonobos (*Pan paniscus*): Repertoire and Use. *American Journal of Primatology, 65(1), pp.39-61*

Pika, S. and Zuberbühler, K. (2008) Social Games Between Bonobos and Humans: Evidence for Shared Intentionality? *American Journal of Primatology, 70(3), pp.207-210*

Pollick, A.S. and de Waal, F.B.M. (2007) Ape gestures and language evolution. *PNAS, 104(19), pp. 8184-8189*

Pollick, A.S., Jeneson, A., de Waal, F.B.M. (2008) Gestures and Multimodal Signalling in Bonobos. In *The Bonobos: Behavior, Ecology, and Conservation,* pp. 75-95 Springer, New York

Power, T.G. (2000) *Play and exploration in children and animals.* L. Erlbaum, New York

Prüfer, K., Munch, K., Hellmann, I., Akagi, K., Miller, J.R., Walenz, B., Koren, S., Sutton, G., Kodira, C., Winer, R., Knight, J.R., Mullikin, J.C., Meader, S.J., Ponting, C.P., Lunter, G., Higashino, S., HObolth, A., Dutheil, J., Karakoç, E., Alkan, C., Sajjadian, S., Rita Catacchio, C.R., Ventura, M., Marques-Bonet, T., Eichler, E.E., André, C., Atencia, R., Mugisha, L., Junhold, J., Patterson, N., Siebauer, M., Good, J.M., Fischer, A., Ptak, S.E., Lachmann, M., Symer, D.E., Mailund, T., Schierup, M.H., Andrés, A.M., Kelso, J., Pääbo, S. (2012) The bonobo genome compared to human and chimpanzee genomes. *Nature, 486(7404), pp. 527-531*

Sharpe, L.L. and Cherry, M.I. (2003) Social play does not reduce aggression in wild meerkats. *Animal Behaviour, 66(5), 989-997*

Sharpe, L.L., Clutton-Brock, T.H., Brotherton, P.N.M., Cameron, E.Z., Cherry, M.I. (2002) Experimental provisioning increases play in free-ranging meerkats. *Animal Behaviour, 64(1), pp. 113-121*

Smith, P.K. (1984) (editor) *Play in Animals and Humans.* Basil Blackwell, Oxford

Sommer, V., Vasey, P.L. (2006) (editors) *Homosexual Behaviour in Animals, an Evolutionary Perspective.* Cambridge University Press, Cambridge

Spencer, H. (1873) *The Principles of Psychology. Second Edition, Volume 2*. Appleton, New York

Špinka, M., Newberry, R.C., Bekoff, M. (2001) Mammalian play: Training for the unexpected. *The Quarterly Review of Biology, 76(2), pp. 141-168*

Stanford, C.B. (1998) The Social Behavior of Chimpanzees and Bonobos. Empirical Evidence and Shifting Assumptions. *Current Anthropology, 39(4), pp. 399-420*

Stevens, J.M.G., Vervaecke, H., de Vries, H., van Elsacker, L. (2006) Social structures in *Pan paniscus*: testing the female bonding hypothesis. *Primates, 47(3), pp. 210-217*

Stevens, J.M.G., Vervaecke, H., de Vries, H., van Elsacker, L. (2007) Sex Differences in the Steepness of Dominance Hierarchies in Captive Bonobo Groups. *International Journal of Primatology, 28(6), pp. 1417-1430*

Stevens, J.M.G., Vervaecke, H., Van Elsacker, L. (2008) The Bonobo's Adaptive Potential: Social Relations under Captive Conditions. Pp. 19-38 in *The Bonobos: Behavior, Ecology and Conservation.* Edited by Furuichi, T. and Thompson, J. Springer, New York

Strier, K.B., Dib, L.T., Figueira, J.E.C. (2002) Social dynamics of male muriquis (*Brachyteles arachnoides hypoxanthus*). *Behaviour, 139(2-3), pp. 315-342*

Stumpf, R. 2007. Chimpanzees and bonobos: Diversity within and between species. Pp. 321-In *Primates in perspective*. Edited by Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M. and Bearder, S.K.. 321–344. Oxford University Press, Oxford

Tinbergen, N. (1951) *The study of instinct.* Oxford University Press, Oxford

Tinbergen, N. (1963) On aims and methods in ethology. *Zeitschrift für Tierpsychologie, 20, pp. 410-433*

Thompson, K.V. (1998) Self assessment in juvenile play. Pp. 183-204 in *Animal play: Evolutionary, Comparative, and Ecological perspectives.* Edited by Bekoff, B. and Byers, J.A. Cambridge University Press, Cambridge

Vehrencamp, S.L. (1983) A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour, 31(3), pp. 667-682*

Vervaecke, H., de Vries, H., van Elsacker, L. (2000) Dominance and its Behavioral Measures in a Captive Group of Bonobos (*Pan paniscus*). *International Journal of Primatology, 21(1), pp.47-68*

de Vries, H. (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour, 50(5), 1375-1389*

de Waal, F.B.M. (1995) Bonobo Sex and Society. The behaviour of a close relative challenges assumptions about male supremacy in human evolution. *Scientific American, 16, pp. 82-88*

de Waal, F.B.M., Lanting, F. (1997) *Bonobo: The Forgotten Ape.* University of California Press, Berkeley

Watts, D.P. and Pusey, A.E. (1993) Behavior of Juvenile and Adolescent Great Apes. Pp. 148-172 in *Juvenile Primates: Life History, Development, and Behavior.* Edited by Pereira, M.E. and Fairbanks, L.A. Oxford University Press, New York

Wrangham, R.W. (1986) Ecology and Social Relationships in Two Species of Chimpanzee. Pp. 352-378 in *Ecological Aspects of Social Evolution. Birds and Mammals.* Edited by Rubenstein, D.I. and Wrangham, R.W. Princeton University Press, Princeton New Jersey