Ontogeny and Variability of Play Behaviour in Wild, Immature Bornean (*Pongo pygmaeus wurmbii*) and Sumatran Orangutans (*Pongo abelii*)



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# Abstract

According to some hypotheses, play serves different functions at different times during ontogeny and therefore the nature and frequency of play are expected to change during the developmental trajectory. With their extended immature phase as well as ecological and behavioural variation among populations, orangutans offer the opportunity to disentangle specific functions of different play types. In my thesis, I compared frequency and qualitative characteristics of social and solitary play of wild, immature orangutans (0.3-13 y) across two study populations (*P.pygmaeus wurmbii*, at Tuanan, Borneo, and *P.abelii* at Suaq Balimbing, Sumatra). Play behaviour was documented by instantaneous and all-occurrence sampling during full-day focal follows. Social play bouts were also video taped in order to evaluate qualitative characteristics of social play.

I found different ontogenetic trajectories of social, solitary locomotor and solitary object play. Solitary object and solitary locomotor play peaked around the age 1 - 3 years and 2 - 4 years, respectively, and ceased around the age of 5 years, whereas social play was generally low but present throughout the entire ontogeny. While solitary play frequency and quality did not differ between sites, social play frequency was higher at Suag Balimbing than at Tuanan. Nonetheless, we could not find any difference in social play motivation between the two populations: First, the higher social play frequencies at Suaq Balimbing were mediated by more frequent associations, especially among non-related females and with unflanged males compared to Tuanan. Second, when being in an association, immatures of the less gregarious population at Tuanan even tended to play more than immatures at Suaq Balimbing. Therefore, higher social play frequency in the population of Suaq Balimbing can be explained by the higher degree of sociability and hence, increased social play opportunities, and not by a difference in the intrinsic motivation to play. Moreover, video analyses of play sequences revealed no differences in qualitative characteristics of social play. Even though higher fruit availability has been made responsible to the more sociable Sumatran orangutans, on a smaller scale, neither social nor solitary play frequencies were affected by fruit availability at either site.

All in all, my thesis suggests that play indeed serves various functions at different times during ontogeny. Different play types follow different, fixed developmental trajectories in orangutans and happen irrespective of the ecological and social circumstances and details. Therefore, play seems to be a crucial element during the ontogeny of orangutans.

# **1** Introduction

"Play behaviour is a paradox in humans and animals, being ubiquitous yet ambiguous." (Graham & Burghardt, 2010)

"Play is...ubiquitous", yet not fully understood. Its omnipresence already suggests its importance. Rather than being a by-product or even a maladaptation, play might provide crucial either immediate or delayed benefits to immature individuals (Martin & Caro, 1985). Play is one of the first social interactions of immatures with unrelated individuals (Palagi, 2011). It might thus allow interesting insights into social behaviour and learning mechanisms about social interactions, such as cooperation and competition. Therefore, if not for the sake of play *per se*, but rather for studying ontogeny, it is crucial to look at play. Moreover, by considering differences in the play repertoire of great apes and humans, especially borderline cases, such as fantasy play (Bjorklund & Gardiner, 2011) and the unique play patterns in humans (e.g. Pellegrini, 2009) might even give important hints about the human evolution (Bateson, 2011). Therefore, the study of play behaviour in great apes is vital. This comparative study aimed at understanding the play behaviour of immature orangutans.

# 1.1 What is play?

# 1.1.1 Phylogeny

Phylogenetically, play behaviour is widespread among animals, especially in mammals. But it has also been observed in reptiles, such as turtles and crocodiles, fish (Burghardt, 1998; Burghardt, 2005), octopuses (Kuba et al., 2003) and birds (e.g. Heinrich & Smolker, 1998; Diamond & Bond, 2003).

Play behaviour is in fact with only some exceptions (Pellis & Iwaniuk, 1999a) nearly ubiquitous in mammals (Fagen, 1981). Play accounts for 1 to 10 % of the time budget in immature mammals (e.g. Fagen, 1981). In primates, it seems to be most prevalent (Müller-Schwarze, 1984) and is present in all species (Fagen, 1993). Great apes typically show more social play than any other primates in captivity, with an average of 14 % of their time budget compared to 8 % in haplorhine primates (Lewis, 2005).

Fagen (1993) points out that play is especially common in animals with a long period of immaturity and long-lasting parental care. In primates, the long immaturity has been associated with the large amount of complex social skills that need to be learned (Joffe, 1997) and thus play might take a role in acquiring these skills. Yet, it has been argued that a large brain connected with the greater proportion of postnatal brain growth is correlated with a longer immaturity and therefore also with play (Pellis & Iwaniuk, 2000). Moreover, in birds, large brain size, altriciality and higher levels of sociability were named preconditions for social play (Diamond & Bond, 2003).

Play has been denoted the hallmark of juvenile period (Groos, 1898). Nevertheless, it can also be observed in adult animals, especially in humans (e.g. Huizinga, 1938; Held & Spinka, 2011). In any case, when studying play behaviour each phase of life needs to be looked at separately (Palagi, 2011). Namely, strong evidence points to different benefits of play during either immaturity or adulthood.

# **1.1.2 Definition**

There have been many attempts to define play (for reviews Fagen, 1981; Burghardt, 2005). Thereby authors have either focused on the functional (e.g. Fagen, 1981, tab. 1) or structural components of play (Burghardt, 2005). Burghardt (2005) points out that it is essential to define play in order to label behaviour "play" in animals where play might not be as obvious to us as in others, for example in fish, reptiles and insects.

Play is often characterised by its seeming uselessness, yet resembling serious behaviour (e.g. Bekoff & Byers, 1981, tab.1)

To sum up, Burghardt (2005) defined five criteria which need to be fulfilled to label a behaviour as play:

- I. Limited immediate function
- II. Intrinsic motivation, autotelic component
- III. Structurally or temporally different to serious behaviour
- IV. Repeated performance of the same play to exclude strange behaviour
- V. Relaxed field: individuals free from stress play more

However, evidence challenging Burghardt's fifth criteria will be presented later on.

Relevance of play during development	"Play is vital to the healthy development of all of the so-called higher animals. Play is a biological imperative Play for your life: The stake are survival." (Preface: Fagen (1981): National Conference on Vital Role of Play in Learning, Development and Survival, Washington DC)
Relevance of play study	"Evolutionary and ecological considerations, along with studies of the brain and play, help explain why some species play and others play less so or not at all." (Burghardt, 2010)
What is known	"No behavioural concept has proven more ill-defined, elusive, controversial, and even unfashionable" (E.O.Wilson, 1975)
What is play?	"it's hard to define, but I know it (play), when I see it" (Dolhinow, 1999)
Functional definition	"I view play as behaviour that functions to develop, practice, or maintain physical or cognitive abilities and social relationships, including both tactics and strategies, by varying, repeating and/or recombining already functional subsequences of behaviour outside their primary context. It is a matter of taste whether behaviours that do not simultaneously satisfy the structural, causal – contextual, functional, and developmental criteria of this definition are to be called play. " (Fagen, 1981)
Structural definition	"Play is all locomotor activity performed postnatally which appears to an observer to have no obvious immediate benefits for player, in which motor patterns resembling those used in serious functional contexts may be used in modified terms. Elements: exaggeration, repetition, fragmentation or disordering of motor act sequences" (Bekoff & Byers, 1981)

 Table 1: Quotations and definitions of play behaviour

# **1.1.3 Subdivision play types**

Not all play is the same. The most common and simplest subdivision of play is into (1) solitary object, (2) solitary locomotor and (3) social play (Bekoff & Byers, 1981). The three play types occur in different conditions, involve different skills and require varying preconditions and hence, need to be looked at separately. Play patterns can further be

distinguished more in detail. For example social play can be split up into wrestling, chasing, play fighting, pseudo-sexual play, play-mothering etc. (Lewis, 2005; Lewis & Barton, 2006), object play can be categorized according to the objects involved in (Myowa-Yamakoshi & Yamakoshi, 2011) or what is done with the object (Pellegrini, 2013) and locomotor play could be differentiated into rhythmic stereotypies, exercise play and rough & tumble play (Pellegrini & Smith, 1998a).

## **1.1.4 Ontogenetic trajectories**

In general, play behaviour in immatures follows a bell-shaped developmental trajectory (Pellis & Pellis, 2009): it increases at the end of infancy, peaks during juvenility and decreases to the end of juvenility. The fact that very young infants hardly play (e.g. Squirrel monkeys: Stone, 2008) might indicate that some basic physical abilities are required to play. Yet, several studies suggest that the three play types follow different ontogenetic trajectories (humans: Pellegrini & Smith, 1998b; antelopes: Thompson: 1998; vervet monkeys: Fairbanks, 2000; gorillas: Maestripieri & Ross, 2004; meerkats: Sharpe, 2005a). With skill development play patterns change and thereby might occur due to different motivations and serve various functions. Generally locomotor play peaks before object play and social play constitutes the last peak (e.g. vervet monkeys: Fairbanks, 2000).

In great apes, there seem to be various peaks of a single play type. Social play peaks during infancy with the mother as play partner and a second time during early juvenility with peers. Moreover, qualitative developmental trajectories can be seen within one single play type (Lewis, 2005). For example, social play in chimpanzees cannot be distinguished by a quantitative, but a qualitative trajectory, in terms of complexity, asymmetry and playmate choice (Cordoni & Palagi, 2011). In wild chimpanzees, social play ceases during adolescence, whereas adolescent individuals still receive play invitations, but do not initiate play themselves anymore (Pusey, 1990).

From another point of view, the three main play types can be combined even within one single play bout, which might indicate a universal function of play (Burghardt, 1998). For example if two animals chase each other, it is social and locomotor play. This fact led some researchers to suggest and to assess play complexity rather than the occurrence of specific play types (e.g. Iwaniuk, Pellis & Nelson, 2001). On the one hand, play complexity may be defined as the number of different types of play patterns within a single play session (Cordoni & Palagi, 2011). On the other hand, play can be argued to become more complex as another animal is involved. Hence social play would generally be more complex, since sophisticated social communication between the play participants might be required (Fagen, 1993; Pellegrini, 2009). For example, Zucker & Clarke (1992) found that the older howling monkey immatures get, the more likely they were to play in larger groups. If one argued that play becomes more complex, the more individuals participate, then we would see an increase of complexity during ontogeny in howler monkeys. Yet, it should also be assessed how complex the social interactions are between individuals.

In summary, play is closely linked to ontogeny either by requiring basic skills as precondition or providing a possibility to learn or practice specific skills required during adulthood.

# 1.1.5 Reciprocity and cooperation in social play

From another angle, if play partners differ in size, there needs to be some restraint or selfhandicapping by the stronger play partner (bonobos: Enomoto, 1990; Biben, 1998; chimpanzees: Flack et al., 2004; gogs: Bauer & Smuts, 2007). Though, most animals show a preference for size-matched play partners and physical symmetry seems to be an important factor to maintain a play relationship over time (e.g. Palagi, 2007b; Thompson, 1996). In any case, cooperation and especially reciprocity is believed to be crucial for maintaining social play, since animals betake themselves into vulnerable situations during play (e.g. Bekoff, 1995a, 2001; Fagen, 1993; Pellis et al., 2010a). Pellis and colleagues (2010a) imply the need of a 50:50 rule between cooperation and competition to keep up social play. Animals should not take advantage of their success and cooperate with the play partner, but there also needs to be some competition. They argue if there is a bias towards cooperation, i.e. 60:40, play serves rather social skill practice. Yet if play is skewed towards competition, i.e. 40:60, individuals might profit in terms of fighting skill practice (Pellis et al., 2010b). As individuals can blunder into vulnerable situations, contact play might also imply trust which could be reflected in the partner choice (Bekoff, 2001). So, there would need to be some basis for the relationship between playmates, such as kinship or friendship. For example, squirrels prefer to play with littermates (Nunes et al., 2004). Yet, golden lion tamarins show a preference for non-related, mixed-aged play partners over their twin. The authors justify this preference by elevated socio-cognitive skill demands and thereby the practice of interactions with individuals (Oliviera et al., 2003). In general, potential play partners, who encounter each other repeatedly, should be more

In general, potential play partners, who encounter each other repeatedly, should be more likely to cooperate in play, because repeated encounters facilitate cooperation (Fagen, 1993). Fairness allows unrestrained playing (Pellis et al., 2010b).

If there are unbalanced play dyads with one player a lot older or stronger than the other, there should be some restraint by the dominant individual. Pereira & Preisser (1998) point out that the less likely a strong individual is to find a matched play partner, the more effort the individual should invest into self-handicapping during play with weaker individuals. In fact, chimpanzees show a high degree of self-handicapping: the older the dominant individual, the more they restrain themselves when playing with a younger individual. Older individuals even show awareness of the play spectators. Namely, they reduce play intensity when interacting with a younger individual whose mother is present (Flack et al., 2004). However, dogs seem to violate the 50: 50 rule. Since they become a lot more violent as they grow bigger, stronger and more dominant to playmates and thereby play bouts turn out very skewed (Bauer & Smuts, 2007). Moreover, third party interventions were observed in dog social play. Yet, the intervening individual tends to support the winning player and hence, no reciprocation can be seen (Ward et al., 2009).

All in all, there needs to be a mechanism which motivates subordinate or weaker individuals to engage in play and thereby to maintain a play relationship. This might be in form of role-reversals or self-handicapping. Opposite, dominant individuals show awareness of the weaker individuals' skills by adapting play intensity.

### **1.1.6 Play signals**

Cooperation during play could also be enhanced by playful signals and hence, these could help to maintain a play bout (eg. Bauer & Smuts, 2007). Such signals can be gestures, facial expressions or vocalisations.

Some students of play even defined play based on such play signals and exclusively considered play-like behaviour with the playful signals as real play (e.g. Myowa-Yamakoshi

& Yamakoshi, 2011). Different taxa exhibit different playful expressions. In carnivores, the play bow is characteristic of social play, whereas in primates, the open mouth display – play face (PF) or full play face (OPF) – is often present during solitary and social play (e.g. Fagen, 1993; Ross et al., 2014). However, play signals do not seem to be compulsory during play, but they might aid to initiate and to maintain play bouts (e.g. Waller & Dunbar, 2005; Lewis, 2005). Play duration is reported to be longer if both players display playfaces (Waller & Dunbar, 2005; Mancini et al. 2013). In several primate species playface frequency was highest during play-fighting and rough playful interactions, which alludes to the necessity to signal benevolent intent (e.g. Pellis & Pellis, 2007; Vettin & Todt, 2005). From an evolutionary perspective, playfaces have been characterized as ritualized forms of biting (Poole, 1977).

Also vocalisations can act as play signals. Play panting in chimpanzees appears to encourage the performer to continue to tickle or chase the other individual and thereby stimulates social play (Matsusaka, 2004). Thus, it would also serve the maintenance or initiation of play. In contrast, visual signals are hypothesized to be emitted unconsciously and to be an honest representation of the individual's emotional state (Waller & Dunbar, 2005; Cordoni & Palagi, 2011). This hypothesis is further supported by the fact that playfaces do not only occur in social play context, but are also exhibited during solitary play (e.g. Ross et al., 2014). Nevertheless, playface frequency increases in adult bonobos with increasing play roughness, whereas in adult chimpanzees playface frequencies do not seem to change with play type and context. However, in immature chimpanzees playfaces increased in the older play partner if the mother of the younger player was closer or play was rougher (Flack et al., 2004), which alludes to a signalling function of the playface. From another point of view, Hobaiter and Byrne (2014) argue that gestures during play could rather serve for learning socially delicate gestures in a relaxed situation.

All in all, there is an ongoing debate whether playful expressions are intentional or simply represent the emotional state of individuals. Nevertheless, the hypotheses are not mutually exclusive (Demuru et al., 2014).

# **1.2 Functions of play**

Since the 19<sup>th</sup> century there is a persisting debate about when, to what extent and how play benefits an individual. Over 30 hypotheses have been proposed for proximate and ultimate causes of play (for a review: Burghardt, 2005). Yet, a lot of the hypotheses are mere theories without empirical support. Most early theorists agreed that play is an instinctive behaviour (Hall, 1904; Groos, 1899; Spencer, 1872). All in all, if not labelled functionless, play is assumed to contribute to physical, social, and cognitive skill development in immature individuals.

# **1.2.1** When and to what extent benefits? – Play paradox

Benefits of play in immature individuals are mostly designated to be delayed and only present during adulthood. Yet, individuals face immediate energetic costs when playing (Byers & Walker, 1995; Bekoff & Allen, 1998; Sharpe et al., 2002; Oliveira et al., 2003). Though, no agreement about the actual energy expenditure of play could be reached yet.

If play benefits animals only delayed, but yields immediate costs, it is a biological paradox. Anyhow, the cost is likely highly variable according to the context and species, as time spent playing varies within and across species (e.g. Fagen, 1981).

But not only the timing, also the magnitude of play benefits is questioned. Benefits would mean that play enhances survival and thereby fitness. Fagen (1981) proposed that play might

enhance fitness only indirectly (Figure 1). He argued that play would influence a specific phenotypic factor which could also be developed by alternative behaviours. Thus, a lack of play does not necessarily lead to an incompetent adult with low fitness. Yet, he focused on the delayed benefits of play.

In contrast, Martin & Caro (1985) proposed immediate benefits of play for juveniles. Meaning that play would already enhance survival during juvenility and thereby increase the individuals' fitness. This seems to be the case in bears: The more juvenile bears played, the more likely they were to survive (Fagen & Fagen, 2009). Another aspect to consider is that adult play likely has immediate benefits, such as tension reduction and social bonding (e.g. Palagi & Mancini, 2011).

Aforementioned, there are different views to which extent play offers benefits to the individual performing it. Graham & Burghardt (2011) proposed three different levels of utility of play. First, play occurs sporadically with an excess of energy due to boredom, but is not necessary for long-term benefits. Second, play helps for the maintenance of physiological, behavioural and perceptual conditions of an animal (motivated and autotelic). Third, play is necessary for reaching developmental milestones, in terms of cognitive, physical and social skills and thus may enhance behavioural innovations. They argue that the three levels can



**Figure 1:** Scheme adapted from Fagen (1981) about the phenotypic effects of play which in turn affect fitness. After Fagen play is only one of many optional behaviour that can affect a specific phenotypic trait.

occur in the same species, indicating that not all play patterns may provide benefits of the same extent. Nevertheless, the fact that play is phylogenetically so wide-spread leads to the evolutionary necessity of a function, otherwise the behaviour should have been eliminated by natural selection (Fagen, 1981). Taken together, it is difficult to disentangle at what stage and to what extent play benefits individuals. If the cost-benefit equilibrium is taken as a proxy, since there are some energetic costs, only the lower boundary of benefits can be estimated.

### 1.2.2 What are the benefits?

#### 1.2.2.1 "Functionless"

A proximate effect of play on an individual seems to be enjoyment or as Martin and Caro (1985) formulated it, during play "means are of higher importance than ends". As discussed beforehand, the behaviour does not seem to serve any apparent immediate benefit and thus is even marked functionless by some theorists. Such perception led Carr (1902) to phrase the *Diversion Theory* hypothesizing that the only reason for play is fun, and that there is no developmental component to play. Hall (1904) classifies play an evolutionary relict (*Recapitulation Theory*), which was once necessary for the development in primitive humans. Still, he does not designate play completely functionless, but rather sees benefits for "perfecting the organism".

#### 1.2.2.2 Physical benefits

Byers and Walker (1995) proposed the *Motor Skill Hypothesis* attributing play a function of physical, muscular training. Yet, since muscle training only has a temporary effect, Byers (1998) refined their hypothesis by adding a neuro-developmental effect. Fairbanks (2000) supported the idea of a physical consequence of play by her study on vervet monkeys showing that play arises simultaneously to neural development (*Neural Selection Model*). Such studies imply a crucial role of play during ontogeny.

From another point of view, Thompson (1996) attributed play a *Self-Assessment* function. He suggests that social play is highly competitive and thereby play would improve the response to an unpredictable or unstable social and physical environment (Thompson, 1998). Hence, play would not be imperative, but offer an additional physical benefit to an individual. The hypothesis is supported by the overall preference of primates for same-aged, same-sexed, same-ranked play partners (e.g. gorillas: Maestripieri & Ross, 2004; great apes: Lewis, 2005). But not only social play, also solitary play could be a *Physical Flexibility Training* for example for arboreal primates (Fontaine, 1994) and hence, provide practice and self-assessment.

As already mentioned above, one of the most prevalent hypotheses about play is the practice for adult life (e.g. *Instinct Practice:* Groos, 1898; also: *Self-assessment:* Thompson, 1998). Since play resembles incomplete serious behaviour (e.g. Fagen, 1981; Bateson, 2005), it is argued to assist the learning of the related serious behaviour, e.g. fighting, mating, maternal care and foraging.

If play contributes to skill development and adult life practice, variation according to age and sex might be present and hence, representative for the species-specific skill repertoire. Thus, it would be expected that a stronger sexual dimorphism connected to sex-specific behaviour as adults within a species would also be represented in variable play (e.g. Fagen, 1993; Pellegrini & Smith, 2005). However, it is still debated if the behaviour differs with sex during infancy/immaturity. In a recent paper, Lonsdorf et al. (2014) found behavioural differences in 3 years old chimpanzees. Yet, in order to decide upon sex differences in play behaviour and their significance, play needs to be compared with the adult behavioural repertoire (Müller-Schwarze, 1984). Smith (1982) predicted that in sexual dimorphic, polygynous species, males engage more in play fighting than females. Not in the amount, but in play fighting style such differences were observed in rats (Pellis, Pellis & Bell, 2010). In contrast, male sugirrels did not engage more in play fighting, but more in sexual play than females (Nunes et al., 1999). However, even though a lot of sex differences are not statistically significant, males generally tend to play rougher and initiate more play bouts (Graham & Burghardt, 2010). Pellegrini & Bjorklund (2004) explain the fact that girls engage in less vigorous and more solitary play than boys by their different strategies to get mating access later on during adulthood. Moreover, social play between like-aged male chimpanzees seems to be more asymmetric than females' play (Palagi, 2007b). Besides, sex differences cannot only be represented in the play behaviour itself, but also in the play partner choice (Fagen, 1981). In Gorillas, both males and females prefer to play with males, which can be explained by motor training for males and the need of females to rely on the males later on during adulthood (Maestripieri & Ross, 2004). Yet, also in solitary play, sex differences were observed. Anecdotal data from chimpanzees report only female juveniles carrying sticks and caring for them as if these were their infants (e.g. Kahlenberg & Wrangham, 2010; Matsuzawa, 2011). Additionally, Lonsdorf et al. (2014a) reported earlier play peaks in male than in female chimpanzee infants and to have more different social (play) partners than females (Lonsdorf et al., 2014b) In contrast, meerkats do not show sex differences in play, because their roles in adults do not vary greatly and both sexes need to fight (Sharpe et al., 2002; Sharpe, 2005a). In conclusion,

there is evidence that play behaviour already reveals behavioural sex differences during immaturity in species with sexual dimorphism and thereby this difference could be evidence for play serving adult skill practice.

#### 1.2.2.3 Socio (-cognitive) benefits

Yet, play could also contribute to the learning of communicative skills and by that assist social assessment, for example the recognition and response to vocal and facial expressions (Lewis & Barton, 2006). Play is said to involve meta-communication, because individuals have to read the play partners' intentions and to give and to understand signs of play (e.g. chimpanzees: Flack et al., 2004; gorillas: Palagi, 2007a; Palagi, 2011). For example chimpanzee immatures revealed to use gestures to initiate play only from a certain age onwards (Bard et al., 2014). Therefore playing requires fine-tuning according to social partner and environmental circumstances, which requires socio-cognitive abilities and might distribute to rehearsing such skills.

Bell and colleages (2010) varied group compositions of immature female rats, either enabling them to play with peers or not. They conclude that peer play is essential for the development of adult social competence, because brain structures of the orbitofrontal cortex - an area known to be essential for social interactions - were better developed. These findings are further supported by an experimental study showing more conflict escalations in rats deprived of play during an early phase in immaturity (Van den Berg et al., 1999). Hence, rank establishment and perception of individuals' rank could be mediated by social play and thereby help social assessment (great apes: Lewis, 2005). Thus, there is likely a socializing function of play in group-living species (e.g. primates: Poirier & Smith, 1974). Also in adult animals, play likely promotes social cohesion, tension reduction and might even

Also in adult animals, play likely promotes social cohesion, tension reduction and might even prevent xenophobic reactions in humans and lemurs (Chimpanzees & Bonobos: Palagi, 2006; Palagi & Paoli, 2007; Tacconi & Palagi, 2009; Cordoni & Palagi, 2011; Humans: Gray, 2009; Lemurs: Antonacci et al., 2010). For example, in solitary species courtship play might serve adults to overcome the stress of being in association (Pellis and Iwaniuk, 1999b). Thus, play is closely linked to social tolerance and social skills.

Yet, Sharpe's (2005b) findings in meerkats do not support this hypothesis, since there is no correlation between the social play frequency and mean number of play partners with group size, frequency of other affiliative behaviour, level of contribution to cooperative group activities and duration of tenancy in natal group.

### 1.2.2.4 Cognitive benefits

On a wider scale play could be central to the evolution of behavioural flexibility, plasticity and social intelligence (Fagen 1981, 1993; Bekoff, 1995b; Pellegrini, 2009; Bateson, 2011). Play requires fine-tuning according to play partner, social context and environmental conditions (Palagi, 2011). During play individuals place themselves into unpredictable situations (e.g. Thompson, 1998; Pellis et al., 2010a), which might lead to novel behaviour. Following that, play might affect evolutionary processes via innovation, by altering the ability to adapt to a new environment (Pellegrini et al., 2007). Pellegrini et al. (2007) even argue that play primarily is for innovations and not for learning, as it offers a low-cost, low-risk potential for innovations. Since behavioural flexibility is correlated with cognitive abilities, which increase monitoring and produce different outputs according to the context (Taborsky & Oliveira, 2012), play should occur more often in intelligent species. Previously mentioned, correlations between brain part sizes and play have been found (also see section 1.2.3.3). Concluding this section on the benefits of play, it is difficult to tear the effects of play apart and classify them into different domains (e.g. social, physical and cognitive). No consensus has been attained about the evolutionary origin of the different play types, whether they have evolved independently (Burghardt, 2010) and if they serve distinct functions. Spinka et al. (2001) offer a more general explanation for play. They argue that all play patterns are a *Training for the unexpected* for immature individuals.

To sum up, play behaviour is likely multifunctional within and across species (Martin & Caro, 1985; Pellis et al., 2010), and it might even have evolved several times (Burghardt, 2010). Nevertheless, most students of play agree that play is important for physical, cognitive and social development (e.g. Spinka et al., 2001).

# **1.2.3 How to study play?**

Regarding the sheer variety of hypotheses, it might be difficult to attribute a function to play behaviour in a species. Previous studies either tested hypotheses experimentally or comparatively.

On the one hand, incurred costs are often taken as an estimate for the benefits of play. On the other hand, play-deprived individuals and the assessment of their adult competence would be another way to find out whether play is essential for (skill) development during ontogeny. Yet how do we measure adult competence? And how can immatures be deprived of play without being deprived of social interactions or crucial environmental factors? There have been experiments with rats. Van den Berg et al. (1999) deprived male rats during their 4<sup>th</sup> and 5<sup>th</sup> week of life of play. They found that more conflicts escalated in deprived rats. The rats did not show appropriate behaviour towards dominant animals and thus, conflicts broke off (van den Berg et al., 1999). Such results suggest delayed benefits of play. However, as their deprivation was basically social isolation and the resocialization happened among socially deprived individuals, the results have to be taken with caution regarding the effect of play on adult behaviour.

Yet, play behaviour varies depending on the individual and environmental and social conditions (Bekoff, 1984). Such variability may allude to which degree play is essential and thus, indicate possible functions. Thus, comparative studies analysing the variability in play rates and styles within and across species might enable researchers to deduce possible functions. On the one hand, play behaviour might differ with internal factors, such as age, sex and individual differences. On the other hand external factors, such as food availability, predation pressure and sociality, have revealed decisive for play occurrence.

# 1.2.3.1 Internal factors

Variation in play behaviour has been linked to different age and sex categories. Thereby there is an intrinsic component to play and Fairbanks (2000) presented evidence that play might be ontogenetically fixed and tightly linked to neurological development (also see section 1.2.3.3). Play urge was even found to be heritable in rats (Siviy & Panksepp, 2011). In several primate species (e.g. chimpanzees: Cordoni & Palagi, 2011; gorillas: Maestripieri & Ross, 2004; vervet monkeys: Fairbanks, 2000), different ontogenetic trajectories of solitary locomotor, solitary object and social play have been found in respect to quality and quantity (for more details see section 1.1.4 on the ontogeny of play).

Trajectories of play might not only be present in frequency, but also in increasing complexity. During solitary play, this might be reflected in a higher variability of movement and object manipulation modes. Social play requires the adjustment to the play partner and the ability to convey playful intentions (section 1.1.5 & 1.1.6). Thus, there has to be a synchronization about changes of play dynamics, a mutual agreement to play and if necessary self-restraint by the stronger play. All these factors reflect play complexity. An additional factor of complexity in social play could be the involvement of objects. It has been shown that the older immature chimpanzees get, the more they use detached objects in social and non-social play (Myowa-Yamakoshi & Yamakoshi, 2011). These triadic interactions between two individuals and an object have been subdivided into 3 levels (Myowa-Yamakoshi & Yamakoshi, 2011):

<u>one-way play</u>: individual manipulates an object in the direction of another playmate
 <u>two-way play</u>: individual manipulates an object jointly with the other playmate
 <u>object or action-role turn-taking play</u>: individual manipulates an object with a playmate while taking turns

The increasing numbers designate increasing complexity of triadic interactions. In chimpanzees, only level 1 and 2 could be found. Yet, a clear pattern of increasing play complexity with age was identified (Myowa-Yamakoshi & Yamakoshi, 2011).

Yet, in the end the challenge is to disentangle whether play promotes skill acquirement *per se* or whether play is only performed if certain skills are already acquired. Thus, in the latter play would act as an additional factor fostering skills or even innovations. Therefore, it is important to put play behaviour within the context of skill development trajectories. As, in their review, Pellegrini and colleagues (2007) state that the developmental trajectories of play resemble immediate and delayed benefits of one play behaviour.

Moreover, certain play may only be present if some basic skills are present, for example independent locomotion in primates. Such limitations may constraint which play types are present in a specific period of immaturity.

#### 1.2.3.2 External factors

The occurrence and frequency of play is not constant within a species and thus variability due to external factors might be an indicator for the importance and thereby possible functions of play. Play frequency highly depends on the ecology and social environment, such as predation, food and play partner availability (e.g. Zucker & Clarke, 1992). Many authors argue that play occurs only under non-stress situations and if there is stress, play frequency drops (e.g. Fagen, 1981; Palagi, 2007b). Bekoff (1984) stated that even though the distribution of play may differ, overall play might be the same for individuals growing up in different conditions. In contrast, Thompson (1998) expects the opposite correlation that animals under stress need to play more to be prepared for the unpredictable environment. His view is supported by the increased play frequency in undernourished rats (Loranca et al., 1999) and neglected kittens (Martin & Caro, 1985).

Yet, in other species the opposite trend has been reported. Food provisioning led to higher play frequencies in squirrels and meerkats (Nunes et al., 1999; Sharpe et al., 2002). Sharpe and colleagues (2002) concluded that not time, but energy is the limiting factor of play. Moreover, play rates were found to vary with season in geladas and squirrel monkeys (Barett et al., 1992; Stone, 2008). In geladas, play rates and play quality declined during dry season, when food is scarce, because more time is needed for food processing and more energy used for thermoregulation (Barett et al., 1992). In squirrel monkeys, the same decrease of social play during either dry season in nature or with artificial food shortage in laboratories can be seen (Baldwin & Baldwin, 1974, 1976; Stone, 2008). Yet, not even food provisioning induced more play during low food availability (Stone, 2008). Additionally, golden lion tamarins do

not seem to minimize daily energy expenditure to play, since they play most during midday, when it is hottest (Oliveira et al., 2003).

Held and Spinka (2011) concluded that most animal play is easily blocked by harmful environmental conditions. Yet, because of its rewarding, self-reinforcing properties, play could become prominent in the behavioural repertoire of infants and juveniles. Though, they propose that play can also increase in stressful situations, e.g. in response to reduced parental care, and therefore is no reliable indicator of favourable conditions (Held & Spinka, 2011).

Nevertheless, not only environmental conditions, but also social factors have an impact on the energy balance of immature animals and with that on the play behaviour. Immediate causes, such as playmate availability, directly control play frequencies. Though, in squirrels social play decreases with increasing litter size, which might be explained by the lower weaning weight, which in turn might be explained by lower maternal investment (Nunes et al., 2004). So maternal investment in terms of energy might be crucial for immatures to engage in play. For example, in horses, extra-nutrition provided by higher maternal investment seems to enable foals to play more (Cameron et al., 2008). Thus, social (mother) and environmental factors are closely interlinked.

On the other hand, there seems to be some previous social competence needed for play to occur. Van Leeuwen et al. (2013) found that even though chimpanzee orphans displayed more play bouts, they were not able to maintain one bout for a long time. In contrast, mother-reared chimpanzees' play bouts lasted longer and did not end as much in aggression as the play between orphans. This result might indicate that the mother is crucial for a normal socialization of the offspring (van Leeuwen et al., 2013). Spijkerman et al. (1996) found similar trends when comparing peer-group raised with zoo-group living immature chimpanzees' social play behaviour. In fact chimpanzee mothers with juveniles associate more often than if they are with infants. The sons even get a higher rank later on, if their mother has associated more with males during the son's juvenile period (Williams et al., 2002).

All in all, there are many factors affecting play frequencies and styles. Bringing all the factors together and assess their relative influence on play might enable us to infer functions to play behaviour.

#### 1.2.3.3 Neurological perspective

More recent studies have focused on the mechanisms of play, in terms of neurological processes. Since the prolonged immature phase is associated with large brains and play (Pellis & Iwaniuk, 2000), play might have an important role in neural development. Play probably occurs when it can alter the terminal phase of synapse formation and elimination in the area of the brain that controls coordinated motor output and thus would have a permanent and age-dependent effect (Byers, 1998). Following this line of argument, Fairbanks (2000) suggested the *Neural Selection Model* acting on play in vervet monkeys. She found locomotor play to peak earliest during infancy when the cerebellum is still developing and only later on, when neural pruning proceeds, object play and social play are most prevalent. Play was found to decline as sex hormones increase. In contrast, Lewis & Barton (2006) propose that there is a link between the brain becoming dimorphic and sex differences in play.

Moreover, the role of the cerebellum, which controls motor activities, in play is further supported by its size positively correlating with social play (Lewis & Barton, 2004). Additionally, more playful individuals tend to have more thickly myelinated brains and thicker cortices (Pellis & Pellis, 2009; Lewis, 2001)

However, most comparative studies investigating play in relation to brain parts only find a positive correlation with social play, and not solitary play, with either neocortex ratio, hypothalamus, amygdala, cerebellum or striatum size (Lewis, 2001; Lewis & Barton, 2006; Graham, 2011). The hypothalamus positively reinforces play by mediating pleasure and motivation, in form of dopamine production (Siviy & Panksepp, 2011). The amygdala is responsible for emotions and social interactions and assessment and thus, might take a crucial role during social play (Lewis & Barton, 2006). Experimental studies on rats point to partial neural incorporation of play and thereby to play taking a crucial role in social skill acquisition (Siviy & Panksepp, 2011). Yet, these are correlations showing a link between play and brain, but not a causal relationship and hence, the actual role of play in the development of these structures is still debatable.

Pellis et al. (2010) propose that in rodents subcortical mechanisms mediate the motivation and behaviour of play, and the cortex provides mechanisms by which the play changes with age and context. Because the amygdala correlates positively with social play on a species level, they name it crucial for reciprocity regulation and thus, the maintenance of play (Pellis et al., 2010a).

In contrast, adult-adult play in primates does not seem to correlate with neither amygdala nor non-visual neocortex (Pellis & Iwaniuk, 2002). This leads to the suggestion that play might be important for neural development and even act like a feedback system on the neurobiological system. In primates a greater proportion of postnatal brain growth correlates with more and more complex play (Fagen, 1993; Pellis & Iwaniuk, 2000). Yet, in birds, no correlation between brain size and play complexity could be found (Diamond & Bond, 2003). In any case, having only correlations, it cannot be excluded that these are by-products of a large brain requiring a higher metabolic rate, which in turn can be regarded as the precondition of play (Spencer, 1872; Graham & Burghardt, 2010).

All in all, during ontogeny, play is either neurologically fixed and thus needs to be performed during a critical period or it is rather for gathering experience and hence not crucial for a normal development, but rather an additional benefit (Bateson, 2011). Since there might be certain neurological requirements for specific play patterns, correlations of neural development and play could also be a consequence of neurological acquirements. These two scenarios are not mutually exclusive, though neural development might be enhanced also by "serious", non-play behaviour (e.g. Fagen, 1981, fig. 1).

# **1.3 Orangutans and play**

Having the correlation between increased postnatal brain growth and play frequency (Pellis & Iwaniuk, 2000) and complexity should foster interest in play behaviour. If play is regarded to be representative for the behavioural repertoire, it may be crucial to take play differences and similarities into account. For example when regarding great apes, play may provide insights into innovation, social affiliation, dominance relationships, cultural transfer, cognitive capacities and self-conception (Lewis, 2005; Bekoff & Allen, 1998; Povinelli & Cant, 1995). Besides, social play and the necessary cooperation among play partners may point to the evolution of fairness and morality (Bekoff, 2004). All these features are affiliated with human evolution and unique human cognitive abilities. Therefore, the study of play in the closest human relatives, the great apes, is crucial. Orangutans have revealed to solve cognitively highly demanding tasks and similar to chimpanzees exhibit cultural variants of behaviours (e.g. van Schaik et al., 2006; Krützen et al., 2011).

However, what can we learn from studying play in a semi-solitary species (van Schaik, 1999)? On average orangutans only spend 5 % of their time in association (van Schaik, 1999). On the one hand, their long dependence on the mother during the first 6 – 8 years of life and their large brain (van Noordwijk & van Schaik, 2005; Wich et al., 2009) are perfect preconditions for play to occur. On the other hand, since immatures depend also on their mothers' willingness to associate with possible play partners (van Noordwijk et al., 2012), there is very little partner choice for the immature orangutans. They have to play with the offspring of the mother's preferred association partners which are related females (van Noordwijk et al., 2012). Mothers do not engage in play with their offspring every day. Of the complete social play time of immature orangutans only one third is with their own mother, but half of it is accounted by play with peers (van Noordwijk et al., 2009). Hence, there seems to be a need for play with peers.

In contrast, associations and social interactions are very scarce among orangutans (van Noordwijk et al., 2009). Though, the Sumatran orangutans (*Pongo abelii*) are more gregarious than the Bornean orangutans (*Pongo pygmaeus*) (van Schaik, 1999). The low association time is mirrored in the low overall social play percentage of immatures: in Tuanan (Borneo) social play accounts for less than 1 % of the immatures' time budget, whereas in Ketambe (Sumatra) 1.5 % (van Noordwijk et al., 2009). However, once mothers associate, their offspring spend up to 50% of their waking time in social play (van Noordwijk et al., 2009).

Against all expectations, mothers with dependent offspring do not change association patterns with food availability, i.e. they still associate even at low food availability (Harrison et al., 2012; van Noordwijk et al., in prep.). As immatures' social play frequencies during associations are not affected by food availability either, a plausible explanation for mothers to still associate is to give their offspring a chance to play (van Noordwijk, pers.comm.). This would imply that play might have a crucial function in the development of the immature orangutans. However, if they remain greatly solitary and without body contact throughout their adult life, except for mating and raising their offspring, why should there be a need to play? Is the social tolerance trained and enhanced by playing (e.g. Fox, 2002) and thus, play only a social instrument? Or could close interactions with peers help to develop sophisticated social skills, which might be decisive during adulthood? And if so, which skills can be affected by play during immaturity?

Davila-Ross et al. (2008) found evidence for rapid facial mimicry during play in zoo-living orangutans which might indicate the capability of emotional contagion. Are these social skills relicts from a more social period or crucial during the development of immature orangutans and decisive for social interactions? Might such refined social skills even be crucial for raising their own offspring later on or for the anticipation of the opponent's actions during male-male encounters?

To sum up, even though orangutans live mostly solitarily, during the few encounters sophisticated social skills might still be required. Play could be a mechanism for immature individuals to practice these skills.

From another point of view, solitary play is not limited by access to a partner. In fact, unweaned immatures spend up to 15 - 45 % of their time budget in solitary object and locomotor play during certain periods of ontogeny (van Noordwijk et al., 2009). If a behaviour is so prevalent, does it maybe contribute to the acquisition of sophisticated techniques or even lead to innovations? Or could it be a compensation for the low social play rates?

# 1.3.1 Aim of the study

Because play behaviour is very prevalent and appears to be essential during the ontogeny of immature orangutans, this comparative study aimed at characterising play and infer possible developmental functions to the multifaceted behaviour. The geographic variation among

orangutans in terms of ecology and thus gregariousness and skill repertoire (Krützen et al., 2011) allowed to analyse the occurrence of play behaviour in different contexts. We investigated the variation of play behaviour with age, sex, food availability, social context and species (*Pongo pygmaeus wurmbii* and *Pongo abelii*). For this purpose, we studied two orangutan populations, one in Suaq Balimbing, Sumatra and the other one in Tuanan, Borneo. The orangutans at these two study sites do not only belong to different species, but also largely vary in their ecology and behavioural repertoire. Hence, the populations present a good framework for elaborating the crucial external factors that might alter play quantity and quality.

Moreover, it is likely that different play types follow different ontogenetic trajectories, if they serve different developmental functions. By comparing the average frequency of specific play behaviour (internal factors) with varying contexts, we may be able to decide how external factors, i.e. the social and non-social environment, influence the frequency and occurrence of play and if they interfere with the internal factors. If there is variability among contexts, it might help to understand the functions of play.

In the subsequent sections, we present hypotheses on how specific factors might alter play behaviour.

### 1.3.1.1 Internal factors – Ontogeny of play

The three main play types, solitary object, solitary locomotor and social play, have been found to follow different developmental trajectories in several species. According to previous studies (see section 1.1.4 "Ontogenetic trajectories" & 1.2.3.1 "Internal factors"), we expected similar trajectories with locomotor play peaking first and then object and social play. van Adrichem et al. (2006) could show that there is a peak of solitary play during the first two years and the peak of social play only occurs at an age of 8 in Sumatran orangutans (Ketambe). Yet his study was conducted with only four individuals. Another study in Suaq Balimbing did not find such a peak of social play at the age of 8 years (van Noordwijk & van Schaik, 2005).

Probably one play type not only exhibits a quantitative peak, but shows development within itself in terms of bout duration, variation in movement modes and context in which it occurs in. Therefore, not only frequency, but also the variation of qualitative characteristics of all the three play types were evaluated in respect to age by considering the activities and the distance to surrounding party members.

For all play types it is difficult to disentangle internal factors conclusively from external factors, but especially for social play external and internal factors are tightly linked (see also section "Mother and Partner"). There is virtually no partner choice for immature orangutans. They can only play if there is an associate and thus, are likely to play with a size-mismatched partner. The larger and stronger individuals thus need to restrain themselves in order not to hurt or endanger the weaker individual and to maintain the play relationship. As aforementioned, self-handicapping can also be a sort of complexity and therefore needs to be taken into account. We assessed the involvement in play of both players in order to evaluate whether older, larger individuals could show signs of self-handicapping. Restraint could not only be needed for keeping up play within the dyad, but also for keeping the careful mothers away from intervening the play.

From another perspective, the motivation to play might be higher when there is a matching association partner rather than a mismatched one. But how can motivation be assessed? In the current study, we investigated how much play occurred in specific dyads during an association, who initiated and ended the play and the party, the level of participation and specific play elements to get a general idea of who is motivated to play.

Moreover, even though there is hardly any partner choice, social play partners were anticipated to change from the very young infants playing mostly with the mother to the older dependent immatures playing predominantly with peers (great apes: Lewis, 2005). This change in play partner could also be reflected in the initiation of play. Namely the older individuals might initiate playing with younger individuals. Whereas the mother mainly starts play when her infant is still very young.

Fagen (1993) explained the reported sex differences in orangutan play by the large sexual dimorphism and related the sex-specific different behaviour during adulthood. Both male and female immatures prefered to play with male partners (Rijksen, 1978). In general, male immatures were observed to engage in more social play than females in a rehabilitation centre, whereas both sexes engaged the same amount in solitary play (Descovich et al., 2011). Nonetheless, van Adrichem et al. (2006) also emphasized the large individual variation in playfulness. Because of the limited access to play partners, we anticipated the absence of sex difference in social play. For solitary play, we did not find any evidence in the literature that would suggest early sex differences in the behaviour of immature orangutans. Therefore, we also predicted no sex differences in solitary play quantity or quality.

All in all, play pattern variation with age were anticipated. On the one hand the relative amount of play types in relation to age and sex were assessed, deciding upon ontogenetic trajectories of each play type. On the other hand, a possible increase in play complexity with increasing age was investigated. Additionally, we evaluated how play dyads might differ by considering the context of social play bouts such as initiation and termination, participation, emission of playful expressions and other play elements as well as age and sex of play partners.



**Figure 2:** Scheme of internal (age) and external (food availability and behavioural repertoire) factors that were expected to affect different play behaviour quantitatively and qualitatively. Especially the external factors vary with species (*Pongo abelii* vs. *Pongo pymaeus wurmbii*) and site (Suaq Balimbing vs. Tuanan) and hence, play behaviour was expected to differ due to that among the sites. Note that sex was not included as an internal factor in this scheme. The scheme was set up based on: Barett et al. (1992), Cameron et al. (2008), Cordoni & Palagi (2011), Fairbanks (2000), Held & Spinka (2011), Koops et al. (in prep.), Loranca et al (1999), Maestripieri & Ross (2004), Meulman & van Schaik (2013), Myowa-Yamakoshi & Yamakoshi (2011), Nunes et al. (1999), Ramsey & McGrew (2005), Schuppli (2012), Sharpe et al. (2002), Stone (2008), van Leeuwen et al. (2013) , van Noordwijk et al. (2009), van Noordwijk et al. (in prep.), van Schaik (1999)

# 1.3.1.2 External factors

We compared the frequency of play behaviour in varying contexts. Yet all these categories are interlinked, too (fig.2). Not only external factors with each other, but also internal and external factors were difficult to tear apart, especially for social play, as previously discussed.

#### Food availability

Food availability is generally higher in Suaq Balimbing, Sumatra, than in Tuanan, Borneo (Marshall et al., 2009). Therefore, on the one hand, the Sumatran orangutans face less energetic constraints, which we anticipated to lead to more play if play was constrained by energy. On the other hand, the Sumatran orangutans will use less time to get their daily food rate and so, play might also occur more often due to more free time.

Yet the orangutan immatures always have additional energy supply by drinking mother milk (van Noordwijk et al., 2013). The mother milk supply might be a buffer during low food availability and provide immatures the energy to maintain play behaviour. Nevertheless, it cannot be excluded that at low food availability the composition or the amount of mother milk changes also affecting the immature's energy and time and thereby, play rates were predicted to alter with food availability.

From another point of view, already at 1 ½ years the dependent offspring feeds on solid food itself (van Noordwijk et al., 2013). If food quality is low and requires longer processing, it might be not the energy only but also the time, which limits the immature's play rates.

#### Sociability

Overall food availability determines association rates of orangutans (van Schaik, 1999). As there is generally a west to east gradient of food availability – with highest values in Sumatra and lowest values in eastern Borneo (Marshall et al., 2009) –, the same pattern in sociability can be found, with most gregarious populations on Sumatra (van Schaik, 1999). Either if play was necessary for the acquisition of social skills or if play was a consequence of a higher degree of gregariousness, overall higher social play rates were expected in Suaq Balimbing, Sumatra, than in Tuanan, Borneo.

On a smaller scale, females preferentially associate with relatives (Singleton et al., 2009, van Noordwijk et al., 2012). Following this, in larger matrilines females have more possibilities to associate with their female kin. Therefore, we expected higher social play rates in immatures of larger matrilines. In Suaq Balimbing the preference towards associations with relatives seems to be absent (Schuppli, pers. comm.). If the kin-biased association patterns were absent in Suaq Balimbing, we predict equal play opportunities for all immatures regardless of their matriline. Overall, this would imply even more social play opportunities for immatures in Suaq Balimbing than in Tuanan.

Yet, to decide upon a pattern, it will be crucial to assess realized or ignored association possibilities, which cannot be covered by this study, because it would require a large amount of simultaneous follows of mother-offspring pairs that are ranging closely together. Instead, social play opportunities were assessed by evaluating realized associations and the presence or absence of social play within these associations. Moreover, we also evaluated if there was any pattern in the association initiations.

#### Mother and Play Partners

The mother greatly decides where a mother-offspring pair travels to and thus, also about whom they encounter (Noordwijk et al., 2012). Therefore, with their associations, the mothers could select the appropriate play partners for their offspring. Aforementioned, primates show a preference for size-matched and like-aged play partners. Hence, it would be essential to see if females with similar aged offspring associate more often than related females with offspring of a large age difference. However, this question is beyond the scope of this study. From another point of view, older offspring could try to pull its mother into an association once a possible association partner is within association reach (van Noordwijk, pers. comm.). Therefore, on the one hand, it was assessed who was responsible to initiate a party and if there was a relation to who initiated play. On the one hand, the age difference between associates was taken into account when classifying the realized and ignored play opportunities, as well as the amount of play within an association in relation to the age difference. Hence, we expected more play and more initiations by both play partners if they had a small age difference.

In chimpanzees, the presence of the mother changes play behaviour and signals within the play dyad (Flack et al., 2004). Since orangutan mothers are critical even only in building associations with other mother-offspring pairs, we could expect even stronger adjustment of the play partners to each other and to the other's mother, if they are interested in maintaining a play bout for a long time, without the mothers' interruption. Thereby, we predicted a high degree of self-handicapping by the larger play partner (see also section 1.3.1.1 on "Internal factors – Ontogeny of play").

#### Tool use

Orangutans are efficient tool users, whereas the Sumatran orangutans, especially the population in Suaq Balimbing, show more sophisticated techniques than the Borneans (Meulman & van Schaik, 2013). Ramsey & McGrew (2005) argue that object play, which includes components such as innovation, repetition, fragmentation and substitution, may benefit the development of tool use. Involving objects into play may hint towards practicing or even a predisposition of tool use (Bjorklund & Gardiner, 2011; Koops et al., in prep). In humans, object play correlates with tool use performance, yet basic motor abilities of eyehand coordination are required for object play to occur. Tool use knowledge is not genetically inherited, but specific learning mechanisms, such as object play, could be adaptive (Ramsey & McGrew, 2005; Bjorklund & Gardiner, 2011). In fact, younger animals seem to be more curious about objects (Ramsey & McGrew, 2005). Moreover, the difference in early object manipulation preferences between tool using species and non-tool using species has been shown in chimpanzees and bonobos. Namely, chimpanzee infants manipulate objects more frequently than infant bonobos (Koops et al., in prep.). Yet it is important to distinguish between *exploration*, which proceeds play, and *object play* (Pellegrini & Smith, 1998b; Bjorklund & Gardiner, 2011; Schuppli et al., 2012). Bjorklund & Gardiner (2011) define exploration as an act to find out what the object itself can do ("What can it do?"), whereas object play serves the purpose of detecting what the individual can do with the object ("What can I do with it?").

Since tool use can partly be defined by the manipulation of detached objects (e.g. Meulman & van Schaik, 2013), the question arises whether there is a pattern of using detached objects during play and becoming a more competent tool user later on. Myowa-Yamakoshi & Yamakoshi (2011) found that the older chimpanzee immatures get, the more they use detached objects during play. If there was a connection between tool use and object play,

Sumatran orangutans were expected to show more complex object play with detached objects than Bornean orangutans. Nevertheless, because tool use is socially learned in orangutans (e.g. Jaeggi et al., 2010; Schuppli et al., 2012; Meulman et al., 2013) and infants in tool using populations are more prone to explore (Schuppli et al., 2012), object play might just be a symptom and not an essential learning mechanism.

#### 1.3.1.3 Playfaces

As already mentioned earlier on in the introduction (section 1.1.6 "Play signals", the function of playfaces is not resolved yet and there is an ongoing debate about playfaces being a communicative signal, which can be controlled, or a pure emotion, and thus an honest sign of joy. Probably, these two hypotheses are not mutually exclusive (Demuru et al., 2014). In this study, we documented playface occurrence in all play types. If there was a communicative function to the facial expression, we expected to find a difference between Sumatran and Bornean orangutans. Either playfaces could signal benevolence or it could be an instrument of play coordination. In the first case, playfaces might be more needed in less gregarious populations, like Tuanan, and hence, we would predict more playfaces in Bornean orangutans. For the second scenario, Sumatran orangutans were anticipated to show more playfaces, because of their higher degree of sociability and thereby the implied better social skills. From another perspective, if playfaces serve any communicative purpose, they are anticipated to change according to the specific dyad composition and the surrounding, such as the proximity to the mothers and other associates (adapted from Flack et al., 2004). Hence, we would expect more playfaces and other play signals during more intense play. In order to convey the mother of the playful intent, the older, stronger play partner should emit more play signals when the mother of the younger player is closer. Moreover, the older play partner may generally exhibit more play signals, because either of the higher competence of social communication or the need to communicate benevolent intent during rougher play bouts.

#### 1.3.1.4 Compensation

If play is crucial during development, how can individuals cope with a lack of play? In orangutans, the limitations to play might be a lack of play partners, energy or time. In case, play could not be replaced by a serious behaviour to acquire specific skills, there are two possibilities that could still lead to a "competent" adult. Either there could be an immediate compensation of a lack of play with another play type or an alternative play partner, or there could be a delayed compensation by the same play type.

First, although it is very unlikely that immatures compensate a lack of peer play with their mothers (van Noordwijk et al., 2009), on a daily basis, there might still be a compensatory effect. Namely, during days when there is an association and play with the associate, there might be no mother-offspring play. Yet, during days without associations, there might be mother-offspring play. Alternatively, if all play types served the same function, there might be less solitary play on a day with an association and a lot of social play, while during days with less social play, there could be more solitary play. This could lead to similar overall play rates of all immatures, which however are composed of different play types. For example an individual with little social play opportunities. Though, such compensation can be labelled unlikely, because there is evidence from other species that time spent in social and solitary play is independent from each other. Hence, no compensation across play types was expected.

Yet, there could be a delayed compensation for a lack of social play opportunities during dependent infancy. If the mother is regarded the "association determining factor" and did not associate often with potential play partners, the immature could try to make up for this deficiency during adolescence. Independent juveniles with less social play during dependency would thus be expected to associate more often to play. If the *Neural Selection Model*, which implies a critical period for play on account of neural development (Fairbanks, 2000), proofs to be valid in orangutans, this hypothesis can be considered unlikely. Previous data showing lower association rates in Bornean than in Sumatran juveniles neither supported this hypothesis on a large scale comparison between the islands (van Schaik et al., 2009). Nonetheless, determining whether there is any kind of compensation will also help to find out if social as well as solitary play is crucial for neural development or rather for mere experience gathering in orangutans.

#### 1.3.1.5 Inferring functions

If the three play types follow different ontogenetic trajectories, there is evidence that they need to be looked at separately, because they could serve different functions. By evaluating the influence of external factors and if there is any compensation pattern, we might be able to infer such functions. On the one hand, if there appears a pattern in the internal factors, and no delayed compensation is seen, play possibly would be ontogenetically fixed and thus, crucial neurological mechanisms could be inferred. On the other hand, if there is no clear ontogenetic pattern and delayed compensation can be seen, play might not be an imperative, but serves to gather experience and offers an additional benefit. Though, attention needs to be paid to external factors, which either enhance or repress play and hence, in turn might influence also ontogenetic trajectories of play. If varying external factors, which have been reported to be decisive for specific play rates, and adult behavioural repertoire correlate with play rates, evidence might be provided for specific developmental functions of play.

#### **1.3.2 Research hypotheses recapitulation**

In order to wrap up the elaboration of the research hypotheses in chapter 1.3.1 "Aim of the study", the main research hypotheses are summarized briefly in this section:

- a) **Age**: We expected different ontogenetic trajectories of the three main play types with solitary locomotor play peaking first, then solitary object play and finally social play.
  - i. Finding different trajectories of the three play types could imply that they are independent of each other and thus, would be evidence for different functions of the three main play types
- b) Age: An increase in play complexity within each play type with age was expected.
  - i. *Locomotor Play*: A larger variation of locomotor patterns with age was predicted.

- ii. *Object Play:* More different object manipulations within a single play bout, increasing bout length and change in object preference with age were expected.
- iii. *Social Play*: A change of play partner preference and play dynamics with age were anticipated.
- c) Site: The three play types were hypothesized to vary with study site:
  - i. *Locomotor Play:* No difference was expected in terms of locomotor play between Suaq Balimbing and Tuanan.
  - ii. *Object Play:* Solitary object play rates were expected to be higher in Suaq Balimbing than in Tuanan. Moreover, the solitary object play was anticipated to involve more sticks and other detached object in Suaq Balimbing.
  - iii. *Social Play:* Higher social play rates were expected in Suaq Balimbing than in Tuanan.
- d) **Fruit availability**: All three play types were anticipated to decrease during low fruit availability.
  - i. Because there was evidence that social play among peers would not drop at low fruit availability, it was anticipated that all three play types would cease around weaning (5.5 7 years of age) when immatures do not get extra energy supply from the mother anymore.
- e) **Sex**: No sex differences in play frequency of all three play types were predicted.
  - i. If there was a preference for play partners of a specific sex as reported in previous studies, it would hardly stand out due to the low number of partners available.

Additionally, we investigated qualitative characteristics of play behaviour such as who starts and ends play, the use of playful expressions and other play elements and the activity and distance to the mother while playing.

# 2 Methods

# 2.1 Study site and study period

The field study was conducted at two different research sites: Suaq Balimbing  $(03^{\circ}02'87'')$ , 97°25'01''E) in the Kluet region of Gunung Leuser National Park, province Aceh, Indonesia and Tuanan  $(02^{\circ}09'06.1'')$ S; 114°26'26.3''E) in the Mawas Reserve, central Kalimantan, Indonesia (fig.3). Tuanan and Suaq Balimbing are both functioning field sites run by the Anthropological Institute of the University of Zurich in collaboration with Fakultas Biologi of Universitas Nasional (UNAS), Jakarta and BOS Foundation for Tuanan, and UNAS, SOCP (Sumatran Orangutan Conservation Program) and Paneco for Suaq Balimbing. Both field sites are situated in peat-swamp forest. Orangutan densities differ greatly between the two sites. Whereas in Suaq Balimbing an orangutan density of 4 - 7.44 individuals per km<sup>2</sup> has been reported (van Schaik et al., 2001), in Tuanan 2.77 – 3.84 individuals per km<sup>2</sup> have been estimated (van Schaik et al., 2005).

At both sites data were collected largely simultaneously during 6 months (Suaq Balimbing: February – June 2014, Tuanan: March – August 2014) by well-trained observers, mainly Sonja Falkner, Caroline Schuppli and myself. The first month of the field study, we dedicated to inter-observer reliability tests and Sonja and my training as observers (for inter-observer reliabilities tests see section 2.2.8). Pilot studies mainly focused on the elaboration of a detailed behavioural protocol of orangutan play behaviour, guaranteeing the consistency of the data collected, given that the subsequent data acquisition was carried out simultaneously in Suaq Balimbing and Tuanan by different observers. There were several full-day follows when Sonja, Caroline and I took simultaneous data of the same infant in order to discuss and define behavioural variants. At the end of the 7-month data collection, Sonja and I conducted again several full-day follows together in Tuanan to ensure congruent data collection.



**Figure 3:** Map showing the distribution of Sumatran (*Pongo abelii*) and Bornean orangutans (*Pongo pygmaeus*). The study sites, Suaq Balimbing and Tuanan, where the data collection for this study took place, are indicated with a red (Suaq Balimbing), respectively blue (Tuanan) circle. Figure adapted from Krützen et al. (2011).

# 2.2 Data collection

# 2.2.1 General procedures

Daily focal sampling was performed following one individual from its morning nest to the evening nest. Standardized methods of focal animal sampling including instantaneous scan sampling at two-minute intervals and ad libitum focal animal sampling was conducted. The established protocol for orangutan data collection was used to record behavioural data (http://www.aim.uzh.ch/Research/orangutannetwork/Field Guidelines.html). I also followed this protocol to collect data on play behaviour in order to be able to conduct subsequent analyses using longterm, instantaneous data from the databases of Tuanan and Suaq Balimbing.

Play behaviour was subdivided into the three main categories of solitary locomotor (APM), solitary object (APO) and social play (SP). Two additional categories, AP nest and AP display, were also recorded (for definitions see section 2.2.5.1). These categories were subsequently analysed for a play activity time budget. However, a more detailed protocol for both solitary and social play was set up in order to study the qualitative characteristics of these behaviour and compare them among different contexts.

# **2.2.2 Solitary play protocol**

Solitary play was recorded using all-occurrence sampling methods. For the broader context, the exact time of occurrence, the duration of the bout, the activity before and after and the activity of and distance to the mother and other party members were documented. The play activity itself was described in details including the movement types, the position of the focal individual and the body parts involved in play. Moreover the presence or absence of playfaces was recorded. Therefore, I controlled for face visibility of the focal individual by applying a score of 0 (not visible), 1 (only partly visible) and 2 (fully visible). Additionally, during solitary object play, a detailed description of how and with which body parts the object is manipulated was documented, eg. "swing", "manipulate", "shake", "rip off" etc. . Moreover, the type of object, its species and if it was detached or attached was noted. The exact definitions can be found in section 2.2.5.

# 2.2.3 Social play protocol

Data collection on social play was conducted by all-occurrence sampling methods. The focal animal was switched, if it was not involved in play, because of social play's rarity. In social play bouts, the initiation and termination was described in detail. It was noted who is responsible for starting and ending the play bout and how play was started and ended. The exact behaviour of each of the play participants was described, including the presence of vocalisations and playfaces. The play participants' level of involvement was assessed separately. On the one hand, the presence or absence of play bites, grabbing, hitting and body-checking was documented for having a measure of the directionality of actions. On the other hand, a scale called the "participant is during play:

-1: individual actively refuses to play. So it retrieves from the other individual who tries to initiate play

**0**: individual "lets" play happen, but there is no active involvement at all (e.g. the play partner allows the focal to play with a hand or a foot, but does not actively move the body part which the focal is playing with)

1: individual is involving in play but only with one "small" body part, such as a foot or a hand

**2**: individual is involving in play with several body parts (eg. two hands, hand and foot etc.)

**3:** individual is involving in play with whole body

This score was set for each participant in each play bout. Moreover, the visibility of each play participant was categorized in 4 levels ( $\mathbf{0}$  = not visible at all,  $\mathbf{1}$  = one body part (some fur) is visible,  $\mathbf{2}$  = body visible, but not fully (e.g. facing the back to the observer, so that face is not visible),  $\mathbf{3}$  = fully visible, also face)

Additionally, the age and sex of the play partners were noted. Also, individuals within 10 metres of the players and their activities were recorded, in order to assess the greater context of play. For the same reason, the play participants' activity before and after the play bout were documented (for more detailed definitions see section 2.2.5).

Generally, we recorded social play with handheld camcorders (Panasonic HC-V130) if the visibility allowed to do so. These videos were subsequently analysed.

# 2.2.4 Video analysis

In order to assess the qualitative elements of social play, like playfaces, hitting and biting, quantitatively, video analyses were conducted with the video coding program INTERACT by Mangold International. The videos were from the aforementioned study period. Additionally, I took all the social play videos from the data bases of the two field sites, in order to increase sample sizes. All the videos were taken in the period between 2010 and 2014. Due to the arbitrary choice of videos (i.e. presence or absence of video) for the dyads, video data could not be used for general statements, but only for the qualitative assessment of play elements in respect to certain dyads.

I ran video coding in two steps. The first round was dedicated to coding the face visibility of the focal and the partner within certain play bouts (sometimes there were several play bouts on one video). Only in the second round, I coded the actual play elements of both the focal individual and the play partner:

- Full playface with duration (see definitions in section 2.2.5.2)
- Grabbing (starts when grabbing, then duration of holding is taken)
- Small playface as an event
- Hitting as an event
- Play biting as an event
- Body-checks as an event

A play bout was defined to end, if there were no playful interactions or body contact anymore between the two players for at least 10s. Play bout durations range from try-initiations of 3 s to 6.6 minutes with a mean duration of 1.05 minutes (median = 47 s) (tab.2).

Play bout	Total	Tuanan	Suaq	Min duration	Max duration	Mean duration
Complete bouts	112	64	48	3 s	5.1 min	62 s
Incomplete bouts	86	67	19	9 s	5.5 min	68 s
Only initiation	24	14	10	11.3 s	2.8 min	54 s
Only termination	100	57	43	6 s	6.6 min	63 s
TOTAL	322	203	120	3 s	6.6 min	64 s

**Table 2:** Overview of the social play video material available for video coding and analysis.

# **2.2.5 Definitions**

### 2.2.5.1 Playtypes

*Solitary object play* (APO): manipulation of objects which seems "non-functional" and is often repetitive, e.g. swinging twigs, ripping off and discarding leaves, shaking and manipulating sticks (fig.6).

*Solitary locomotor play* (APM): repetitive movement of body parts or the whole body, like twirling up-side-down or swinging arms and legs. APM can be in one spot, but also includes moving around with no obvious directional goal.

*Solitary nest play/nest practice* (APnest): Immatures attempt to build a nest by pulling branches towards themselves, yet do not necessarily succeed in doing so. APnest also includes playing with old nests and deconstructing them in a vigorous, "uncontrolled" manner which is not exploring.

*Solitary display play* (APdisplay): Solitary play and display directed at another individual (often the observers) without the obvious interaction of the other individual, e.g. shaking branches or swinging arms, often with a detached branch, in the direction of the target.

*Solitary play bout*: A solitary play event which starts with the first vigorous movement or contact to the object that is played with and ends when either i) there is no contact with the object or activity directed at this object anymore for at least 10 s, ii) the vigorous moving is ended for at least 10 s or, iii) a new activity other than play is being started. The same object play bout is however maintained if the object is changed or new objects are taken while continuing playful manipulation of one of the objects.

*Social play:* Non-aggressive interaction between two or more individuals that does not serve any apparent, immediate purpose, often including body contact. Social play is often accompanied by playfaces or play vocalisations (e.g. Suaq Balimbing: "play oh") (fig.5).

*Social play bout:* A play bout starts with the first playful interaction, which can be starting body contact, but also intense watching from a short distance and then starting to play. A play bout ends when has not been any playful interaction between the players for at least 10 s.

*Social play duration:* Exact play duration in seconds or minutes was not available for all the social play bouts. Because most social play was long enough to be present in the 2-min scan data, approximate durations by the amount of 2-min intervals was taken into account. For the social play bouts where exact durations were known, the durations were recalculated into 2-min intervals (e.g. "360s" became "3").

### 2.2.5.2 Play elements

*Playface*: Relaxed open mouth display with teeth exposed ("full playface") or without teeth visible ("small playface") (van Hooff, 1962). Mostly seen during social play, but also occurs during solitary play (Fagen, 1993; Ross et al., 2014) (fig.4).

*Grab:* Active grabbing and holding of the social play partner, often includes pushing and pulling while holding the partner. In the video-coding grabbing (holding) duration was also measured and can be taken as proxy for active initiation and maintenance of body contact by either play partner.

*Hit*: Playful slapping of the play partner with a hand/arm.

Playbite: Mock-biting of play partner during social play (fig.5).

*Body-check*: Impulsive pushing of the play partner with the entire body (weight). Also includes the sudden pulling down of the partner, so that the partner falls down a few metres.



Figure 4: Full playface: "relaxed open mouth display with teeth exposed"



**Figure 5:** Social play with a play bite (individual on the upper right corner)



Figure 6: Solitary object play with an attached twig with leaves while hanging on a liana.

#### 2.2.5.3 Age classes

Generally, immatures were defined as all the individuals unweaned or weaned which were not yet reproducing/mating. When referred to infants in the text, unweaned immatures are meant. Whereas weaned immatures are generally called juveniles (still in constant association with the mother) and adolescents (mostly roams independent of the mother).

However, for the analyses, more detailed age class categories were set up according to the proximity and dependence onto the mother (van Noordwijk et al., 2009, p.193)(tab.3).

Age class	From	То	Description
Dependent	0 y	2 у	Offspring is completely dependent on the mother during travel and is always in cling
Infant	2 у	4 y	Offspring is partly in contact with the mother during travel, but already tries to move on its own. Generally, infants are still a lot within 10m of the mother
Immature	4 y	New sibling born	Offspring is still in constant association with the mother, but travels mostly independently with some assistance from the mother. The offspring is still unweaned, but towards the end of this phase is being weaned.
Juvenile	New sibling born	~ 10 y	Offspring has a younger sibling, is now weaned feeds and travels without assistance from the mother. But a juvenile is still in near constant association with the mother.
Adolescent	~10 y	$\sim \! 14y$	Offspring has left constant association with mother, but is not reproducing yet.

Table 3: Age class definitions based on locomotor skills and dependency on the mother (van Noordwijk et al., 2009).

For analysing play and association partners, there were additionally the age classes *mother*, *female* (without dependent offspring), *unflanged male*, and *flanged male*. Moreover dyad types of social play were defined as *mother* (mother-offspring), *sibling* and *associate* (play with any other individual than the mother or the sibling).

Because the exact age is unknown for most adult orangutans, mothers were generally incorporated as 25 y of age (300 months), except for Kondor who is known to be younger. This age was only used to calculate an absolute age difference and to have the mothers as far outliers. Unflanged males were generally incorporated as 17 years old (200 months), with the exception of Ekko who has been known for a very long time and is certainly older than that. However, these ages were only used to calculate age differences. In order to avoid biases by these rather arbitrary ages, the age differences were calculated by age class differences whenever possible.

# 2.2.5.4 Context data

For assessing the context in which play occurred, I greatly respected the general protocol. The distances and activities of the party members (mostly the mother) were documented using the established data collection protocol.

*Distances* to other individual were recorded in the categories of 0m, < 2m, < 5m, < 10m, < 50m, and the additional category of not present ("NP"). Because these distance categories are not proportionate to each other, they were treated as categories during the analyses and not as absolute, numeric values.

*Distance changes* during the course of a single play bout were assessed by taking the distance to the mother at the beginning and the end and putting them into the categories *"stay"*, *"leave"* and *"approach"*.

Activities of the mothers were also reported according to the established protocol. For later analyses the activities were subdivided into *stationary* (feeding, resting), *moving* and *social* activity types. If there were several activities reported during one single play bout, the activity types were implemented in hierarchical order with social as the highest, then moving and lastly stationary activities.

#### 2.2.5.5 Data manipulations

*Visible follow hour:* Total follow hours of a specific individual corrected by the proportion of 2-min bouts with a visibility score of 1 or 2 (not 0).

*Play Index:* Total play time during an association divided by the total time in association. Play Index =  $\frac{\text{total } 2 - \text{ min bouts spent in SP with specific partner}}{\text{Total } 2 - \text{ min bouts in party}}$ 

*Hinde Index for play initiation and termination (PHI)*: Measurement of who is controlling/motivated to play

$$PHI = \frac{\text{Initiations by focal} + (\frac{\text{Initiations by both players}}{2})}{\text{known initiations}} - \frac{\text{Terminations by focal} + (\frac{\text{Terminations by both players}}{2})}{\text{known terminations}}$$

*Fruit Availability Index* (FAI): Total count of trees with fruits divided by the total trees surveyed. FAI was assessed once a month at both field sites along constant line transects.

*Age differences:* Absolute age differences were calculated (focal age – partner age), but also age differences by taking the above age classes (section 2.2.5.3): if the individuals were of the same age class or differed by one age class, they were called "peers", otherwise they were put into categories of "focal older" and "partner older".

*Number of object manipulations:* Total count of different object manipulations within one single object play bout.

Locomotor pattern diversity: Total number of different locomotor modes during one single locomotor play bout.

*Opportunity for social play:* Association that lasts at least 30 minutes of which at least 10 min are within 10 metres.

## 2.2.6 Study subjects, collected data

#### 2.2.6.1 Tuanan

Form 20 March 2014 to 24 August 2014, we collected data on 11 infants and juveniles of different sex and ranging from 6 to 98 months of age, giving us a total of 701 focal-follow hours. Most observations were conducted on mother-offspring pairs of one single matriline (haplotype B) inhabiting the central part of the study area. Nevertheless, data on 4 mother-offspring pairs and one juvenile from matrilines of (two) different haplotypes (A, C) could be obtained. The minimum requirement of 5 full day follows per individual could be achieved for 8 of the 11 observed individuals (~60 follow hours) (Table 4, Figure 7).

Individual	Estimated birth	Sex	Mother	Sibling in contant association	Haplo- group	Haplo-         Total follow         Total N-N           group         hours         follows w           (hh:mm)         reliable o	
Charlie	15.07.09	male	Cinta	No	А	23.3	2
Danum	15.07.10	male	Desy	No	С	60.2	5
Ipsy	15.06.07	female	Inul	Yes (Ivan)	С	59.3	5
Ivan	31.12.13	male	Inul	Yes (Ipsy)	С	72.5	6
Jane	01.07.13	female	Juni	Yes (Jip)	В	76.6	6
Jip	10.02.06	male	Juni	Yes (Jane)	В	33.7	2
Joya	15.06.11	male	Jinak	No	В	61.7	5
Kahiyu	28.02.12	female	Kondor	No	В	59.4	5
Kino	01.01.07	male	Kerry	No/ Yes (Ketambe)	В	103.6	9
Mawas	15.07.08	female	Mindy	No	В	83.9	8
Sony	28.03.10	male	Sidony	No	А	109.9	10

**Table 4:** All infants followed in Tuanan, Mawas Reserve, during the period of 20 March – 24 August 2014 including information on age, sex, relationships and the total follow hours.



**Figure 7:** All the observed immatures in Tuanan during the period from March – August 2014: Charlie, Danum, Ipsy, Ivan (with Inul), Jane (with Juni), Jip, Joya, Kahiyu, Kino, Mawas and Sony (from top left to bottom right)

## 2.2.6.2 Suaq Balimbing

From 11 February to 15 June 2014, we collected data on 4 infants ranging from 11 to 44 months of age (tab.5). We could get a total of 300 focal-follow hours. Due to *Neesia* season during May and June, most orangutans left the study area to feed on *Neesia* fruits elsewhere. Therefore, data collection during these months was difficult and animals often got lost because they travelled far outside the study area, giving us little overall full-day follows. Unfortunately, the minimum requirement of 5 full-day follows could only be reached for Lois and Rendang. In order not to loose information from Cinnamon and Frankie, the influence of total follow hours and days available was assessed in subsequent analyses.

Individual	Estimated birth	Sex	Mother	Sibling in contant association	Haplo- group	Total follow hours ( <i>hh:mm</i> )	Total N-N follows with reliable observer
Frankie	15.07.12	male	Friska	Yes (Fredy)	2	51.3	4
Lois	01.08.10	male	Lisa	No	1	115.1	7
Rendang	15.07.13	male	Raffi	Yes (Ronaldo)	2	109.8	9
Cinnamon	05.05.12	female	Cissy	No	1	13.8	1

**Table 5:** All infants followed in Suaq Balimbing, Taman Nasional Gunung Leuser, during the period of 11 February – 15 June 2014 including information on age, sex, relationships and the total follow hours.



Figure 8: All the observed immatures in Suaq Balimbing during the period from February – June 2014: Frankie, Lois, Cinnamon, Rendang (from left to right)

# 2.2.7 Longterm data

For setting up a daily play budget, a total of 351 full-day follows from 26 different immatures from both Tuanan (N=210) and Suaq Balimbing (N=141) were available. The data was collected in a period between 2010 and 2014. The length of full-day follows did not differ significantly between the two sites (W=6309.5, p=0.135).

In addition, the extensive Tuanan database containing data on infants since 2003 to 2014 was used. With these longitudinal data on 6 immatures (Jerry, Jip, Kino, Mawas, Milo, Susi), I could set up individual play trajectories. For the analyses only data points composed of the average daily play proportion of at least 5 full-day focal follows that were collected within a 4 months period, were used. Moreover, follows of which the daily APO and APM proportions deviated more than one standard deviation from the mean of a specific individual and age, were excluded (tab.6). After these corrections, I excluded Kino and Mawas from the data set, because of the lower sample size compared to the other 4 individuals.

Name	Estimated birth	Total N-N follows	Total selected follows	Total data points
Jerry	15.06.2003	337	281	34
Jip	10.02.2006	173	157	20
Kino	01.01.2007	133	102	4
Mawas	15.07.2008	98	83	7
Milo	15.06.2001	332	291	35
Susi	31.12.2002	169	141	15

**Table 6:** The 6 individuals from Tuanan with most full-day follows during their immature phase with the total number of full-day follows during the period 2003-2012 and 2014, the selected total follow count (when excluding the follows with solitary play proportions deviating more than a standard deviation from the mean of the specific individual and age) and the resulting data points composed of at least 5 N-N full-day follows for one specific month.

#### 2.2.8 Inter-observer reliability

Inter-observer reliabilities between Sonja, Caroline and me were high for the instantaneous scan data collection (tab.7). On the one hand, we assessed the Index of Concordance on bout, as well as total count level.

Exact match IC =  $\frac{Total \ count \ of \ matches \ at \ each \ 2-min \ interval}{Total \ 2-min \ intervals}$ 

Total bout IC =  $\frac{Total \ overall \ overlaps \ in \ categories \ for \ each \ group}{Total \ 2-min \ intervals}$ 

	Total	A	ctivity	(	Cling		Visibility	
	Exact match	Exact match	Total Bout IC	Exact match	Total Bout IC	Exact match	Total Bout IC	coefficient (overall)
	IC	IC	Dout IC	IC	Dourie	IC	Dout IC	(0,0,0,0,0,0)
Sonja-Julia	0.56	0.54	0.96	0.65	0.79	0.48	0.85	0.90
Caco - Julia	0.67	0.68	0.98	0.80	0.90	0.54	0.83	0.92
Sonja- Caco	0.76	0.67	0.95	0.84	0.82	0.78	0.87	0.84

**Table 7:** Indices of Concordance among Sonja, Caco and Julia for the immatures' activities, cling and visibility scores and the overall match. The first column "Exact match IC" of each group (activity, cling and visibility) indicates the proportion of exact scan matches among observers, the second column "Total bout IC" indicates the proportion of matches of overall counts of different activities, cling (cling, unsure, non-clinging) and visibility (0, 1, 2) scores.

For the all-occurrence data, there were no detailed data available from simultaneous follows, therefore follows by different observers of the same individuals at different days were compared (Frankie, Ipsy, Ivan, Jip, Joya, Lois, Sony). The individuals ranged across a wide age spectrum (1 - 9 y). Wilcoxon signed rank tests were conducted in order to see if there was a significant bias in reporting solitary play in the all-occurrence data between Sonja and me. For both solitary locomotor (V=15, p=0.43) and object (V=21, p=0.29) play, the tests showed no significant difference in reporting solitary play frequencies between Sonja and me.

# 2.3 Data analysis

Previous to analysis, most data were corrected by the corresponding visibilities. In order to calculate a play activity budget, follow hours were corrected by the proportion of visible 2-minute bouts (> 0). Subsequently "visible follow hours" were used to calculate proportions of specific behavioural patterns. This correction could be made for the more detailed data from 2014. However, because the visibility assessment was only recently introduced into the

established protocol, the unknown activity bouts were taken as a proxy for visibility bias in the longterm data sets. Unknown activity bouts and 0 visibility score correlate strongly (1.06  $\pm$  0.12, t=9.23, p <<0.0001, F<sub>1.71</sub>=84.98, p<0.0001, N=73).

For the videos, as already mentioned before, face visibility was assessed, and playfaces and playbites were subsequently corrected for "visible-face" play duration and not by play duration itself, when calculating frequencies.

I conducted data analysis using the statistics program R. For most analyses, I carried out *Linear Mixed-effect Models* (LMMs) using the package nlme (Pinheiro et al., 2015) or *Generalized Linear Mixed-effect Models* (GLMMs) for the binomial presence-absence-data using the package lme4 (Bates et al., 2015).
# **3 Results**

# 3.1 Play activity budget

From the instantaneous 2-min scan data, a play budget was calculated per individual and age with longterm data (2010 - 2014). All play behaviour was pooled into the three categories of solitary locomotor, solitary object and social play. When an immature manipulated branches as if it was building a nest (*nest practice*), it was included as object play (see also section 2.2.5.1 for definitions).

I set up linear mixed models with site, age, sex and fruit availability as fixed factors and the individual identity as a random factor. The complete model is always reported, as well as the best fitting model, which I evaluated by hierarchical entry of the fixed factors according to hypotheses and visual inspection of the exploratory graphs.

Furthermore, the analysis of the play budget was conducted with three different data sets depending on observers. The first data set included all observers. The second consisted only of very selected observers who were concentrating on immature behaviour. The third data set was composed of a mixture between the first two data sets. Follows of immatures below 7 years were only taken from selected observers, whereas all the follows of older individuals were included. Generally, data points were average daily frequencies of at least 5 full-day follows. To prevent a loss of data, I had to take average ages over several months (at most 4 months) for some individuals in order to have a minimum 5 full-day follows. Due to the fact that most ages are estimates anyways, this procedure should not have a large impact on the results. However, it also implied that also the monthly Fruit Availability Index was averaged. A separate analysis controlling for all the other fixed factors was conducted with individual follow days to evaluate the effect of the real, non-averaged FAI (3.1.4 "Play and fruit availability"). Moreover, because the data set for the very selected observers would have been very limited and would have lacked large age ranges of certain sites, I included less reliable observers, if there were at least 4 follows by highly reliable observers and the less reliable observer's reported frequencies were within the range of the highly reliable observers of a specific 5 day follow period. In all analyses, I transformed the daily proportions using the arcsin-square-root-transformation in order to normalize the residuals.

# 3.1.1 Solitary play

### 3.1.1.1 Solitary object play

Solitary object play (APO) is high during the first 4 years of age and then sharply drops to near 0 (fig.9, fig.10). In Suaq Balimbing, the APO trajectory seems to decrease less steeply than in Tuanan. However, there is only one data point for Suaq Balimbing between the age 4 and 8 years of age. Accordingly, for all three data sets, average daily solitary object play was best explained by age, site and the interaction between the two (1.  $\chi^2(6)$ = 43.24, p<0.0001, AIC= -34.54, N =37, gr=21; 2.  $\chi^2(6)$ = 43.32, p<0.0001, AIC= -34.5, N=37, gr=21; 3.  $\chi^2(6)$ = 44.23, p<0.0001, AIC= -57, N =59, gr=24) (tab.8). Adding neither Fruit Availability Indices (FAI) nor sex improved the model (tab.9). Only the results of the data set with very selected observers are presented here. The others can be found in the appendix. The reason for the different sample sizes reported in table 8 and table 9 is that the Fruit availability Indices (FAI)

were not available for all the months of the year 2011 in Suaq Balimbing. Omitting these data points did not change the best fitting model.

	Value	SE	DF	t	р
Intercept	0.6124	0.0597	19	10.2622	*0.0000
Site Tuanan	0.0925	0.0861	19	1.0749	0.2959
Age*	-0.0039	0.0007	14	-5.9995	0.0000*
Site Tuanan:Age*	-0.0023	0.0011	14	-2.1603	0.0486*

**Table 8:** Best fitting model for average daily solitary object play proportions with data from selected observers only ( $\chi^2 = 43.32$ , p<0.0001, AIC= -34.5, N=37, gr=21).

	Value	SE	DF	t	р
Intercept	0.6200	0.1944	16	3.1891	0.0057*
Age*	-0.0040	0.0010	11	-4.1739	0.0016*
Site Tuanan	0.1417	0.2173	16	0.6521	0.5236
Sex m	0.0027	0.0764	16	0.0359	0.9718
av.FAI	0.0012	0.0173	11	0.0722	0.9437
Age:Site Tuanan	-0.0023	0.0013	11	-1.7936	0.1004
Site Tuanan:av.FAI	-0.0162	0.0335	11	-0.4842	0.6378

**Table 9:** Complete tested model for average daily solitary object play proportions with data from selected observers only  $(\chi^2(9) = 40.26, p < 0.0001, AIC = -23.99, N = 34, gr = 19)$ .



**Figure 9:** Average daily solitary object play proportion (proportion of time per 2-min activity bout) by age and site. Data points are composed of at least 5 full-day follows of an individual at a specific age. Individuals can be several times represented in the graph. Data from all observers are considered in this graph. The lines were added to the graph using the *loess*-function.



**Figure 10:** Average daily solitary object play proportion (proportion of time per 2-min activity bout) by age and site. Data points are composed of at least 5 full-day follows of an individual at a specific age. Individuals can be several times represented in the graph. Data from very selected observers only are considered in this graph. The lines were added to the graph using the *loess*-function.

Exploration was only recorded as a separate behavioural element in the data collection protocol in Tuanan from July 2012 onwards (before this explorative behaviours were most likely labelled as solitary object play). Even when correcting for this potential definitional difference by analysing the general object manipulation proportion, the best fitting model was with age only ( $\chi^2(4)=34.34$ , p <0.0001, AIC=-27.27, N=34, gr=19). Even though the site\*age interaction did not improve the fit significantly, there was a trend towards improving the model ( $\chi^2(6)=4.97$ , p=0.083, AIC=-28.24, N=34, gr=19) (tab.10, tab.11).

	Value	SE	DF	t	р
Intercept *	0.6778	0.0703	17	9.6364	0.0000*
Site Tuanan	0.0443	0.0973	17	0.4555	0.6545
Age *	-0.0041	0.0008	13	-5.0967	0.0002*
Site Tuanan:Age	-0.0022	0.0012	13	-1.7994	0.0952

**Table 10:** Model for average daily object manipulation proportions with data from selected observers only ( $\chi^2(6)=4.97$ , p=0.08, AIC=-28.24, N=34, gr=19).

	Value	SE	DF	t	р
Intercept *	0.7334	0.1758	16	4.1725	0.0007*
Age *	-0.0041	0.0010	12	-4.2194	0.0012*
Site Tuanan	0.0053	0.1368	16	0.0386	0.9697
Sex m	0.0151	0.0778	16	0.1935	0.8490
av.FAI	-0.0073	0.0147	12	-0.4943	0.6300
Age:Site Tuanan	-0.0022	0.0013	12	-1.6993	0.1150

**Table 11:** Complete tested model for average daily object manipulation proportions with data from selected observers only ( $\chi^2(9)$ =40.26, p<0.0001, AIC=-23.99, N=34, gr=19).



**Figure 11:** Average daily solitary object manipulation (play and exploration) proportion (proportion of time per 2-min activity bout) by age and site. Data points are composed of at least 5 full-day follows of an individual at a specific age. Individuals can be several times represented in the graph. Data from all observers are considered in this graph. The lines were added to the graph using the *loess*-function.



**Figure 12:** Average daily solitary object manipulation (play and exploration) proportion (proportion of time per 2-min activity bout) by age and site. Data points are composed of at least 5 full-day follows of an individual at a specific age. Individuals can be several times represented in the graph. Data from very selected observers only are considered in this graph. The lines were added to the graph using the *loess*-function.

#### 3.1.1.2 Solitary locomotor play

Solitary locomotor play (APM) proportion varied greatly across the three data sets. In the two restricted data sets, average daily locomotor play proportion was best explained by age only ( $\chi^2(4)=25.92$ , p <0.0001, AIC=2.90, N=37 of 21 individuals) (tab.12). In contrast to solitary object play, a clear peak of APM can be seen around age 2.5 y (fig.13, fig.14). Yet, the quadratic model was not significantly better than the linear model ( $\chi^2(5)=0.80$ , p=0.37, AIC=5.7). In Tuanan, the peak of solitary locomotor play tended to be stronger, however neither site per se, nor the interaction between age and site were significant (tab.13).

	Value	SE	DF	t	р
Intercept*	0.6359	0.0606	20	10.4960	0.0000*
Age*	-0.0047	0.0008	15	-5.9593	0.0000*

**Table 12:** Best fitting model for average daily solitary locomotor play proportions with data from selected observers only ( $\chi^2(4)=25.92$ , p<0.0001, AIC=2.90, N=37 of 21 different individuals).

	Value	SE	DF	t	р
Intercept*	0.7086	0.2916	16	2.4300	0.0272*
Age*	-0.0048	0.0014	12	-3.4189	0.0051*
Site Tuanan	-0.0179	0.2201	16	-0.0815	0.9360
Sex m	-0.0325	0.1018	16	-0.3196	0.7534
av.FAI	0.0008	0.0261	12	0.0297	0.9768
Age:Site Tuanan	-0.0012	0.0019	12	-0.6240	0.5443

**Table 13:** Complete tested model for average daily solitary locomotor play proportions with data from selected observers only ( $\chi^2(8)=26.49$ , p<0.001, AIC=10.60, N=34 of 19 different individuals).



**Figure 13:** Average daily solitary locomotor play proportion (proportion of time per 2-min activity bout) by age and site. Data points are composed of at least 5 full-day follows of an individual at a specific age. Individuals can be several times represented in the graph. Data from all observers are considered in this graph. The lines were added to the graph using the *loess*-function.



**Figure 14:** Average daily solitary locomotor play proportion (proportion of time per 2-min activity bout) by age and site. Data points are composed of at least 5 full-day follows of an individual at a specific age. Individuals can be several times represented in the graph. Data from very selected observers only are considered in this graph. The lines were added to the graph using the *loess*-function.

# 3.1.2 Social play

#### 3.1.2.1 Overall

Social play trajectories greatly varied between Tuanan and Suaq Balimbing. In Suaq, there was a peak of social play between the age of 2 and 4 years, whereas in Tuanan no clear peak of social play could be seen (fig.15, fig.16). After the age of 8 years, there was hardly any social play in Suaq Balimbing, while in Tuanan, there were still some high social play proportions (fig.15, fig.16). Accordingly, in all three data sets, the best fitting model for explaining average daily social play proportions included age, site and the interaction between the two (selected observers:  $\chi^2(6)=18.29$ , p<0.001, AIC=-32.6, N=37 of 21 different individuals) (tab.14, tab.15). I could not find any effect of sex or fruit availability on social play proportions.

	Value	SE	DF	t	р
Intercept*	0.3770	0.0500	19	7.468	0.0000*
Age*	-0.0020	0.0006	14	-4.053	0.0012*
Site Tuanan*	-0.2380	0.0750	19	-3.161	0.0051*
Age:Site Tuanan*	0.0020	0.0010	14	2.268	0.0396*

**Table 14:** Best fitting model for average daily social play proportions with data from selected observers only  $(\chi^2(6)=18.29, p<0.001, AIC=-32.6, N=37 \text{ of } 21 \text{ different individuals}).$ 

	Value	SE	DF	t	р
Intercept	0.3726	0.1859	16	2.0040	0.0623
Age*	-0.0028	0.0008	11	-3.5190	0.0048*
Site Tuanan	-0.1996	0.2099	16	-0.9509	0.3558
Sex m	-0.0213	0.0582	16	-0.3670	0.7184
av.FAI	0.0074	0.0171	11	0.4309	0.6748
Site Tuanan:av.FAI	-0.0126	0.0353	11	-0.3585	0.7267
Age:Site Tuanan*	0.0026	0.0011	11	2.3879	0.0360*

**Table 15:** Complete tested model for average daily social play proportions with data from selected observers only  $(\chi^2(9)=21.53, p<0.01, AIC=-26.68, N=34, gr=19)$ 



**Figure 15:** Average daily social play proportion (proportion of time per 2-min activity bout) by age and site. Data points are composed of at least 5 full-day follows of an individual at a specific age. Individuals can be several times represented in the graph. Data from all observers are considered in this graph. The lines were added to the graph using the *loess*-function.



**Figure 16:** Average daily social play proportion (proportion of time per 2-min activity bout) by age and site. Data points are composed of at least 5 full-day follows of an individual at a specific age. Individuals can be several times represented in the graph. Data from very selected observers only are considered in this graph. The lines were added to the graph using the *loess*-function.

#### 3.1.2.2 Social play partners

To find out to whom the surplus of social play in Suaq Balimbing has to be attributed to, I evaluated play proportions spent with specific play partner types (dyad type), i.e. the mothers, the siblings and associates, which can be peers or also a lot older individuals (fig.17). In the graph, associate play was further subdivided by related and non-related play partners, however for the analysis all associates were lumped together due to the small sample sizes. The average daily social play proportion was significantly higher with associates than with

mothers and siblings (tab.16). However, only dyad type was significant in the best fitting model for the average daily social play proportion with specific play partners ( $\chi^2(5)=79.91$ , AIC=-81.18, p<0.0001, N=97 of 20 different individuals). The model did not improve if site, focal age or the interaction between dyad type and site was added. Yet, looking at the full-model (tab.17), there is a significant site difference.



**Figure 17:** Average daily proportion of social play (proportion of time per 2-min activity bout) spent with specific play partner type (mother, sibling, related and non-related associates) in Tuanan (a) and Suaq Balimbing (b). Data points are averages of an individual at a specific age per dyad type. Individuals can be represented in the graph several times. The lines were added to the graph using the *loess*-function.

	Value	SE	DF	t	р
Intercept*	0.4561	0.0329	75	13.8474	0.0000*
Dyad type mother*	-0.2700	0.0398	75	-6.7847	0.0000*
Dyad type sibling*	-0.1839	0.0411	75	-4.4766	*00000

**Table 16:** Best fitting model for explaining the average daily social play proportion with different dyad types ( $\chi^2(5)$ = 79.91, AIC=-81.18, p<0.0001, N=97 of 20 different individuals)

	Value	SE	DF	t	р
Intercept	0.3291	0.0562	72	5.8592	0.0000
Dyad type mother	-0.1296	0.0696	72	-1.8607	0.0669
Dyad type sibling	-0.0845	0.0700	72	-1.2064	0.2316
focal age	0.0005	0.0005	72	1.1146	0.2687
Site Tuanan	0.1516	0.0683	18	2.2190	0.0396
Dyad type mother: Site Tuanan	-0.1992	0.0844	72	-2.3601	0.0210
Dyad type sibling: Site Tuanan	-0.1529	0.0853	72	-1.7916	0.0774

**Table 17:** Complete tested model model for explaining the average daily social play proportion with different dyad types ( $\chi^2(9)$ = 88.34, AIC=-81.18, p<0.0001, N=97 of 20 different individuals).

Because associates are not available during the entire activity time, I defined the Play Index as the total time spent in social play with a specific partner during the total time in association (definition see section 2.2.5.5).

Mothers played significantly more with their 0 – 2 year old offspring in Suaq Balimbing than in Tuanan (-0.0735±0.0291, t<sub>7</sub>=-2.53, p<0.05, N=11 of 9 different individuals ( $\chi^2(4)$ =2.85, AIC=-29.76, p<0.05)) (fig.19a). Yet, the dependent offspring (0 – 2 y) in Suaq Balimbing tended to be older than in Tuanan (W=25, p=0.08, N=11). When considering all the mother-

offspring play of 0 – 4y old immatures, the site difference vanished (-0.0072±0.0478,  $t_{10}$ =-0.15, p=0.88). Overall, mother-offspring Play Indices however tended to increase from 0 – 2y old dependents to 2 – 4y infants (0.0587±0.0291,  $t_{11}$ =2.02, p=0.07). Therefore, only the model with age class and not with site was the best fitting model for explaining average Play Indices among mother-offspring dyads ( $\chi^2(4)$ =4.05, p<0.05, AIC=-40.73, N=24 of 12 individuals).

No difference in Play Indices among sibling across the two sites could be found ( $F_{1,8}$ =0.62, p=0.45, N=17 of 10 different individuals). Only dependent (0 – 2 years) and infant (2 – 4 years) age classes were considered. The opposite direction (juveniles and adolescents) of sibling play was not analysed. There was also no trend of Play Indices increasing more steeply in Suaq Balimbing than in Tuanan, as would have been expected by looking at the figure 19b ( $F_{1,5}$ =2.05, p=0.21, N=17 of 10 different individuals).

Because, older siblings are generally not in constant association anymore with their mothers when their younger siblings are around 2 - 4 years, I separately looked at sibling play when the younger sibling was below 1 year of age. There was no difference between sites in how much the siblings played with each other ( $F_{1,2}=0.48$ , p=0.56, N=6 individuals with 3 different ages). However, sample size was very small and unfortunately, there is an imbalance in sexes across the sites. For Suaq Balimbing, only male-male siblings were present, whereas in Tuanan 3 male infants of which only one had a male older sibling (Sony, Danum, Ivan). The fourth infant was a female with an older brother (Jane, Jip).

Play Indices of associate play did not significantly differ between the sites when only taking the immature individuals below age 4 years into account ( $F_{1,4}$ =0.25, p=0.65, N=11 of 7 different individuals). Play Indices were neither explained by age nor by the interaction between age and site ( $F_{1,3}$ =0.14, p=0.73;  $F_{1,3}$ =1.19, p=0.35, N=11 of 7 individuals). Yet, in Suaq Balimbing, there was a lot more play among unrelated individuals observed. Especially already young infants (below 2 years of age) were observed to play with other non-related infants or unflanged males (fig.19d). In Tuanan, only immatures older than 4 years were observed to play with unrelated individuals and there was also only one instance of a



**Figure 18:** Proportion of all social play spent with mother in Suaq and Tuanan. Only infants below age 4y are included in the graph and datapoints are average daily proportions of social play with the mother by individual and age (individuals are several times in the graph). The lines were added to the graph using the *glm*-function.

dependent infant (0 - 2 years) playing with an associate.

This tendency of very young infants playing with others than the mother more frequently in Suaq Balimbing was also reflected in the proportion of social play attributed to the mothers. Mothers in Tuanan contributed proportions close to 1 to the play budget of their offspring in the first 4 years of life. Whereas social play proportions with the mothers were close to significantly lower in Suaq compared to Tuanan ( $F_{1,10}$ =4.73, p=0.055, N=32 of 12 different individuals)(fig.18). The model with age and site was best for explaining the proportion of play with the mother by the total social play ( $\chi^2(5) = 41.39$ , p<0.0001, AIC=78.35).



**Figure 19 a – d:** Play Indices (total time spent in social play per time in association) for inidividuals of a specific age class by dyad type (mother (a), sibling(b), related associate (c) and non-related associate (d)). Play Indices are averages per individual at a specific age and by dyad type. All data points are illustrated as jittered points around the boxplots.

# 3.1.3 Associations as opportunities for social play

### 3.1.3.1 Association patterns in Suaq Balimbing and Tuanan

The association patterns were evaluated in order to assess the opportunities immature individuals get for social play and which one they take advantage of. Therefore, the associations were only assessed with the data used for the play budget assessment which gave a corresponding picture to the other findings of this study.

A viable opportunity for social play was defined as an association which lasted at least for 30 minutes of which at least 10 minutes had to be within 10m distance of each other.

#### Kin-biased associations

Previous studies showed a kin-biased association pattern among females in Tuanan (van Noordwijk et al., 2012). In Suaq Balimbing a substantial amount of associations between non-related females has been observed and thus, it is assumed that the kin-preference is not as strong as in Tuanan. Because this has not yet been shown and because I had a relatively small data set for the social play and association patterns, I set up graphs and tested if this variation could be seen in my data set for immature individuals, too (fig.20).



**Figure 20:** Counts of associations (of only immature follows) with specific party classes in respect to kinship (colours) and site (Suaq Balimbing (a), Tuanan (b)).

Only the proportions of associations with related mothers with dependent offspring were analysed. Thereby, I intended to avoid pseudo-replication, by also analysing the association of the mothers' offspring. In Suaq Balimbing a higher proportion of immatures' associations with mother-offspring pairs could be accounted to non-related dyads (Tuanan:  $1.35\pm0.62$ ,  $t_{13}=2.18$ , p<0.05, N=21 of 15 different immature individuals).

When considering separately the associations between immatures (which are often mediated by their mothers), Tuanan individuals were still significantly more in association with relatives than Suaq Balimbing immatures (1.90±0.32,  $t_{17}$ =6.00, p=0.0000, N=52 of 20 different individuals). However, there was also an effect of the party's age class on the kinbiased associations. Additionally, the model with the interaction between the party's age class and site was the best fitting model ( $\chi^2(10)$ =27.47, p<0.001, AIC=160.27, N=52 of 20 different individuals) (tab.18).

	Value	SE	DF	t	р
Intercept*	3.1416	0.7371	26	4.2619	0.0002*
Site Tuanan	0.0000	1.0425	17	0.0000	1.0000
Party age class infant*	-2.0944	0.9516	26	-2.2009	0.0368*
Party age class immature*	-3.1416	0.9516	26	-3.3013	0.0028*
Party age class adolescent*	-2.2814	0.7880	26	-2.8951	0.0076*
Site Tuanan:Party age class infant	1.0472	1.2767	26	0.8202	0.4196
Site Tuanan:Party age class immature*	3.1416	1.2589	26	2.4955	0.0193*
Site Tuanan:Party age class adolescent	2.0397	1.1171	26	1.8259	0.0794

**Table 18:** Best fitting model for the association proportion of immature individuals with related other immature individuals ( $\chi^2(10)=27.47$ , p<0.001, AIC=160.27, N=52 of 20 different individuals)

#### Mother – offspring associations

Mother-offspring dyads are in constant association when the immatures are still unweaned (dependent, infant and immature age classes). The Tuanan immature outlier is Sony, when Sidony was injured (fig.21).



Sibling association

Figure 21: Proportion of total follows when mother and offspring were in association. The immature class outlier is Sony when Sidony was injured. Data points are total follows with association by total follow days per individual and age. This is a boxplot with the jittered data points added in colour.

**Figure 22:** Proportion of total follows when siblings were in association. Data points are total follows with association by total follow days per individual and age. The lines were added to the graph using the *loess*-function.

#### Associations with siblings

When a new offspring was born, siblings were still around. When their sibling was around 2y, they started to range more independently (fig.22). When testing the association proportion of siblings with absolute age, the cubic model with age, site and the interaction between the two was significantly better than the 0 model ( $\chi^2(8)$ = 21.10, p<0.001, AIC=28.9, N=50 of 22 different individuals). However only the age components of the model significantly affected the association frequencies of sibling pairs (tab.19).

	Value	SE	DF	t	р
Intercept*	1.0238	0.1506	24	6.7975	*00000
Age *	-0.0360	0.0090	24	-3.9932	0.0005*
Age <sup>2</sup> *	0.0007	0.0002	24	4.2595	0.0003*
Age <sup>3</sup> *	0.0000	0.0000	24	-4.2997	0.0002*
Site Tuanan	0.2361	0.1636	20	1.4436	0.1643
Age: Site Tuanan	-0.0027	0.0024	24	-1.1376	0.2665

**Table 19:** Best fitting model for explaining the association frequency between sibling pairs ( $\chi^2(8)$ = 21.10, p<0.001, AIC=28.9, N=50 of 22 different individuals).

I did analyse the sibling associations by absolute age and not age classes, because there is an imbalance in ages represented in each age class and site. When analysing the association patterns by age classes, there was a significant age class difference. Namely, immatures spent significantly less time in association with their siblings (-0.7115± 0.1353,  $t_{25}$ =-5.2591, p<0.0001). Additionally, the model with site and age class was the best fitting model ( $\chi^2(7)$ =28.97, p<0.0001, AIC=19.03, N=52 of 22 different individuals). Sibling associations were significantly more frequent in Tuanan than in Suaq Balimbing (0.2862±0.0983,  $t_{20}$ =2.91,

p<0.01). However, this result might be attributed to the younger dependent (0 - 2y) siblings in Tuanan. There was no interaction between site and age class.

#### Associations with others

Associations with others increased with age (0.0086±0.0019,  $t_{37}$ =4.50, p<0.001, N=61 of 22 different individuals) and there were significantly less associations in Tuanan than in Suaq Balimbing (-0.6548±0.1957,  $t_{21}$ =-3.35, p<0.01, N=61 of 22 different individuals). The model with age and site was good for explaining the amount of follows in association with others ( $\chi^2(5)$ =21.63, AIC=142.63, p<0.0001, N=61 of 23 different individuals). However, with the addition of a site\*age interaction, the model became even better ( $\chi^2(6)$ =5.66, p<0.05, AIC=138.96, N=61 of 22 different individuals). Yet, the interaction was not significant anymore, when omitting the oldest individuals from Suaq Balimbing for which no comparison to Tuanan was possible (fig.23a).

When analysing the same with age classes instead of absolute age, there was no age difference anymore and only a site difference could be seen (-0.5337 $\pm$ 0.2016, t<sub>20</sub>=-2.65, p<0.05, N=58 of 22 different individuals) (fig.23b). Of course the oldest Suaq Balimbing individuals were also removed for this analysis.



**Figure 23:** Association frequencies of immature individuals with other individuals than the mother or the sibling by age (a) and age class (b) (x-axis) and site (red: Suaq Balimbing, blue: Tuanan). The lines were added to graph a) using the *loess*-function. The data points in plot b) are illustrated as jittered points around the boxplot.

In order to see if associations with specific party classes were more frequent in one site than the other, association rates were looked at separately for each party age class.

#### Unflanged males

There were significantly less associations with unflanged males in Tuanan than in Suaq (- $0.4557\pm0.1600$ , t<sub>17</sub>=-2.85, p<0.05, N=39 of 19 different individuals) (fig.24a). There was no difference among immatures' age classes, and the model with site only explained the association rates with unflanged males best (( $\chi^2(4)$ = 7.62, p<0.01, AIC=61.83, N=39 of 19 different individuals).

#### Adolescents (non-siblings)

The model with age class only was the best fitting model for the association rates with adolescents ( $\chi^2(6)=27.25$ , p<0.0001,mAIC=11.98, N=27 of 15 different individuals) (fig.24c). Adolescents associated significantly more frequently with each other than with younger dependent individuals (0.4392±0.1474, t<sub>13</sub> =2.98, p<0.01, N=27 of 15 individuals). There was no site difference and no interaction between age class and site.

#### Dependent immatures

Unfortunately there were not enough data to compare the association rates of unweaned immatures across the two sites, because there were very little data only. When conducting tests only within age classes of which more than just one data point per site were available, I could only compare adolescents (fig.24b).

For the adolescent age class, no site difference in respect to association rates with unweaned immatures emerged ( $0.0457\pm0.2396$ , t<sub>2</sub>=0.19, p=0.87, N=8 of 4 different individuals).



**Figure 24:** Association rates (total counts of associations with specific party age class individuals/total follow days) with unflanged males (a), adolescents (that are not siblings) (b) and other unweaned immatures (c) by the age class of the immature individuals (dependent (0-2y), infant (2-4y), immature (4y-when new sibling born), adolescent (weaned offspring)). All data points are illustrated as jittered points around the boxplots.

#### 3.1.3.2 The chance of social play within associations

#### Chance of play with associates

Overall, neither site nor the focals' age affected the chance of play within an association. The average Play Index of a specific association dyad had a significant effect on the play proportion of days with association ( $F_{1,97}$ =106.74, p<0.0001, N=130 with 23 different individuals). Also the party's age class ( $F_{8,97}$ =18.65, p<0.001, N=130 with 23 different individuals) and if the dyad was related ( $F_{1,97}$ =9.91, p<0.01, N=130) had an effect on the proportion of associations with play. And thus, the proportion of associations with play for all possible party types, was best explained by the model with these 3 components ( $\chi^2(13)$ = 172.77, p<0.0001, AIC=231.72, N=130, of 23 different individuals).

Yet, there were still all possible party age classes included in the analysis. Flanged males and the females with dependent offspring, the two age classes which play was never seen with in the current sample, were excluded. However, the best fitting model did not change. Thus, the proportion of playful associations was still best explained by the average Play Index, kinship

and the party class ( $\chi^2(9)$ = 110.78, p < 0.0001, AIC=189.09, N=87 of 23 different individuals) (tab.20). Even though the proportion of playful associations was arcsin-square-root transformed, the residuals were not normal distributed and thus, this result should be treated with caution. Moreover, there could well be interactions between the terms, yet due to the low sample size, no interactions could be tested reliably.

Moreover, I could not assess the proportion of associations with play within a single focal age class with specific association partners, because I did not have enough data to do so (fig.25). Only in Suaq Balimbing, social play between unweaned immatures and unflanged males was observed in the current data set (fig.25a).

	Value	SE	DF	t	р
Intercept	-0.5349	0.4057	58	-1.3185	0.1925
Party age class infant*	0.9796	0.4343	58	2.2554	0.0279*
Party age class immature	0.8406	0.4358	58	1.9289	0.0586
Party age class adolescent	0.3314	0.3701	58	0.8955	0.3742
Party age class unflanged	0.8155	0.4185	58	1.9487	0.0562
Related yes*	0.4685	0.2247	58	2.0845	0.0415*
Average Play Index*	6.3691	0.7500	58	8.4920	0.0000*

**Table 20:** Best fitting model for the proportion of associations that were playful ( $\chi^2(9)$ = 110.78, p < 0.0001, AIC=189.09, N=87 of 23 different individuals)



**Figure 25 :** Proportion of associations with play of immature individuals with a given party age class: a) unflanged males b) adolescents that are not the immature's sibling and c) unweaned immatures. On the x-axis is the age class of the immature focal animal and the two sites are in colours (red: Suaq Balimbing, blue: Tuanan). All data points are illustrated as jittered points around the boxplots.

#### Sibling associations and play proportions

Dependent infants (0 – 2 years) tended to play less with their older siblings in Tuanan than in Suaq Balimbing (-0.3427±0.1533,  $t_8$ =-2.24, p=0.056, N=16 of 10 individuals) (fig.26). No age effect was tested, because there was a significant difference of sibling associations across age already and thus the play proportion would be biased by this difference.



**Figure 26:** Proportion of associations with social play with the older or younger sibling in respect to age class (x-axis) and site (colour). All data points are illustrated as jittered points around the boxplot.



**Figure 27:** Proportion of days with social play with mothers in respect to age class of the offspring (x-axis) and to site (colour). All data points are illustrated as jittered points around the boxplot.

#### Mother associations and play proportions

The proportion of associations, i.e. days, with social play with the mother significantly decreased with age of the offspring (-0.0026±0.0007,  $t_{49}$ =-3.79, p<0.001, N=75 of 25 different individuals). There was no significant difference between the two sites (-0.1004±0.0785,  $t_{23}$ =-1.28, p=0.21, N=75 of 25 individuals). The model with age only was the best fitting model to explain the proportion of days with social play with the mother ( $\chi^2(4)$ =10.06, p<0.01, AIC=7.12) (fig.27).

## **3.1.4 Play and fruit availability**

Because for some individuals I took the average Fruit Availability Index (FAI) for more than one month in order to have at least 5 full-day follows for one data point, I repeated the analyses for the solitary and social play frequencies without any FAI averages. I set up a model, which controlled for site, age and individual identity. However, the Fruit Availability Indices did not improve the 0 model neither for solitary nor for social play frequencies (solitary play:  $\chi^2(6)=0.32$ , p=0.57, AIC=101.28; social play:  $\chi^2(6)=0.06$ , p=0.81, AIC=-62.47; N=312, with 74 different combinations of site, age and individual identity).

# **3.1.5** Compensation

#### 3.1.5.1 Relation among play types

There was a positive, quadratic relation among social and solitary play frequencies on a daily basis when controlling for individual identity and age ( $\chi^2(6)=7.79$ , p<0.05, AIC= 25.91, N=263 of 69 age and individual combinations) (tab.21). The analysis was conducted with data from very selected and highly reliable observers only.

	Value	SE	DF	t	р
Intercept*	0.4149	0.0672	192	6.1740	0.0000*
Social play*	0.4071	0.1521	192	2.6770	0.0081*
Social play <sup>2</sup> *	-0.5393	0.1965	192	-2.7444	0.0066*

**Table 21:** Model for daily solitary play frequency by daily social play frequency ( $\chi^2(6)=7.79$ , p<0.05, AIC= 25.91, N=263 of 69 age and individual combinations). There was no difference between the two sites. Data from very selected observers only were considered. Both solitary and social play frequencies were transformed using arcsin-transformations in order to normalize the residuals.

Using the same restricted data set, we found that on a longterm view (averages of at least 5-full day follows for each play type) there was also a positive, quadratic correlation among solitary and social play ( $\chi^2(6)=17.55$ , p<0.001, AIC=6.48, N=26 of 18 individuals and 26 different ages) (tab.22).

	Value	SE	DF	t	р
Intercept*	0.2165	0.0894	17	2.4211	0.0269*
Social play*	3.2343	0.8720	6	3.7093	0.0100*
Social play <sup>2</sup> *	-3.9421	1.5049	6	-2.6194	0.0396*

**Table 22:** Model for average solitary play frequency by average social play frequency of a specific follow period per individual ( $\chi^2(6)=17.55$ , p<0.001, AIC=6.48, N=26 of 18 individuals and 26 different ages). There was no difference between the two sites. Data from very selected observers only were considered. Both solitary and social play frequencies were transformed using arcsin-transformations in order to normalize the residuals.

When looking at the separate solitary play types in relation to social play, we found similar trends. There was a positive correlation between solitary locomotor play and social play frequency on a daily, as well as on longterm basis (tab.25, tab.26). For solitary object play, we discovered a positive correlation which was even stronger in Tuanan than in Suaq on a longterm basis ( $\chi^2(7)=17.53$ , p<0.001, AIC=-7.38, N=26 of 18 individuals and 26 different ages) (tab.23). But the model with the correlation between solitary object and social play frequency on a daily basis was not significant, however the quadratic correlation itself was ( $\chi^2(6)=4.11$ , p=0.13, AIC=-138.75, N=263 of 69 age and individual combinations) (tab.24).

	Value	SE	DF	t	р
Intercept*	0.2383	0.0798	16	2.9869	0.0087*
Social Play*	0.3130	0.1159	6	2.7010	0.0355*
Site Tuanan	-0.1152	0.1554	16	-0.7410	0.4695
Social Play:Site Tuanan*	2.8269	0.8490	6	3.3298	0.0158*

**Table 23:** Model for average solitary object play frequency by average social play frequency of a specific follow period per individual ( $\chi^2(7)$ =17.53, p<0.001, AIC=-7.38, N=26 of 18 individuals and 26 different ages). Data from very selected observers only were considered. Both solitary object and social play frequencies were transformed using arcsin-transformations in order to normalize the residuals.

	Value	SE	DF	t	р
Intercept*	0.2855	0.0497	192	5.7479	0.0000*
Social play*	0.2544	0.1258	192	2.0212	0.0447*
Social play <sup>2</sup>	-0.3105	0.1653	192	-1.8780	0.0619

**Table 24:** Model for daily solitary object play frequency by daily social play frequency ( $\chi^2(6)$ =4.11, p=0.13, AIC=-138.75, N=263 of 69 age and individual combinations). There was no difference between the two sites. Data from very selected observers only were considered. Both solitary object and social play frequencies were transformed using arcsin-transformations in order to normalize the residuals.

	Value	SE	DF	t	р
Intercept*	0.1584	0.0512	17	3.0961	0.0066*
Social play*	1.0903	0.1963	7	5.5537	0.0009*

**Table 25:** Model for average solitary locomotor play frequency by average social play frequency of a specific follow period per individual ( $\chi^2(5)=17.94$ , p<0.0001, AIC=-8.24, N=26 of 18 individuals and 26 different ages). There was no difference between the two sites. Data from very selected observers only were considered. Both solitary locomotor and social play frequencies were transformed using arcsin-transformations in order to normalize the residuals.

	Value	SE	DF	t	р
Intercept*	0.2559	0.0460	192	5.5658	0.0000*
Social play*	0.3622	0.1251	192	2.8959	0.0042*
Social play <sup>2</sup> *	-0.4650	0.1613	192	-2.8825	0.0044*

**Table 26:** Model for daily solitary locomotor play frequency by daily social play frequency ( $\chi^2(6)$ = 8.79, p<0.05, AIC=-133.57, N=263 of 69 age and individual combinations). There was no difference between the two sites. Data from very selected observers only were considered. Both locomotor object and social play frequencies were transformed using arcsin-transformations in order to normalize the residuals.

#### 3.1.5.2 Relation between social play with different partners

Social play frequency with neither associates nor siblings correlated with the motheroffspring play frequency on a daily basis ( $\chi^2(7)=0.36$ , p=0.95, AIC= 349.99, N=120 of 19 different individuals with 45 different ages) (tab.27). Total play bout counts with the mother were log-transformed for the analysis. Moreover, I controlled for individual identity and age.

	Value	SE	DF	t	р
Intercept	0.4719	0.2750	103	1.7159	0.0892
Total play bouts with other than mother	0.0000	0.0141	103	-0.0023	0.9982
Dyad type sibling	-0.0530	0.3069	103	-0.1727	0.8632
Total play bouts with other than mother: Dyad type sibling	0.0093	0.0196	103	0.4734	0.6369

**Table 27:** Complete model fitted for total daily play bouts with the mothers ( $\chi^2(7)=0.36$ , p=0.95, AIC= 349.99, N=120 of 19 different individuals with 45 different ages).

# 3.1.6 Individual trajectories Tuanan

From Tuanan, longitudinal 2-min scan data from 2003-2012 and 2014 of 4 individuals (Jerry, Jip, Milo, Susi) were available. Play trajectories were set up on an individual level (fig.28). The reported proportion of solitary object play seemed to be consistently lower in the years 2003 – 2009 whereas solitary locomotor play was a lot higher compared to the data I used throughout my thesis (fig.29). Because I could not exclude that this variation in the data could result from definitional issues and changing research foci, I decided to lump solitary locomotor and object play together to solitary play for the subsequent analysis. Analyses were conducted with monthly means for each individual. Only data points composed of at least 5 full-day follows were taken into account. However, because the amount of full-day follows included for one specific data point still significantly affected solitary and social play proportion (solitary:  $\chi^2(5)=11.07$ , AIC=108.1, p<0.01; social:  $\chi^2(5)=6.7$ , AIC=-61.1, p<0.05; age and individual identity were included as random factors), the total follow count was included as a random factor in all analyses. Linear mixed models were set up without interaction terms, because for some individuals (e.g. Milo) not the entire ontogenetic trajectory was available and significant interactions could result from this lack of data.



**Figure 28:** Individual play trajectories: average daily solitary (dark blue) and social (light blue) play frequencies. Data points are composed of at least 5-full day follows. The lines were added to the graph using the *loess*-function.

Solitary play was best explained by a quadratic model with age only ( $\chi^2(5)=78.04$ , p<0.0001, AIC=116.9, N=104). The individual identity and the Fruit Availability Indices (FAI) did not significantly improve the model ( $\chi^2(9)=4.59$ , p=0.33, AIC=120.3, N=104) (tab.28).

	Value	SE	DF	t	р
Intercept*	0.8440	0.1382	89	6.1070	0.0000*
Age	0.0040	0.0043	89	0.9301	0.3548
Age <sup>2</sup> *	-0.0001	0.0000	89	-3.4985	0.0007*
FAI	0.0198	0.0125	89	1.5861	0.1163
Name Jip	0.1427	0.1170	89	1.2201	0.2257
Name Milo	-0.0248	0.1301	89	-0.1906	0.8493
Name Susi	-0.0664	0.1275	89	-0.5206	0.6039

**Table 28:** Complete model for solitary play frequencies. Data points are averages of an individual at a specific age during a specific month (exact FAI values).  $\chi^2(9)=82.6$ , p<0.0001, AIC= 120.3, N=104 with 9 different follow day counts (from 5 full-day follows upwards).

Social play proportions were best modelled by the cubic function of age and individuals' identity ( $\chi^2(9)=46.8$ , p<0.0001, AIC= -80.3, N=104) (tab.29). Fruit Availability Indices (FAI) did not significantly improve the model for social play frequencies.

	Value	SE	DF	t	р
Intercept	0.0070	0.0522	89	0.1333	0.8943
Age*	0.0118	0.0034	89	3.441	0.0009*
Age <sup>2</sup> *	-0.0002	0.0001	89	-2.8248	0.0058*
Age <sup>3</sup> *	0.0000	0.0000	89	2.7435	0.0074*
Name Jip	-0.0195	0.0440	89	-0.4431	0.6588
Name Milo*	-0.1097	0.0510	89	-2.1519	0.0341*
Name Susi*	-0.1499	0.0490	89	-3.0584	0.0029*

**Table 29:** Complete model for social play frequency ( $\chi^2(10)$ =46.9, p<0.0001, AIC=-78.4, N=104 with 9 different follow day counts (> 5 N-N follows)). Interactions were not included.

When Susi was excluded from the analysis, the social play proportion among different individuals did not vary anymore ( $F_{2.75}=2.28$ , p=0.11). The cubic function of age only was the best fitting model ( $\chi^2(6) = 20.72$ , p<0.0001, AIC=-50.46, N=89 with 9 different full-day follow counts (>5 N-N follows at least)).



**Figure 29:** Play trajectories from Tuanan data of 11 different individuals over a 10 years span (2003-2012 + 2014). Data points are composed of at least 5 full-day selected follow-days.

# **3.2 Details on solitary play**

### **3.2.1 Play budget with all-occurrence data**

Because solitary play bouts are often very short and therefore could be underrepresented in the instantaneous data set, the play budget analysis was redone with all-occurrence data. Unfortunately, the duration of individual play bouts was not always reported and therefore I could only use bout frequencies, but not overall play duration for a reliable analysis. However there was a strong, positive correlation between bout frequencies and total play duration (slope= $52.2\pm6.6$ , t=7.88, p<0.0001, F<sub>1.20</sub>=62.11, p<0.00001, R<sup>2</sup>=0.74).

Additionally, the more detailed all-occurrence data also allowed me to conduct analyses on rarer play behaviour, such as AP nest. Moreover, I could assess the inter-linkage between different play types and other behaviour, which is not noted as such in the 2-min scan data. Because the 2-min scan data is collected in a hierarchical order and thereby according to the protocol only one behaviour should be reported at one 2-min bout.

Because we could not collect data of 5 full-day follows for all the individuals, I always assessed first if the total follow days had an effect on overall hourly play frequencies and then included the total follow days as random effects in the linear mixed models.

To evaluate if there was an influence of daytime on solitary play frequencies, I took all hourly average counts of solitary play per individual and set up a linear mixed model with age and site as random factors. I took only the time between 6 a.m. to 3 p.m. avoiding the hours during which certain individuals would have slept still or already. No effect of daytime on overall hourly solitary play bout frequency was found ( $\chi^2(5)=1.67$ , p=0.20, AIC=677.09, N=146 by 21 different ages).

#### 3.2.1.1 Solitary object play

For the analysis of solitary object play (APO), I could incorporate data collected in previous years by Caroline Schuppli, Sofia Forss and Ellen Meulman. For normalizing the residuals, APO frequency was log-transformed.

First, I tested how many full-day follows per individual and age were necessary in order to avoid an impact of the follow amount on the hourly APO frequency. A model with total fullday follows as fixed effect and individual identity and age as random effects was set up to test this. If I included all full-day follows, the total amount of full-day follows per individual and age had a significant effect on the hourly APO frequency ( $\chi^2(4) = 4.25$ , p<0.05, total follows:  $0.038\pm0.018$ , t<sub>17</sub>=2.109, p=0.05, N=40 of 18 different individuals and 40 age-individual combinations). If there were at least 2 full-day follows per individual, the effect of total follows vanished (( $\chi^2(5)=0.63$ , p=0.43, N=35 of 21 individuals with 34 different ageindividual combinations). Therefore, I tested the hourly APO frequency in relation to age, site and FAI based on at least 2 full-day follows per individual and age. The model with age as a fixed effect and individual identity as a random effect was the best fitting model ( $\chi^2(4)$ =36.05, p<0.0001, AIC=21.6, N=35 of 21 individuals). Age had a significant effect on APO frequency  $(-0.014\pm0.001, t_{13}=-11.43, p=0)$  (fig.30). Previous work had set the minimum necessary full-day follow days to 5 for a normalized activity budget of adult female orangutans (van Noordwijk, pers. comm.). Yet, this more conservative approach did not change the best fitting model ( $\chi^2(4)=34.3$ , p<0.0001, AIC=12.16, N=24 of 18 different individuals). Solitary object play frequency was still best explained by age only (-0.0154 $\pm$ 0.0015, t<sub>5</sub>=-10.6, p<0.001).

Even though, not all the durations of solitary object play were available, I evaluated if the average duration of a play bout varied across age. For this analysis I took the average play bout duration per individual and its average age. Object play bouts became significantly shorter with age (-0.4769±0.2144, t=-2.22, p<0.05, R<sup>2</sup>=0.22, F<sub>1,13</sub>=4.95, p<0.05, N=15) (fig.31).



**Figure 30:** Solitary object play bouts per visible follow hour. Data points are composed of an average count per individual and age (some individuals are represented twice in the graph). The lines were added to the graph using the *loess*-function.



Figure 31: Average duration of an APO bout. Data points are composed of the average duration per individual and its average age. The lines were added to the graph using the *loess*-function.

#### 3.2.1.2 Solitary locomotor play

Neither total amount of full-follow days ( $\chi^2(5)=1.65$ , p=0.2), nor total visible follow hours ( $\chi^2(5)=0.4742$ , p=0.5) affected the average reported solitary locomotor play frequency per visible hour. It was controlled for individual identity and age by adding them as random factors. Yet, the total number of follow days was still added as a random factor in the analysis, because of the aforementioned 5 days baseline, which I did not have for 3 individuals.

For the analysis, the hourly locomotor play frequencies were log-transformed. The quadratic model with age only was the best fitting model ( $\chi^2(6)=15.71$ , p<0.001, AIC= 25.7, N=21 of 15 individuals) (tab.30). APM showed a peak around age 3 years (fig.32). APM frequencies were not affected by sex, site and fruit availability (tab.30).

The average locomotor play bout duration decreased significantly with age (-0.825±0.166, t=-4.97, p<0.01,  $R^2$ =0.63,  $F_{1,13}$ =24.71, p<0.001, N=15) (fig.33). The average duration was calculated by individual and average age.

	Value	SE	DF	t	р
Intercept*	1.0970	0.2006	14	5.4682	0.0001*
Age	0.0116	0.0102	4	1.1362	0.3193
Age <sup>2</sup>	-0.0002	0.0001	4	-2.3648	0.0773

**Table 30:** Best fitting model for hourly solitary locomotor play frequencies ( $\chi^2(6)=15.71$ , p<0.001, AIC= 25.7, N=21 of 15 individuals)

	Value	SE	DF	t	р
Intercept*	1.4017	0.6362	12	2.2033	0.0479*
Age	0.0188	0.0162	1	1.1640	0.4518
Age <sup>2</sup>	-0.0002	0.0001	1	-1.2851	0.4210
Sexm	0.0149	0.2011	12	0.0742	0.9421
Site Tuanan	-0.1955	0.6973	12	-0.2804	0.7840
FAI	-0.0587	0.0516	1	-1.1378	0.4590
Age: Site Tuanan	-0.0154	0.0163	1	-0.9435	0.5185
Site Tuanan:FAI	0.0629	0.0627	1	1.0025	0.4992

**Table 31:** Complete tested model for hourly solitary locomotor play frequencies ( $\chi^2(11)=20.2$ , p<0.01, AIC=31.23, N=21 of 15 individuals)



**Figure 32:** APM bouts per visible follow hour. Data points are composed of an average count per individual and age (some individuals are represented twice in the graph). The lines were added to the graph using the *loess*-function.



Figure 33: Average duration of an APM bout. Data points are composed of the average duration per individual its average age. The lines were added to the graph using the *loess*-function.

### 3.2.1.3 Solitary nest practice play

The analysis of nest play (AP nest) was conducted by taking average frequencies per individual and its average age, because nest play is not observed very frequently. Moreover, if there was an average taken by each age of an individual, the number of full-day follows affected the AP nest frequency. However when lumping all the data of an individual, neither the total amount of full-day follows ( $\chi^2(5)=0.32$ , p=0.57, random effects=Name/Age), nor total visible follow hours ( $\chi^2(5)=0.18$ , p=0.67) had an impact on the average hourly AP nest frequency. Again, to keep the analysis more conservative, the total follow day number was still added as a random factor in the analysis.

No model was significantly better than the 0 model. However visual inspection of the graph revealed a peak of AP nest between the age of 2 and 4 years (fig.34).



**Figure 34:** AP nest bouts per visible follow hour. Data points are composed of an average count per individual its average age. The lines were added to the graph using the *loess*-function.

# 3.2.1.4 Solitary display play

Less habituated individuals exhibited more AP display towards observers (e.g. Danum and Sony). Therefore, AP display rather seems to be a measure of habituation, or over-habituation respectively (e.g. Joya), than of playfulness of an individual.

# **3.2.2** Combinations of solitary play types

#### 3.2.2.1 Solitary object-locomotor play

Solitary object and locomotor play were often combined within a single bout (APO-APM). The APO-APM trajectory followed a similar pattern as locomotor play and exhibited a peak around the age of 3 years (fig.35). Accordingly, the quadratic model with age only revealed the best fit ( $\chi^2(6)=9.34$ , p<0.01, AIC=13.55, N=20 of 15 individuals). However, there was only a trend towards age affecting APO-APM frequencies (tab.32).

	Value	SE	DF	t	р
Intercept	0.3533	0.1856	14	1.9035	0.0777
Age	0.0119	0.0089	3	1.3483	0.2703
Age <sup>2</sup>	-0.0002	0.0001	3	-2.0708	0.1301

**Table 32:** Best fitting model for hourly APO-APM frequencies ( $\chi^2(6)=9.34$ , p<0.01, AIC=13.55, N=20 of 15 individuals).

#### 3.2.2.2 Solitary object play and try-feeding

The cut-off line between try-feeding and object play tends to be very narrow. Because immatures mouth objects during manipulating them or play with the objects which they try-feed on, solitary object play and try-feeding are frequently interconnected. Age, site and the

interaction between the two, best described the APO-TF frequencies ( $\chi^2(7)=22.05$ , p<0.001, AIC=-28.92, N=20 of 15 individuals) (tab.33, tab.34). The interconnection of try-feeding and solitary object play was highest during the first 4 years of age and then ceased quite abruptly (fig.36). Thus, it followed a similar trajectory like object play.

Pre-analyses have also been conducted and there was neither an effect of the amount of followdays nor of total follow hours on the APO-TF frequencies, when controlling for age and individual identity ( $\chi^2(5)=0.8254$ , p=0.3636, AIC=-2.95; ( $\chi^2(5)=0.1723$ , p=0.68, AIC=-2.3).

	Value	SE	DF	t	р
Intercept	0.0664	0.1031	13	0.6436	0.5310
Age	0.0102	0.0038	3	2.7109	0.0731
Site Tuanan	0.1951	0.1117	13	1.7463	0.1043
Age: Site Tuanan*	-0.0130	0.0038	3	-3.3961	0.0426*

**Table 33:** Best fitting model for hourly APO-TF frequencies ( $\chi^2(7)=22.05$ , p<0.001, AIC=-28.92, N=20 of 15 individuals).

	Value	SE	DF	t	р
Intercept	0.3290	0.2023	12	1.6264	0.1298
Age	0.0063	0.0044	1	1.4271	0.3891
Sex m	0.0464	0.0469	12	0.9899	0.3417
Site Tuanan	-0.0974	0.2161	12	-0.4510	0.6600
FAI	-0.0237	0.0144	1	-1.6418	0.3483
Age: Site Tuanan	-0.0092	0.0045	1	-2.0460	0.2894
Site Tuanan: FAI	0.0246	0.0172	1	1.4270	0.3891

**Table 34:** Complete model tested for hourly APO-TF frequencies ( $\chi^2(10)=26.3$ , p<0.001, AIC=-27.18, N=20 of 15 individuals).



**Figure 35:** APO-APM bouts per visible follow hour. Data points are composed of an average count per individual and age (some individuals are represented twice in the graph). The lines were added to the graph using the *loess*-function.



**Figure 36:** APO-TF bouts per visible follow hour. Data points are composed of an average count per individual and age (some individuals are represented twice in the graph). The lines were added to the graph using the *loess*-function.

# 3.2.3 Details of solitary object play

In order to see if there were qualitative differences of object play during ontogeny and among the two sites, I assessed the type of objects immatures played with. Additionally, I counted the number of manipulation modes within a single solitary play bout. However, because the terms used for describing the object play were not consistent among observers, as the definitions were not set strictly, I could not assess the variety of object manipulation across sites.

#### 3.2.3.1 Object manipulation diversity

Only data from Tuanan were taken into account for this analysis. Because of the small sample size (N=11), I conducted an ANOVA with one data point for each individual. When transforming the average number of object manipulations with log-transformations, the variance did not differ across age classes (Levene test:  $F_{3,7}$ =0.79, p=0.535) and therefore, a parametric ANOVA could be conducted. The number of object manipulations varied significantly with age class ( $F_{3,7}$ =5.86, p=0.03, N=11). However, the differences between age classes were not significant. Infants tended to manipulate objects most diversely within one play bout (2 – 4 y) (0.118±0.054, t=2.176, p=0.066). The total visible follow hours of an individual did not significantly affect the average manipulation modes per play bout when controlling for age class ( $F_{1,10}$ =0.08, p=0.788).

Because duration correlated with the object manipulation diversity ( $48.59\pm10.47$ , t=4.64, p<0.001, R<sup>2</sup>=0.52, F<sub>1,18</sub>=21.54, p<0.001), I corrected manipulation diversity by play time (manipulations per s). When taking the average for each individual and transforming the manipution rates by the arcsin-function, there was a positive correlation between age (months) and manipulation rates ( $0.0027\pm0.0010$ , t=2.64, p<0.05, R<sup>2</sup>=0.37, F<sub>1.9</sub>=6.98, p<0.05).

#### 3.2.3.2 Detached objects

I calculated the proportion of solitary object play bouts with at least one detached object involved per individual. Because older individuals generally played less, I controlled for the total amount of solitary play bouts by setting them as a random factor in the model. There was a significant increase of detached object use with age  $(0.007\pm0.002, t_{13}=3.38, p<0.01)$  (fig.37). The model with age only was the best fitting model ( $\chi^2(4)=9.48, p<0.005$ , AIC=6.53, N=15) (tab.35, tab.36). There was no site difference in detached object use. However, from Suaq Balimbing only data for individuals below the age of 4 years were available.

	Value	SE	DF	t	р
Intercept*	1.1599	0.1170	13	9.9128	*00000
Age*	0.0073	0.0021	13	3.3849	0.0049*

**Table 35:** Best fitting model for detached object use proportion during solitary object play ( $\chi^2(4)=9.48$ , p<0.005, AIC=6.53, N=15).

	Value	SE	DF	t	р
Intercept	0.0808	1.3510	9	0.0598	0.9536
Age	0.0146	0.0099	9	1.4729	0.1749
Site Tuanan	0.1716	0.3159	9	0.5433	0.6002
Duration	0.0035	0.0041	9	0.8343	0.4257
Stick involved	0.5758	1.3182	9	0.4368	0.6725
Age: Site Tuanan	-0.0057	0.0106	-9	0.5389	0.6030

**Table 36:** Complete tested model for detached object use proportion during solitary object play ( $\chi^2(8)$ =14.88, p<0.01, AIC=9.13, N=15).



Figure 37: Proportion of solitary object play bouts with at least one detached object involved. One data point per individual and its average age. The lines were added to the graph using the glm-function.



**Figure 38:** Proportion of solitary object play bouts with multiple objects involved. One data point per individual and its average age. The lines were added to the graph using the *loess*-function.

# 3.2.3.3 Multiple objects

Younger individuals tended to play more frequently with several objects at a time (age:  $-0.0044 \pm 0.0023$ ,  $t_{13}$ =-2.01, p=0.065) (fig.38). There was no effect of site and only the linear model with age was significantly better than the 0 model ( $\chi^2(4)$ = 4.07, p <0.05, AIC=7.4, N=15) (tab.37). I again put total solitary play bouts as random effects into the model and analysed the average proportion of multiple object use per individual and its average age.

	Value	SE	DF	t	р
Intercept*	0.8099	0.1204	13	6.7252	0.0000*
Age	-0.0044	0.0022	13	-2.0121	0.0654

**Table 37:** Best fitting model for multiple object use proportion during object play ( $\chi^2(4) = 4.07$ , p <0.05, AIC=7.4, N=15).

# 3.2.3.4 Sticks

I could not find any overall patterns for stick play. Neither age, average bout duration nor site improved the 0 model of stick use proportion during solitary object play (fig.40).



However when looking at the bouts individually, play bouts with sticks tended to last longer than if there was no stick, but any other object involved (fig.39). However, no significant relationship could be found.

**Figure 39:** Average duration of a solitary object play bout by stick involvement (yes or no). Suaq Balimbing is in red, Tuanan is represented in blue.

## 3.2.3.5 Leaves

Very young individuals exhibited a significantly higher proportion of play bouts with leaves involved ( $\chi^2(4)=8.37$ , p<0.01, AIC=8.78, N=15) (tab.38). There was no difference between the two sites (fig.41).

	Value	SE	DF	t	р
Intercept*	1.1820	0.1261	13	9.3774	0.0000*
Age*	-0.0072	0.0023	13	-3.1170	0.0082*

**Table 38:** Best fitting model for leave use proportion during object play ( $\chi^2(4)$ = 8.37, p<0.01, AIC=8.78, N=15).





**Figure 40:** Proportion of solitary object play bouts with a stick involved. One data point per individual and its average age. The lines were added to the graph using the *loess*-function.

**Figure 41:** Proportion of solitary object play bouts with leaves involved. One data point per individual and its average age. The lines were added to the graph using the *loess*-function.

# **3.2.4 Details of solitary locomotor play**

#### 3.2.4.1 Locomotion patterns

The diversity of locomotion patterns was assessed only within Tuanan. The amount of visible follow hours available for an individual did not affect the locomotion patterns seen when controlling for age class ( $F_{1,9}$ =0.13, p=0.73, N=15). The average number of locomotion patterns was log-transformed for the analysis. The locomotion pattern diversity significantly decreased with age (-0.0063± 0.0023, t=-2.76, p<0.05, R<sup>2</sup>=0.42, F<sub>1,8</sub>=7.63, p<0.05, N=15). In order to control for the play bout duration, I assessed the locomotion patterns per seconds (locomotion pattern rate). Arcsin-transformed locomotion pattern rates increased slightly, but not significantly with age (0.0041±0.0020, t=2.06, p=0.07, R<sup>2</sup>=0.24, F<sub>1,9</sub>=4.23, p=0.07, N=15).

#### 3.2.4.2 Body parts used

When immatures were below 4 years of age, their whole body was involved in up to half of solitary locomotor play bouts. Later on, the whole body involvement dropped to 0 - 10 % of the play bouts (fig.42).

Unfortunately, the model with total play bouts as a random effect did not work and therefore I fitted a simple linear model without any random effects. The data did not significantly deviate from a normal distribution (W=0.93, p=0.25) and therefore I used a parametric linear model. Age only explained the whole body involvement proportion best ( $F_{1,13}$ =17.99, p<0.001, R<sup>2</sup>=0.55, N=15).



**Figure 42:** Proportion of APM bouts with the whole body involved. Data points are composed of an average proportion per individual its average age. The lines were added to the graph using the *loess*-function.

# 3.2.5 Playfaces during solitary play

Different playful expressions were observed during solitary play, such as playfaces and different vocalisations. Yet, vocalisations only occurred rarely and strongly differed among individuals. Lois was observed about 3 times to make "play ohhs" and Danum few times produced a "raspberry"-like sound in the context of solitary play. Therefore, only playfaces could be analysed more quantitatively. For calculating the playface frequency in the solitary play context, I employed two different approaches. On the one hand, I analysed playfaces per play bout which I corrected by the proportion of visible 2-min bouts (*"Playface frequency"*). Because not for all the play bouts, the durations were available, I could not calculate playface rates by total solitary play time. Thereby play bout counts were taken as a proxy for play duration. On the other hand, my second approach was to look at the playfaces, which were occurring exclusively during solitary play, by visible follow hour (*"Playface occurrence"*).

#### 3.2.5.1 Playface frequency

Playface frequency generally did not change much over age, and only decreased little with age. With all data included, the model with age, site and the interaction between the two was the best fitting model ( $\chi^2(6)=14.97$ , p<0.01, AIC=-8.07, N=15). Age, as well as the interaction between age and site were significant (tab.39). However, Lois, a 4-year old male infant from Suaq Balimbing, figured as an extreme outlier (fig.43).

By excluding him from the analysis, only age had a negative effect on playface frequency ( $\chi^2(4)=7.58$ , p<0.01, AIC=-9.36, N=14) (tab.40), and the site effect and the interaction between age and site were not improving the model anymore. In all models, I controlled for the total play bout count.

	Value	SE	DF	t	р
Intercept	0.1099	0.1558	11	0.7051	0.4954
Age*	0.0139	0.0057	11	2.4396	0.0328*
Site Tuanan	0.3663	0.1791	11	2.0449	0.0655
Age: Site Tuanan*	-0.0179	0.0059	11	-3.0566	0.0109*

**Table 39:** Best fitting model of playface frequency per solitary playbout corrected by overall visibility when Lois is included in the analysis ( $\chi^2(6)$ = 14.97, p<0.01, AIC=-8.07, N=15).

	Value	SE	DF	t	р
Intercept*	0.4407	0.0673	12	6.5535	0.0000*
Age*	-0.0036	0.0012	12	-2.9356	0.0125*

**Table 40:** Best fitting model for playfaces per solitary play bouts corrected by visibility ( $\chi^2(4)$ = 7.58, p<0.01, AIC=-9.36, N=14) when Lois is excluded from the analysis.

#### 3.2.5.2 Playface occurrence

When taking the playface rate in solitary play context corrected by visible follow hours, the same pattern as in the playface frequency arose. When Lois was included in the analysis, the model with age, site and the interaction between the two was the best model ( $F_{2,11}=7.26$ , p<0.01, N=14). With the exclusion of Lois, the model with age only became the best model ( $F_{1,12}=12.84$ , p<0.01, N=13) (tab.41).

	Estimate	SE	t	р
Intercept *	0.9300	0.1417	6.563	<0.0001 *
Age *	-0.0092	0.0026	-3.589	0.0037 *

**Table 41:** Best fitting model for playface occurrence (F<sub>1,12</sub>=12.84, p<0.01, N=13).



**Figure 43:** Proportion of solitary play bouts (corrected by visibility) with a playful expression. One data point per individual and its average age (N=13). The lines were added to the graph using the *glm*-function.



**Figure 44:** Playface occurrence per visible follow hour in the context of solitary play. One data point per individual (N=13) and its average age. The lines were added to the graph using the *glm*-function.

# 3.2.5.3 Solitary play types and playfaces

Playfaces mostly occurred during solitary play when more than one play type was interlinked or when there was a social interaction during a solitary locomotor play bout (tab.42). The mothers' distance did not explain the proportion of solitary play bouts with playfaces ( $\chi^2(7)=3.71$ , p=0.45, AIC=24.44, N=54 of 15 individuals) (fig.45).

	Value	SE	DF	t	р
Intercept	-0.0154	0.1201	78	-0.1284	0.8981
Play class AP nest	0.0105	0.1909	78	0.0548	0.9564
Play class APM	0.2117	0.1465	78	1.4458	0.1523
Play class APM combined	0.0990	0.1675	78	0.5909	0.5563
Play class APM/SP*	1.1606	0.2277	78	5.0964	*00000
Play class APO	0.1786	0.1465	78	1.2196	0.2263
Play class APO combined	0.0401	0.1527	78	0.2625	0.7936
Play class APO/APM *	0.3190	0.1482	78	2.1528	0.0344*
Play class APO/APM combined*	0.6756	0.1629	78	4.1475	0.0001*
Play class APO/APM/SP	0.0116	0.1920	78	0.0607	0.9518
Play class APO/SP	0.2356	0.1629	78	1.4462	0.1521

**Table 42:** Playface frequency during different solitary play types. LMM with individual identity as random factor ( $\chi^2(13)=60.51$ , p<0.0001, AIC=84.17, N=103 of 15 different individuals). All the play types which are named "combined" are solitary play interlinked with either try-feeding or exploration. All playface frequencies of different play types have been compared to playface frequencies during APM.



**Figure 45:** Playface per solitary play bout by the different solitary play classes (x-axis) and site (colour). Data points are playface counts per individual and play class (=total playface per play class / total bouts per play class). All data points are illustrated as jittered points around the boxplot.



**Figure 46:** Proportion of solitary play bouts with a playface by the distance to the mother. One data point per individual and distance category to the mother (if avialable). All data points are illustrated as jittered points around the boxplot.

# **3.2.6 Circumstances of solitary play**

#### 3.2.6.1 Mothers' activity budget

There was some evidence that the mothers' daily activity budget would influence the amount of solitary play of their offspring (fig.49). I looked at the activity budget of the mothers on a daily basis in relation to their offsprings' total solitary play bouts (all-occurrence), which I corrected for visibility. I set up models with individual identity as a random effect and added the mothers' activity proportions (moving, feeding and resting) to the best model for overall solitary play budget which includes age, site, and the interaction between the two ( $\chi^2(6) = 23.51$ , p<0.0001, AIC=629.25, N=70 of 15 individuals). However, the mothers' activities did not significantly improve the fit for the daily play bout counts of their offspring compared to the best overall play budget model ( $\chi^2(9) = 4.93$ , p=0.2, AIC=630.32, N=70 of 15 individuals). Because the mothers' activities might influence play of immatures differently at different times during ontogeny, I added the interaction between the mothers' activities and the age of the immature. Yet, the interaction did not improve the overall model ( $\chi^2(12) = 6.32$ , p=0.39, AIC=634.93, N=70 of 15 individuals) (tab.43).

	Value	SE	DF	t	р
Intercept	-110.6207	314.5748	47	-0.3517	0.7267
Age	5.6979	7.0104	47	0.8128	0.4204
Site Tuanan	36.5944	18.6302	13	1.9643	0.0712
Mother moves	183.2546	314.5676	47	0.5826	0.5630
Mother feeds	179.3535	327.4473	47	0.5477	0.5865
Mother rests	130.3757	329.2857	47	0.3959	0.6939
Age: Site Tuanan *	-1.4828	0.5813	47	-2.5509	0.0141*
Age: Mother moves	-5.9772	6.9849	47	-0.8557	0.3965
Age: Mother feeds	-5.1601	7.1979	47	-0.7169	0.4770
Age: Mother rests	-4.9333	7.2411	47	-0.6813	0.4990

**Table 43:** Overall model tested for total daily solitary play bouts in relation to the mother's activity budget corrected by visibility. The model was not significantly better than the 0 model ( $\chi^2(14) = 19$ , p=0.06, AIC=560.6, N=70 of 15 individuals). It was also not better than the basic overall model tested for the play budget of immatures, which includes age, site, FAI and sex ( $\chi^2(14) = 5.96$ , p=0.43, AIC=560.6, N=70 of 15 individuals).

Overall immatures exhibit most solitary play, when their mother was feeding or resting (fig.47). Nonetheless, because these behaviours are also the most frequent behaviour in a typical orangutan activity budget, I compared the proportion of play bouts with a specific behaviour of the mother to the overall abundance of this behaviour in the mother's activity budget ("relative proportion of activity" =proportion of solitary play bouts with a specific activity of the mother/proportion of this activity in the activity budget of the mother). A relative activity abundance of 1 indicates an expected abundance of solitary play during the specific behaviour of the mother (fig.48).

Overall the activity ratios differed significantly from 1 ( $\chi^2(5)=17.03$ , p<0.001, AIC=297.59), indicating that there is a bias towards certain activities of the mother during which infants play more (tab.44). Yet, this tendency to play during specific activities changes over age, which is indicated by the significant activity age interaction.



**Figure 47:** Difference between the proportion of daily solitary play bouts during a specific behaviour of the mother and the mothers' daily activity proportion of this behaviour. The lines were added to the graph using the *loess*-function.



**Figure 48:** Ratio between the proportion of daily solitary play bouts during a specific behaviour of the mother and the mothers' daily activity proportion of this behaviour. The lines were added to the graph using the *loess*-function.



**Figure 49:** Total solitary play bouts by the offspring corrected by visibility (y-axis) in relation to the mother's activity budget (daily proportion of specific activity) (x-axis) and the offspring's age class (colours). One data point for each day and individual. The lines were added to the graph using the *lm*-function.

	Value	SE	DF	t	р
Intercept*	1.0111	0.1266	136	7.9863	0.0000*
Ratio activity M*	-0.7819	0.2314	136	-3.3798	0.0009*
Ratio activity R	0.1034	0.1875	136	0.5513	0.5824
Age	-0.0024	0.0024	136	-0.9725	0.3325
Ratio M : Age*	0.0171	0.0043	136	3.9860	0.0001*
Ratio R : Age*	0.0081	0.0038	136	2.1551	0.0329*

**Table 44:** Best fitting model for explaining ratios between the mother's actual activity budget and the proportion of solitary play bouts during specific activities of the mother ( $\chi^2(5)=17.03$ , p<0.001, AIC=297.59).

# 3.2.6.2 Distance to the mother

In the behavioural protocol, the distance to the mother is reported by distance classes (see method section 2.2.5.4). Therefore the analysis was conducted by average distance classes, and not by the averages of the absolute numbers of these classes (<0m, <2m, <5m, <10m, <50m). The distance to the mother during solitary play increased with increasing age (0.0516±0.0063, t<sub>61</sub>=8.16, p<0.0001, N=97 of 15 individuals). Moreover, the play type was component of the best fitting model ( $\chi^2$ (14)=82.8, p<0.0001, AIC=141.9, N=97 of 15 individuals). Namely, all the solitary play with a potential social component were closer to the

mother than the other play types (fig.50). Additionally, the model with the interaction between play class and age would have been even better ( $\chi^2(24)=136.24$ , p<0.0001, AIC=108.47, N=97 of 15 individuals). Yet, because of the low sample size for certain play types, I did not include the interaction in the table that is reported in this study (tab.45).

	Value	SE	DF	t	р
Intercept	1.7216	0.2206	71	7.8052	0.0000
Age *	0.0259	0.0031	71	8.2499	0.0000*
Play class AP nest	0.1942	0.2601	71	0.7463	0.4579
Play class APM	-0.3566	0.1863	71	-1.9140	0.0596
Play class APM combined	0.0916	0.2460	71	0.3724	0.7107
Play class APM/SP *	-1.0603	0.2923	71	-3.6267	0.0005*
Play class APO	-0.3558	0.1863	71	-1.9096	0.0602
Play class APO combined	-0.3291	0.1941	71	-1.6954	0.0944
Play class APO/APM	-0.3016	0.1881	71	-1.6038	0.1132
Play class APO/APM combined	-0.1619	0.2141	71	-0.7560	0.4522
Play class APO/APM/SP *	-1.2393	0.2484	71	-4.9881	0.0000*
Play class APO/SP *	-1.0182	0.2163	71	-4.7075	*00000

**Table 45:** Model output for the average distance (class) to the mother during solitary play ( $\chi^2(14)=82.8$ , p<0.0001, AIC=141.9, N=97 of 15 individuals). The play classes are all compared to the play class "AP display".

### 3.2.6.3 Party size

The absolute party size count did not alter hourly solitary play frequency (-0.3499±0.2312,  $t_6$ =-1.51, p=0.18, N=29 of 15 different individuals with 22 different ages). It was controlled for age in the analysis. There was also no site difference in average hourly solitary play frequency with increasing party size (-0.4543±0.5132,  $t_5$ =-0.89, p=0.42, N=29 of 15 different individuals with 22 different ages) (fig.51). The identity of the party members were not considered.



**Figure 50:** Distance to the mother during solitary play by age of the infant (months). The distance to the mother is given in classes: 1 = "0m", 2="< 2m", 3 ="<5m", 4="<10m", 5="<50m". One data point is the average of these classes by individual, its average age and play class. The lines were added to the graph using the *lm*-function.



**Figure 51:** Residuals of the average hourly solitary play bout count by age by the hourly party size. The party size count always includes mother and offspring. Hence a party size of 2 indicates that only the mother and the offspring were present. All data points are illustrated as jittered points around the boxplot.

# **3.3 Details on social play**

For the analysis, social play bouts were subdivided according to dyad type: mother-offspring, sibling or associate play. For subsequent analyses, associate play was further subdivided according to age differences and age classes of the players.

# 3.3.1 Social play duration

Overall play bouts of associate play partners lasted longer than sibling and mother-offspring play ( $\chi^2(6)=6.02$ , p<0.05, AIC=654, N=126 of 18 individuals with 48 partners). There was no overall difference in play duration between Tuanan and Suaq Balimbing and thus, adding the site did not improve the model significantly ( $\chi^2(7)=0.88$ , p=0.34, AIC=655, N=126 of 18 individuals with 48 partners) (tab.46). Play duration also did not vary with focal age and thereby, age did not improve the model either ( $\chi^2(7)=0.47$ , p=0.49, AIC = 737.44, N=126 of 18 individuals with 48 partners).

	Value	SE	DF	t	р
Intercept*	4.0281	0.5774	77	6.9758	0.0000*
Mother*	-1.5195	0.6186	29	-2.4565	0.0203*
Sibling	-1.6268	0.8315	77	-1.9565	0.0540
Site Tuanan	0.5233	0.5652	16	0.9259	0.3683

**Table 46:** Model output of average play bout duration by dyad type and Site ( $\chi^2(7)$ =6.9, p=0.075, AIC=655, N=126 of 18 individuals with 48 partners).

# 3.3.2 Participation and age difference

The absolute participation difference between the two players increased with increasing age difference ( $\chi^2(5)=51.19$ , p<0.0001, AIC = 124.25, N=44 of 17 individuals with 24 partners) Neither site nor dyad type further improved the model for the absolute participation difference. Moreover, there were also no interactions between the components. However, because there were missing data in the social play all-occurrence report, this analysis was repeated with the video data of which all the participation scores were present.

# 3.3.3 Play Index

The Play Index (=total time spent playing per total time in association) revealed the same pattern as the average play bout duration. Namely, generally higher Play Indices for associate dyads than for sibling and mother-offspring dyads. Because the mother and siblings are in constant association with very young infants, the Play Index is lower than for associate play  $(\chi^2(6)=23.04, p<0.0001, AIC=27, N=112 \text{ of } 19 \text{ individuals with } 47 \text{ partners}) (fig.52).$ Moreover, in Tuanan Play Indices were generally higher than in Suaq Balimbing  $(\chi^2(9)=30.69, p<0.0001, AIC=25.8, N=112 \text{ of } 19 \text{ individuals with } 47 \text{ partners}) (tab.47).$ However, this difference was mainly mediated by the interaction between site and dyad type. Play among associates in Tuanan was characterised by significantly higher Play Indices than when playing with the mothers compared to Suaq Balimbing and the same tendency could be seen for sibling play, too.

	Value	SE	DF	t	р
Intercept*	0.5035	0.0871	64	5.7805	0.0000*
Dyad type mother*	-0.2652	0.1239	25	-2.1397	0.0423*
Dyad type sibling	-0.2127	0.1313	64	-1.6194	0.1103
Site Tuanan *	0.3307	0.1184	17	2.7928	0.0125*
Dyad type mother: Site Tuanan *	-0.3443	0.1608	25	-2.1412	0.0422*
Dyad type sibling: Site Tuanan	-0.3037	0.1804	25	-1.6833	0.1048

**Table 47:** Complete model of Play Index by dyad type and site ( $\chi^2(9)=30.69$ , p<0.0001, AIC=25.8, N=112 of 19 individuals with 47 partners)





Figure 52: Play Indices per dyad (total play time per association time) in respect to dyad type (associates, mother-offspring play and sibling play) and site (red: Suaq Balimbing, blue: Tuanan). Data points are averages per dyad.

**Figure 53:** Play Index of associate play in relation to their absolute age class difference (x-axis) and across the two sites (red: Suaq Balimbing, blue: Tuanan). Data points are averages per dyad. The lines were added to the graph using the *glm*-function.

When only considering Play Indices from associate play, there was a trend of more play per association in Tuanan in infants (2 -4 y) and juveniles ( $\sim 7 - 9/10$  y) compared to Suaq Balimbing. Only the age classes available at both sites were put into a model. Focal identity nested in play partner identity was set as a random factor. The model with site only was the only model which was significantly better than the 0 model ( $\chi^2(5)=4$ , p<0.05, AIC=45.13, N=34 of 12 different individuals with 24 play partners) (tab.48).

	Value	SE	DF	t	р
Intercept	0.5197	0.1083	8	4.8003	0.0014
Focal age class infant	0.1638	0.1636	4	1.0017	0.3732
Focal age class juvenile	-0.3683	0.2292	4	-1.6068	0.1834
Site Tuanan	-0.2519	0.3056	4	-0.8242	0.4561
Focal age class infant: Site Tuanan	0.7907	0.3721	4	2.1249	0.1008
Focal age class juvenile: Site Tuanan	1.0630	0.3932	4	2.7034	0.0539

**Table 48:** Complete model for Play Indices of associate play ( $\chi^2(9)$ = 8.2, p<0.05, AIC=18.9, , N=34 of 12 different individuals with 24 play partners).



**Figure 54:** Play Indices of the three different dyad types by the participation difference between players. Data points are daily Play Indices by averages of daily participation differences. a) all data is included, b) only data points with 50% or more bouts of known participation scores. The lines were added to the graph using the *glm*-function.

There seemed to be a trend of lower average participation differences with higher Play Indices (fig.54). Unfortunately, most of the data points with high Play Indices did not contain the minimum of 50% known participation levels. As soon as the data was limited to the most complete data points only, there was no trend anymore of high Play Indices with low participation differences between players, in neither associate nor sibling and mother play. However, I will get back to this relationship in the video analysis section.

Play Indices did not change with varying Fruit Availability Indices (FAI). To see if fruit availability affected the "playfulness" of an association or in general the energy for play, the Play Index was compared across different FAIs within different dyad types (mother-offspring, sibling and associate play) (fig.55). Models were set up with FAI as a fixed effect and focal identity and focal age as random effects. Play Indices were transformed with arcsin-square-root transformations.

Play Indices were not affected by FAI in neither mother-offspring ( $\chi^2(5)=1.58$ , p=0.21, estimate<sub>FAI</sub>= 0.007 ± 0.005, t<sub>2</sub>=1.23, p=0.34), sibling-play ( $\chi^2(4)=0.18$ , p=0.67, N=16 of 9 IDs, estimate<sub>FAI</sub>= 0.005 ± 0.012, t<sub>6</sub>=0.4, p=0.7) nor associate play ( $\chi^2(4)=1.33$ , p=0.25, N=30 of 12 IDs, estimate<sub>FAI</sub>=-0.025 ± 0.022, t<sub>17</sub>=-1.16, p=0.26).


**Figure 55:** Daily Play Indices by monthly Fruit Availability Indices (FAI) for mother-offspring (a), sibling (b) and associate dyads (c) and across the two sites (red: Suaq Balimbing, blue: Tuanan). Data points are averages per dyad and monthly FAI. The lines were added to the graph using the *lm*-function.

## **3.3.4 Hinde Index of play – Intiation and termination**

The Play Hinde Index (PHI) was defined to describe the balance between players (+1: play initiated by focal and terminated by partner, -1: opposite). The model with the dyad type was significantly better than the 0 model ( $\chi^2(6)=6.3$ , p<0.05, AIC=108.96, N=60 of 18 different focal individuals and 43 different play partners) (fig.56a). Focal identity nested in play partners was taken as random factor. There was neither a significant site difference nor an interaction between site and dyad type ( $\chi^2(7)=6.3$ , p=0.098, AIC=110.96 (repeated-measures ANOVA: F<sub>1,16</sub>=0.00, p=0.98);  $\chi^2(9)=10.54$ , p=0.06, AIC=110.73 (repeated-measures ANOVA: F<sub>2,23</sub>=2.00, p=0.16).

Compared to associate play, the Hinde Index of the younger siblings during sibling play was significantly higher and tended to be higher in mother play, too (tab.50).

	Value	SE	DF	t	р
Intercept	-0.0334	0.2096	22	-0.1593	0.8749
Dyad type mother*	0.6085	0.2710	22	2.2457	0.0351*
Dyad type sibling	0.3943	0.2884	16	1.3673	0.1904
Location Tuanan	0.1363	0.2660	16	0.5125	0.6153
Dyad type mother: Site Tuanan	-0.5366	0.3389	22	-1.5833	0.1276
Dyad type sibling: Site Tuanan	0.1791	0.3775	22	0.4745	0.6398

**Table 49:** Complete model for the focals' Hinde Indices in respect to partner type and site (for mother and sibling play always the dependent infant was taken as focal individual) ( $\chi^2$  (9)=10.54, p=0.06, AIC=110.73, N=60 of 18 different focal individuals and 43 different play partners).

	Value	SE	DF	t	р
Intercept	0.0534	0.1270	24	0.4201	0.6781
Dyad type mother	0.2534	0.1657	24	1.5287	0.1394
Dyad type sibling*	0.4918	0.1895	16	2.5955	0.0195*

**Table 50:** Best fitting model for the focals' Hinde Indices in respect to partner type (for mother and sibling play always the dependent infant was taken as focal individual) ( $\chi^2(6)=6.3$ , p<0.05, AIC=108.96, N=60 of 18 different focal individuals and 43 different play partners).

This difference could possibly have been attributed to age differences and the younger individuals tending to be more likely to initiate play. Yet, when looking at the focals' Hinde Index in respect to age difference between associate play partners, no correlation could be

found (fig.56b). Neither the absolute age difference nor the age class difference significantly improved the 0 model for the Hinde Indices of associate play (absolute age difference:  $\chi^2(5)=1.87$ , p=0.17, AIC=52.78; age class difference:  $\chi^2(6)=2.46$ , p=0.29, AIC=55.99, N=26 of 10 different focal individuals and 23 different play partners).



**Figure 56:** Play Hinde Index by a) Type of play partner, b) age class difference between the players (focal age class – partner age class), c) Party initiator and d) Party terminator. The Play Hinde Index was calculated for each play dyad. All data points are illustrated as jittered points around the boxplot.

Not enough data were available to test if the party initiator exhibited a higher or, respectively, the party terminator a lower Play Hinde Index (fig.56c+d). Neither the focals' participation nor the participation score difference revealed clear patterns with the Play Hinde Index. This could also be due to the low sample size for reliable Play Hinde Indices of associate play (N=26).

The absolute Play Hinde Index, which I took as a measure of equal interest in play (0) or onesided interest in play (1), did not predict the playfulness of an association (Play Index) (estimate<sub>PHI</sub>=0.009±0.071,  $t_{42}$ =0.13, p=0.89, N=81 of 18 individuals with 38 different partners) (fig.57). Also when omitting mother and sibling play which are often one-sided, there was no pattern of more play among associates with a more balanced (0) Play Hinde Index (estimate<sub>PHI</sub>=0.183±0.136,  $t_6$ =1.34, p=0.23, N=22 of 10 individuals with 17 different partners).



**Figure 57:** Play Index by absolute Play Hinde Index among a dyad. The dyad type is represented in colours (red: associates, green: mother; blue: siblings). The lines were added to the graph using the *loess*-function.



**Figure 58:** Initiations among mother-offspring play dyads per full-day follows. The offspring is represented in green the mothers in blue. The lines were added to the graph using the *loess*-function.

### 3.3.4.1 Initiations during mother-offspring play

Infant age, initiator identity and the interaction between the two best predicted the initiation proportion during mother-offspring play ( $\chi^2(6)=29.62$ , p < 0.0001, AIC=-16.31, N=66 of 17 different mother-offspring pairs). The model with additionally site and sex was also better than the 0 model ( $\chi^2(10) = 34.5$ , p<0.0001, AIC=-17.2), but not better than the aforementioned model. The infants were more likely to initiate play with their mothers than vice versa (tab.51, fig.58). Yet, Kondor was the exception and initiated play with Kahiyu (infant) more often. There was a peak of play initiations by the infant just after 20 months of age (fig.58).

	Value	SE	DF	t	р
Intercept	0.0205	0.0789	44	0.2596	0.7964
Initiation Infant	0.4871	0.1116	44	4.3662	0.0001
Initiation Mother	0.1245	0.1116	44	1.1157	0.2706
Age	-0.0003	0.0013	44	-0.2024	0.8405
Initiation Infant: Age	-0.0052	0.0019	44	-2.7575	0.0085
Initiation mother : Age	-0.0014	0.0019	44	-0.7175	0.4769

**Table 51:** Best fitting model for proportion of initiations ( $\chi^2(6)=29.62$ , p < 0.0001, AIC=-16.31, N=66 of 17 different mother-offspring pairs.)

### 3.3.4.2 Initiations during sibling play

What was already shown by the Play Hinde Index, younger siblings initiated play significantly more often with their older sibling than vice versa ( $F_{1,7}$ =8.68, p<0.05, focal identity was taken as random effect). Thus, the best fitting model for describing initiation proportions during sibling play was with age difference only ( $\chi^2(4)$ =6.38, p<0.05) (fig.59). Neither site ( $F_{1,9}$ =0.23, p=0.64) nor focal age ( $F_{1,6}$ =0.578, p=0.476) affected the proportion of initiation by the younger, respectively the older sibling.

No such pattern could be observed for play termination. Older and younger siblings exhibited an equal proportion of play termination ( $F_{1,3}=1.27$ , p=0.34).

Moreover, play bouts tended to last longer if the older sibling had initiated play (random effect: focal identity,  $F_{1,59}$ =3.89, p=0.053) (fig.60). For this analysis, the play duration was log-transformed, but the residuals did still not perfectly fit a normal distribution.



**Figure 59:** Initiation proportion by either the older or the younger sibling during sibling play.



**Figure 60:** Social play duration (in 2-min bouts) depending on the play initiatior during sibling play (younger or older sibling)

# 3.3.5 Playface presence during social play

Playful expressions were observered at both sites, Tuanan and Suaq Balimbing. Only in Suaq Balimbing, vocalisations ("play ohh") were heard during social play. Thus, only the playface presence during social play was assessed and this was done in two different ways. On the one hand, I calculated the proportion of play bouts with playfaces present on a dyad level to assess if there were any age, dyad or other overall patterns. On the other hand, I performed generalized linear mixed models (GLMMs) to evaluate possible reasons for playface presence on the level of single play bouts. In all the analyses focal and partner identity were included as random effects.

The proportion of play bouts with playfaces present did not change over age ( $F_{1,22}$ =0.74, p=0.3999, N=52 of 12 individuals and 29 different play partners). The absence of any age effect on playface presence remained, when excluding the data points of which more than 50% of the recorded play bouts did not have information on playfaces ( $F_{1,6}$ =0.078, p=0.7898, N=17 of 8 individuals and 10 different play partners).

Also the dyad type (mother-offspring, sibling or associate play) did not affect the playface presence significantly ( $\chi^2(5)=0.649$ , p=0.72, AIC=69.37, N=17 of 8 different individuals). Yet, by using the entire data set without the exclusion of the more than 50% unknown playface data points, the dyad type tended to improve the model for focal playface presence proportion ( $\chi^2(5)=5.39$ , p=0.052, AIC=183.74, N=52 of 12 different individuals). There was a trend of lower playface presence proportions during mother and sibling play than during associates play.

Within play bouts, the play duration (in 2-min bouts), the focals' participation score and the presence of play bites by the focal best explained the presence or absence of playfaces ( $\chi^2(5)=97.17$ , p <0.0001, N=67 of 12 different focal individuals) (tab.52, fig.61-64). Because of the low sample size, the model components had to be added according to a hierarchical method and could not be tested by forced entry methods. Adding the focals' or the partners' age, age differences between the players, the partners' participation score, the partners' playface presence or absence (fig.63), visibility (fig.61), site (fig.62) or relatedness to the model did not wield any improvement of the model.

	Estimate	SE	Z	р
Intercept	-6.1128	2.5683	-2.38	0.0173
Duration (in 2-min bouts)	0.8135	0.6128	1.327	0.1843
Average participation focal	1.4304	1.0890	1.313	0.1890
Presence of play bites by focal	3.5866	2.0413	1.757	0.0789

**Table 52:** Best fitting model (GLMM) for explaining playface presence on the play bout level ( $\chi^2(5)=97.17$ , p <0.0001, N=67 of 12 different focal individuals)



**Figure 61:** Social play duration by different visibility scores and playface presence of the focal. Data points are individual play bouts. The lines were added to the graph using the *loess*-function.



Figure 62: Playface presence or absence by play duration and site. Data points are individual play bouts.



FALSE

Figure 63: Social play duration (in 2-min bouts) by focal and partner playface presence. Data points are individual play bouts. All data points are illustrated as jittered points around the boxplot.

**Figure 64:** Playface (y-axis) and playbite (colours) presence by focal and focal participation scores (x-axis). Data points are individual play bouts.

## 3.3.6 Context of social play

#### 3.3.6.1 Distance to the mother

Play among associates mostly happened closer to the younger player's mother (fig.65). When setting up the model for distance difference between the two mothers, focal age class and the age difference between the two players composed the best fit ( $\chi^2(9)=16.71$ , p <0.001, AIC=354.17, N=113 of 9 different focal individuals and 13 partners) (tab.53).

	Value	SE	DF	t	р
Intercept	0.5792	1.2551	96	0.4614	0.6455
Partner older	0.9042	1.1774	96	0.7680	0.4444
Same aged (within 3 y)	1.0638	1.1077	96	0.9603	0.3393
Focal age class Infant *	-2.8708	0.7695	7	-3.7306	0.0074*
Focal age class Immature *	-1.6122	0.7808	96	-2.0649	0.0416*
Focal age class Juvenile	-0.5461	0.7995	96	-0.6831	0.4962

**Table 53:** Best fitting model for explaining the distance difference between the players' mother ( $\chi^2(9)=16.71$ , p <0.001, AIC=354.17, N=113 of 9 different focal individuals and 13 partners).





Figure 65: Distance difference between the focal's and the partner's mother in respect to the age differenct between the two players (colours) and the focals' age class. Data points are individual play bouts. Positive distance differences mean the players are closer to the focal's mother.

**Figure 66:** Average distance to the mother while social play by focal age and site. Distances are in classes, 0 corresponds to 0m, 13 to 50m. The lines were added to the graph using the *lm*-function.

When considering all the play bouts and the distance to the focal's mother, the distance to the focal's mother was best explained by the age of the focal only ( $\chi^2(4)=10.62$ , p=0.001) (fig.66). Age difference between the players, play partner age class, site, and relatedness did not result in a better fitting model ( $\chi^2(11)=17.41$ , p<0.05) than the model with focal age as fixed effect and focal identity as a random effect (fig.67). The distance of the mother to the playing offspring significantly increased with focal age (estimate<sub>age</sub>=0.019±0.005, t<sub>23</sub>=3.79, p=0.001, N=35, gr=11) (tab.54).

	Value	SE	DF	t	р
Intercept *	2.6235	0.6098	16	4.3021	0.0005*
Focal age	0.0062	0.0100	16	0.6167	0.5461
Age difference	0.0112	0.0086	16	1.3014	0.2115
Partner class infant	0.5970	0.7204	16	0.8287	0.4194
Partner class immature	1.1127	0.7189	16	1.5477	0.1413
Partner class juvenile	1.5038	0.9477	16	1.5868	0.1321
Partner class mother	3.9872	2.6649	16	1.4962	0.1541
Partner class unflanged	1.7955	1.7769	16	1.0105	0.3273
Same matriline TRUE	- 0.9068	0.4589	16	-1.9761	0.0656

**Table 54:** Complete tested model to evaluate the distance to the focals' mother during social play ( $\chi^2(11)=17.41$ , p<0.05, N=35 of 11 different individuals)



Figure 67: Proportion of play bouts with specific distance to the younger (a), same aged (b) and the older (c) players' mother.

The partners' identity did not seem to have an impact on the distance to the mother. Moreover, the proximity of the mother connected with the partner type did not affect the playface presence in the play partner ( $\chi^2(8)=3.93$ , p=0.41).

When considering the mothers' change of distance to the players in respect to age difference between the players, no clear pattern emerged (fig.68). The mother mostly maintained the same distance during play.



**Figure 68:** Distance change by the mother during social play of the offspring divided by play with peers (within at most 1 age class difference) (a), with older play partners (b) and with younger play partners (c).

#### 3.3.6.2 Activity of the mother



**Figure 69:** Proportion of play bouts with different types of activities by the mother (move, social, stationary) by focal age. Data points are averages by dyad (only associate play). The lines were added to the graph using the glm-function.

The mothers' activities were also looked at according to distance changes. Feeding and Resting were stationary activities, while moving and social activities were put each into separate categories. Stationary activities of the mothers were generally most prevalent during social play, but slightly decreased with offspring age (fig.69). In contrast, mothers tended to move more often with increasing offspring age (0.0076  $\pm 0.0043$ , t<sub>7</sub>=1.73, p=0.12, N=13 of 5 differenct individuals). Social activities occurred only at a very low rate and therefore were not further analysed.

# 3.4 Video data

The video coding was mainly done to have a more detailed picture of the nature and abundance of play elements such as playfaces, play bites, holding, hitting, checking etc. of varying play dyads. Unfortunately, not all the videos available could be matched with the exact play bout of the focal follow data and thereby only the Play Index and the Play Hinde Index, which are a characteristics of the overall association, could be matched to the videos, but not the distances to the players' mothers. Generally, the younger player was taken as the focal individual during video coding.

Because I could assess all the play components including the participation scores directly from the video, I repeated some of the analyses which I already had conducted with the focal follow data.

### 3.4.1 Participation and age difference

The greater the age difference between the two players was, the higher was the participation difference (fig.70). For the analysis the partner age class "infants" was excluded, because I only had 3 data points for this partner age class. Participation differences were best explained by the absolute age difference between the players and the partner age class and the interaction between the two ( $\chi^2(15)=74.33$ , p<0.0001, AIC=149.3, N=80 of 19 different individuals with 48 different partners) (tab.55).

	Value	SE	DF	t	р
Intercept	-0.3839	0.2155	29	-1.7810	0.0854
Age difference *	-0.0096	0.0031	23	-3.1225	0.0048*
Partner age class juvenile	-0.0275	0.5706	23	-0.0482	0.9619
Partner age class adolescent	0.5783	0.5174	23	1.1178	0.2752
Partner age class unflanged	-0.0706	0.4400	23	-0.1604	0.8739
Partner age class mother	0.7246	0.3771	23	1.9217	0.0671
Age difference: juvenile	-0.0003	0.0084	23	-0.0368	0.9709
Age difference:adolescent	0.0144	0.0076	23	1.8863	0.0719
Age difference:unflanged *	-0.0153	0.0057	23	-2.6636	0.0139*
Age difference:mother *	0.0148	0.0051	23	2.8833	0.0084*

**Table 55:** Best fitting model for participation differences between two players within a dyad ( $\chi^2(15)=74.33$ , p<0.0001, AIC=149.3, N=80 of 19 different individuals with 48 different partners



**Figure 70:** Average participation score difference between the players in respect to their age difference (focal age – partner age). The age partner is in colours. Data points are averages per dyad. The lines were added to the graph using the *lm*-function.

### 3.4.2 Playfaces

Because of the noisy jungle sounds and the varying quality of video recordings, I could not reliably assess the presence or absence of playful vocalisations during the video coding. Thus, also in the video data, the playful expression analysis was limited to playfaces. Playface occurrence during social play was assessed using playface counts, which were corrected by the play bout duration during which the face was visible.

$$Playface rate = \frac{Playface count}{visible play s} = \frac{Playface count}{(play duration (frames)*proportion of face visible during play)/30}$$

For the playface rate analysis, small and full playfaces were lumped.

When playfaces were corrected by face visibility, there was still a significant difference between different visibilities (0 - 3) of the players (H<sub>3</sub>= 9.34, p < 0.05). However, after post hoc tests, no significant difference between any visibility category and playface rate could be detected anymores.

Playface rates were analysed at a dyad, as well as, at a bout level. To avoid pseudoreplication, in both cases the two players' (focal and partner) identities were included as random factors in all analyses.

Because the video material available for specific dyads varied greatly, the influence of video material amount on recorded playface frequency was analysed. There was no correlation between the amount of available play bouts from the video analyses and the playface rates (playface/visible play second) neither in the focal animal ( $F_{1,81}$ =0.10, p=0.75, R<sup>2</sup>=-0.01) nor the play partner ( $F_{1.78}$ =0.38, p=0.54, R<sup>2</sup>= -0.01).

#### 3.4.2.1 Distribution of playfaces across play course

To assess when playfaces occur during play, only the videos with complete play bouts were considered. I could use 54 different play bouts where a total of 245 small and full playfaces were seen. The time when a playface occurred was divided by the total play duration, in order to get a *relative position of the event* within play bouts. In this manner, all play bouts of different lengths could be lumped together. Playface distribution over the play course did not significantly deviate from a uniform distribution ( $\chi^2(248)=37.48$ , p=1) (fig.71).



Figure 71: Playface occurrences by both play partners through out the play course. 0 corresponds to the play start and 1 to the play end (N=54 play bouts with 245 playfaces).

**Figure 72:** Playface frequency per visible second by focal by play duration (s). Each data point is a separate complete play bout (N=111). The lines were added to the graph using the *lm*-function.

## 3.4.2.2 Playfaces and play duration

Play with playfaces by the younger individual was significantly longer than without playfaces  $(53.4\pm 9.9 \text{ s}, t_{80}=5.41, p=0, N=111 \text{ of } 14 \text{ individuals with } 30 \text{ different play partners})$ ( $\chi^2(5)=26.37, p<0.0001, AIC=1197.43$ ) (fig.72). Playface display by the older partner did not have an impact on play duration and the model including playface presence or absence by the play partner did not improve compared to the model with focal playfaces only ( $\chi^2(6)=0.09, p=0.77, AIC=1199.34$ ). Yet, also playface rates significantly increased with increasing play bout duration  $(0.0012 \pm 0.0004, t_{50}=3.35, p=0.002)$  ( $\chi^2(5)=10.74, p=0.001, AIC=-36.1, N=74$  of 14 individuals with 23 different play partners). This tendency did not differ among sites, neither adding site ( $\chi^2(6)$  =2.67, p=0.1, AIC= -36.8) nor the interaction between duration and site ( $\chi^2(7)$  =4.9, p=0.09, AIC= -37.02) improved the model with duration only.

#### 3.4.2.3 Average playface rates among dyads

The average playface rate of the younger play participant was best modelled by its age, the partner's age class and the interaction between the two (focal age and partner age class)  $(\chi^2(15)=30.8, p=0.001, AIC=106.29, N=75 \text{ of } 18 \text{ individuals with } 39 \text{ different play partners}).$  Overall, only the play partners' age class and the interaction between partner age class and focal age significantly affected the playface rate (F<sub>5,24</sub>=3.76, p=0.01; F<sub>5,24</sub>=2.7, p<0.05). However, no separate component of the model (i.e. specific partner age class) had a significant effect on playface rates (fig.75, fig.76). Moreover, there was no significant playface rate variation among sites, varying Play Indices and participation differences and thus, these factors did not improve the playface rate model.

Alternatively, playface rate could also be explained by the dyad type, i.e. mother-, sibling- or associate-play ( $\chi^2(6)=14.01$ , p<0.001, AIC=105.1) (fig.73). Yet, the aforementioned model with focal age and partner age class was almost significantly better ( $\chi^2(15)=16.8$ , p=0.052, AIC=106.29). One reason which might explain the importance of dyad type is that playface rates were significantly lower when playing with the mother than with somebody else.



**Figure 73:** Focal playface frequency per visible second by the dyad type and the age difference between players. Data points are average playface frequencies on a daily play dyad basis.



Figure 74: Play partner playface frequency per visible second by the dyad type and the age difference between players. Data points are average playface frequencies on a daily play dyad basis.



**Figure 75:** Focal playface frequency per visible second by the age class of the two players (x-axis: focal age class, and colours for the partners' age class). Data points are average playface frequencies on a daily play dyad basis. Only associate play dyads are represented in this graph (no sibling and no mother-offspring play). All data points are illustrated as jittered points around the boxplot.



**Figure 76:** Focal playface frequency per visible second by the focal's age class and the age difference of the players (x-axis: focal age class, and colours for the age difference (the darker the colour, the larger the age difference). Data points are average playface frequencies on a daily play dyad basis. Only associate play dyads are represented in this graph (no sibling and no mother-offspring play). All data points are illustrated as jittered points around the boxplot.

#### 3.4.2.4 Individual playface frequencies

#### Playfaces of younger focal individual

In the second analysis, I also considered play elements, which could co-occur/correlate with playface display of the focal. Because the videos varied largely in length and quality, I decided to take daily averages of the play elements, rather than single play bouts. This could result in a loss of resolution.

Corresponding to the previous finding, immatures made more playfaces when playing with their siblings or associates than when playing with their mothers (estimate<sub>mothers</sub>= -0.4918± 0.1282, t<sub>30</sub>=-3.84, p<0.01). Moreover playface frequency increased significantly with increasing overall holding duration during play (longer grabbing bouts) (0.5067±0.2043, t<sub>33</sub>=2.48, p<0.05). The best fitting model ( $\chi^2(8)=23.3$ , p<0.0001, N=87 of 19 focal individuals and 51 play partners) for playface frequency included additionally partner playface frequency, which did not significantly affect playface frequency in the focal, but showed a trend to increase with increasing frequencies in the focal (tab.56, fig.77).

	Value	SE	DF	t	р
Intercept *	0.4257	0.1693	33	2.5150	0.0170*
Partner type mother *	-0.4918	0.1282	30	-3.8373	0.0006*
Partner type sibling	0.0000	0.1573	30	-0.0003	0.9998
Playface partner	0.5357	0.3289	33	1.6287	0.1129
Focal active hold duration *	0.5067	0.2043	33	2.4798	0.0184*
Focal age	-0.0017	0.0018	33	-0.9598	0.3442

**Table 56:** Best fitting model for focal playface frequency ( $\chi^2(8)=23.3$ , p<0.0001, N=87 of 19 focal individuals and 51 play partners).

The playface frequency during mother-offspring play did not increase with increasing holding duration (fig.78). Yet, when adding an interaction between holding proportion and partner type, the model was only close to significantly better than the aforementioned model ( $\chi^2(10)=5.94$ , p=0.05). However the diagnostic plots looked better for the first model.



**Figure 77:** Relation between playface frequency per visible second of the two players. Data points are average playface frequencies on a daily play dyad basis.



**Figure 78:** Relation between active holding and playface frequency per visible second by the focal. Data points are averages of playface frequencies and active holding proportion on a daily play dyad basis. The lines were added to the graph using the *glm*-function.

#### Playfaces of older play partner

The model with partner age class, focal age, the interaction between the two and the proportion of play bites by the partner best explained playface frequencies by the (older) play partner ( $\chi^2(16)=57.77$ , p<0.0001, AIC=85.37, N=83 of 19 individuals and 51 different play partners). The ANOVA for all components was very significant. However within the model only the increasing partner playface frequency with focal age and the partners' play bite rates were significant (tab.57).

	Value	SE	DF	t	р
Intercept	0.1160	0.1257	32	0.9222	0.3633
Immature	0.2754	0.3252	20	0.8466	0.4072
Juvenile	-0.4757	0.3199	20	-1.4868	0.1527
Adolescent	-0.3845	0.2873	20	-1.3384	0.1958
Unflanged	-0.3555	0.2623	20	-1.3557	0.1903
Mother	0.1659	0.2670	20	0.6211	0.5416
Focal age *	0.0156	0.0068	20	2.2938	0.0328*
Partner play bites *	22.8221	8.0527	20	2.8341	0.0103*
Immature: Focal age	-0.0374	0.0236	20	-1.5825	0.1292
Juvenile: Focal age	0.0296	0.0216	20	1.3717	0.1853
Adolescent: Focal age	0.0005	0.0151	20	0.0324	0.9745
Unflanged: Focal age	0.0052	0.0086	20	0.5977	0.5568
Mother: Focal age	0.0016	0.0047	20	0.3370	0.7396

**Table 57:** Best fitting model for the older players' playface display frequency ( $\chi^2(16) = 57.77$ , p <0.0001, AIC = 85.37, N=83 with 19 focals and 51 different play partners)

#### 3.4.2.5 Playfaces during mother-offspring play

In Suaq Balimbing, the offspring already displayed playfaces at very young age, when playing with their mothers, whereas in Tuanan only later on, infants made playfaces when playing with their mothers (fig.79). There was no significant difference between the variance of the offsprings' playface frequency across site ( $F_{1,7}=0.5126$ , p=0.50, N=9). Because I took individual averages and the individuals were not represented twice in the data set, a normal linear model was conducted and the model with site, focal age and the interaction between these two was the best model ( $F_{3,5}=8.23$ , p<0.05, R<sup>2</sup>=0.73, N=9) (tab.58). The playface frequency by mothers when playing with their offspring was generally close to 0 (fig.80).

	Estimate	SE	t	р
Intercept *	0.066	0.014	4.862	0.005 *
Site Tuanan *	-0.099	0.021	-4.76	0.005 *
Offspring age	-0.001	0.001	-1.855	0.123
Site Tuanan: offspring age *	0.003	0.001	3.825	0.012 *

**Table 58:** Best fitting model for explaining the offsprings' playface frequency per visible second when playing with its mother ( $F_{3,5}=8.23$ , p<0.05, R<sup>2</sup>=0.73, N=9)



**Figure 79:** Playface frequency by offspring when playing with the mother by offspring age (months) (x-axis) and site (red:Suaq Balimbing, blue:Tuanan). Data points are average of each individual (by average age). The lines were added to the graph using the *glm*-function.



**Figure 80:** Playface frequency by mothers when playing with their offspring in relation to the offsprings' age (x-axis) and the site (red: Suaq Balimbing, blue: Tuanan). Juni is the outlier on the top right, when playing with Jip on the ground.

#### 3.4.2.6 Playfaces during sibling play

Tuanan infants seemed to display playfaces more frequently when playing with their older sibling than in Suaq Balimbing, however this trend was not significant (W=1, p=0.27, N=6) (fig.81a). Unfortunately, only a very small sample size was available (Suaq: N=4: Simba, Frankie, Rendang, Lois; Tuanan: N=2 Jane, Mawas (and Mawas a lot older)). However the older siblings did not show any difference between displaying playfaces at their younger sibling while playing (W=3, p=0.8057, N=6) (fig.81b).

I also set up a linear mixed model in order to avoid pseudo-replication by having Mawas twice in the data set. The model with site, age and the interaction between the two was the best model ( $\chi^2(6)=11.68$ , p<0.05, AIC=26.9, N=8 of 7 different individuals). However, the exact output could not be displayed.



**Figure 81:** Average playfaces per visible play second by the younger (a) and the older (b) sibling when playing with each other in relation to the younger siblings age (x-axis) and site (red: Suaq Balimbing, blue: Tuanan). Data points are averages of eache individual by ist average age by age class. Mawas is twice in the plot, once as infant and once as immature. The lines were added to the graph using the *glm*-function.

# **3.5 Summary table of results**

Play type	Data set	What	Age	Site	FAI	Sex	Age: Site	Remarks
APO	2-min scan data	Daily	<b>N</b> *	×	×	×	S <t *<="" td=""><td></td></t>	
	selected observers	proportion						
(solitary		Daily prop.	<b>\</b> *	×	×	×	×	
object		obj. man.						
play)		Bouts/	<b>\</b> *	×	×	×	×	
		visible h						
		Duration	<b>N</b> *	×	×	×	×	
		of bout	_					
		Detached	<b>7</b> ∗	×	×	×	×	
	All-occurrence	obj. prop.		~				Duration A <sup>ns</sup> with
		SUCK	x	×	x	x	×	$\frac{Duration}{T}$ with
		Leave	<b>\</b> *	~	~	~	~	SUCK
		proportion		^	^	^	^	
		Multiple	N ns	×	x	x	×	
		obi, prop.		~	~	~	~	
	All-occurrence	Obj. man.	7*	×	×	x	×	
	only Tuanan	per second	• /					
APM	2-min scan	Daily	<b>N</b> *	×	×	x	×	
	selected observers	proportion						
(solitary		Bouts/	<b>↑</b> <sup>ns</sup>	×	×	×	x	
loco-		visible h	(3y)					
motor	All-occurrence	Duration	<b>\</b> *	×	×	×	×	
play)		of bout						
		Whole	7*	×	×	×	×	
	4 11	body	<b>—</b>					
	All-occurrence	Locomotor		×	×	×	×	
Salitany	Tuenen 2002 2014	patterns/s	<b>A</b> 14	NLA			NI A	No individual
Sontary play	selected observers	proportion	$\mathbf{T}^*$	INA	×	×	INA	differences
piay	selected observers	Playface	(Jy)	~	~	~	~	uniciclices
	All-occurrence	occurrence		^	^	~	^	
	without Lois	Plavface	<b>N</b> *	×	×	x	x	
		frequency						
	All-occurrence	Playface	7*	×	×	x	S>T *	Lois is outlier
	with Lois	frequency						
Mixed		APO-APM	<b>↑</b> <sup>ns</sup>	×	×	×	x	
solitary		bouts/h	(3y)					
play	All-occurrence	APO-TF	<b>N</b> ns	×	×	×	×	
		bouts/h	<b>A</b> 100					
		AP nest	$\mathbf{\Lambda}^{\text{ns}}$	×	×	×	×	ns, only graph(fig.34)
SP	2-min scan	Daily	N*	S>T	x	x	S>T *	
	selected observers	proportion		*				
(Social	Tuanan 2003-2014	Daily	<b>→</b> <sup>3</sup>	NA	×	×	NA	Individual differences
play)	selected observers	proportion	*					
	All-occurrence	Play Index	×	S <t< td=""><td>×</td><td>×</td><td>×</td><td></td></t<>	×	×	×	
		-		*				
	2-min scan	Play within	×	×	NA	NA	×	Play Index, kinship &
	selected observers	association						party identity crucial
Associa-	2-min scan	All parties	7*	S>T	NA	NA	×	Party identity crucial
tion	selected observers	1	1	*	1			

**Table 59:** Summary of the main results tested for effects of age, site, FAI and sex. Signs:  $\neg$ =positive correlation;  $\checkmark$ =negative correlation;  $\uparrow$ =quadratic correlation with peak which is indicated in brackets;  $\rightarrow$ =effect; <sup>ns</sup>=component of best fitting model, but not significant; \*=significant; S= Suaq Balimbing; T=Tuanan; x=no effect; NA=not tested/testable. Note that details on social play, associations, context of play (mother activity and distance) and playfaces are not represented in this table because those are also explained by a large range of factors.

# **4** Discussion

The main interest of this study was to evaluate the timing and quality of different play behaviour in wild orangutans. Different external and internal factors, such as age, sex, varying ecology and behavioural repertoire, were hypothesized to alter play frequency and quality (tab.59). Because previous studies could not conclude if different play types are independent of each other, the discussion of the results is organized by the solitary and social play types and the hypotheses within these play types. It will also enable us to consider all internal and external factors that might alter a specific play behaviour at once and how these might be intertwined.

The data sets consisted of at most 3 years of data, with the exception of the longitudinal play trajectories in Tuanan. Moreover, there was a lack of data on individuals between 4 and 8 years in Suaq Balimbing. In the appendix, there are additional analyses with some more data from Suaq Balimbing. However even with the increased data set, data on the previously mentioned ages are still very scarce (only one additional data point in this range). Because in the scope of this study it was not possible, I strongly suggest to repeat the analyses with a larger data set for both sites.

# 4.1 Compensation across play types

As reported in the results, there were positive, or quadratic (with a peak) correlations among solitary object play and social play and among solitary locomotor play and social play on both daily and longterm basis. Hence, it seems as if there was a reinforcing mechanism between solitary and social play. We did not test a correlation between the two main solitary play types, because they often occur interlinked within the same bout (also see section 4.3.3). As there was no evidence for any negative correlation between solitary (object and locomotor) and social play, we infer that there is no compensation mechanism between the play types. Particularly, if social play proportions are low, there does not seem to be more solitary play. The absence of compensation and the different trajectories suggest that the three main play types are independent of each other, at least on a functional level. Of course, the play types are often interlinked at instances. Such combinations will be discussed in the course of the discussion section (section 4.3.3).

# 4.2 Play and fruit availability

Strikingly, the frequencies of all the three play types were not altered by fruit availability. These findings are inconsistent with a large range of previous studies (e.g.: squirrels: Nunes et al., 1999; meerkats: Sharpe et al., 2002; sea lions: Burghardt, 2005). Especially in primates, the energy supply has been found to have major impacts on social play behaviour (e.g. Fagen, 2011; squirrel monkeys: Baldwin & Baldwin, 1974 and Stone, 2008; gelada baboons: Barrett et al., 1992; Hanuman langurs: Sommer & Mendoza-Granados, 1995; capuchin monkeys: Robinson, pers.comm. (2001) in Burghardt, 2005). However, so far most studies were exclusively looking at social play and did not include solitary play in their studies. In

orangutans the solitary play, however, is the predominant play behaviour and therefore, it is essential to look at it, too. Either solitary and social play are not as energetically demanding as previously assumed or the infants do not face the costs themselves by having a prolonged milk supply. Particularly, in orangutans the provisional situation is different than in other primates, where mostly social play has been studied in immatures around or after weaning. The long mother milk supply in orangutans (van Noordwijk et al. 2013) might give the immatures the additional energy to play and thus, the infants might not be affected by low fruit availability. Hence, mothers might act like an energy buffer and pay for the play of the immatures (Noordwijk, pers.comm.). Nevertheless, from the age of 1 - 1.5 years infants start to feed on solid food, while they still get the extra milk supply until around the age of 6.5 years (van Noordwijk et al., 2013). Thus, already from the age of 1 - 1.5 years onwards immatures already need additional energy supplies from solid food. Unfortunately, the energetic requirements of play are not yet fully understood, and in field studies it is impossible to disentangle how much energy infants get from the mother milk and how much from solid food. Nevertheless, as solitary play greatly ceases when immatures are competent of processing all feeding items and just before weaning (see also sections 4.3.1 & 4.3.2 on solitary locomotor and object play), we might infer that the mother provides the additional energy and time for solitary play. Similar findings of the mothers' investment being crucial for the extra-energy to play have been reported in horses (Cameron et al., 2008) and squirrels (Nunes et al., 2004).

Even so, weaned immatures did not exhibit any correlation between their social play frequency and fruit availability, which further alludes to the importance of social play during development (also see section 4.4.1). Moreover, the lack of correlation between play frequency and fruit abundance cannot be attributed to an inappropriate measure of food abundance, because fruit availability correlates with how much orangutans feed and what they feed on (Falkner, pers. comm.).

From another perspective, food provisioning during lean seasons did not increase social play in squirrel monkeys (Stone, 2008). Further, immature lion tamarins did not minimize energy expenditure during play as they played during the hottest period of the day (Oliviera et al., 2003). Thus, there seems to be a kind of an innate adaptation to how much immatures can afford to play. On a larger scale, Thompson (1998) even argued that individuals in an unstable environment should show more play because of the higher need for behavioural flexibility. However, we did not find any difference in the response to fruit availability between the two study sites.

# **4.3 Solitary Play**

# 4.3.1 Solitary locomotor play

Solitary object and locomotor play significantly changed with age in all analyses (alloccurrence data, comparative data (2010-2014) and longitudinal data Tuanan). Solitary object play was generally high during the first 3.5 years, whereas locomotor play revealed a distinct peak around the age of 3 years. This peak coincides with the age, at which immatures practice to move on their own and are less frequently clinging to the mother (van Noordwijk et al., 2009) (fig.82). Additonally, the peak of locomotor play corresponds with a peak of motheroffspring conflicts in the context of travel and tree gap crossing (Falker, 2015). Not only solitary locomotor play frequencies peak at the age of 3 years, but also the whole body involvement is highest during the first 3 years of life. Thus, locomotor play could indeed play a role in the acquisition of locomotor skills. This hypothesis further is supported by the fact that locomotor play often involves loosing and regaining control and vigorous swinging, which as a matter of fact could figure as *Training for the unexpected* (Spinka et al., 2001). Yet, no conclusive evidence can be presented in the scope of this study. It will be crucial in the future to also examine the complexity of locomotor play. There is evidence of more diverse locomotor patterns depending on forest structure (Manduell et al., 2012), which could also be reflected in more diverse locomotor play in Suaq Balimbing than in Tuanan. Yet, the infants in Tuanan and Suaq Balimbing did not differ in their locomotor play frequencies and also no variation concerning the age trajectories became apparent across the two sites.



**Figure 82:** "The percentage of time offspring of different ages is clinging to their mother's body while she travels throught the canopy for 4 different populations... Solid symbols are used for Sumatran populations, open symbols for Bornean populations." Figure from van Noordwijk et al. (2009).

Moreover, as already mentioned at the beginning of the discussion, locomotor play did not change with varying Fruit Availability Indices (FAI). Thus, it can be inferred that locomotor play is generally important for all the immatures to acquire locomotor skills and it could potentially even be ontogenetically fixed, because we could not find any individual differences in the longitudinal data of Tuanan.

Of course, we cannot conclusively proof with our findings that locomotor play is obligatory for reaching locomotor competence. Alternatively, practicing how to move by moving might be sufficient (Fagen, 1981). However, this is very difficult, if not impossible to test, because all immatures seem to exhibit locomotor play. Additionally, play could be a mechanism to increase locomotor activity, while the mother is stationary, and by that, locomotor skills are acquired relatively faster than just by moving. Following the same line of argument, locomotor play could even be a learning mechanism adapted to the mother's activity. If the infant would only learn how to move while travelling, the mother would have to adjust and hence, reduce her travelling speed, which would imply more time for travelling and less time for feeding.

All in all, the locomotor play peak is consistent with the hypothesis of locomotor play assisting acquisition of locomotor skills.

## 4.3.2 Solitary object play

As mentioned before, solitary object play is generally high during the first 3.5 years of life without a clear peak and then ceases quite quickly (fig.30). From the comparison between Suaq Balimbing and Tuanan, a difference in the object play age trajectories among the two sites was found, but no difference in absolute frequencies. From the more detailed, all-

occurrence data set, however, no interaction between site and age became apparent and there were also no absolute differences between the two sites. Nevertheless, because Sumatran orangutans generally show a slower life history (Wich et al., 2009), a prolonged phase of object play would fit into the picture. Even so, more data on 4 - 8 y old immatures are needed to complete the object play trajectory of the orangutans in Suaq Balimbing and thereby, to evaluare if there is in fact a prolonged play trajectory. Currently only one data point of a 6-year old individual was included in the 2-min scan data and the all-occurrence data set. No effect of food availability on solitary object play frequencies was detected, at either study site. During the first 3 - 5 years of life, the immatures learn how to process all the food items as their mothers' do but still improve in processing velocity after (Dunkel, 2006; van Noordwijk et al., 2009; Schuppli et al., in prep.) (fig.83).



**Figure 83:** Feeding rates of immatures in relation to feeding rate of adult female by age in Tuanan (left) and Suaq Balimbing (right). The items fed on are further subdivided by processing steps (0 - 3 steps), which are represented in colours. Moreover the average age at weaning and of first reproduction are highlighted. Graphs by courtesy Schuppli et al. (in prep).

Because the food niche of the Suaq Balimbing orangutan with the habitual stick tool use is more complex, we would have expected higher object play frequencies, if object play would assist tool use acquisition, as was found in a comparative study across bonobos and chimpanzees (Koops et al., in prep.). However, it might not be the frequency, but rather the prolonged object play trajectory that is connected to the acquisition of more sophisticated skills, such as tool use. Namely, tool use competence is only reached around the age of 4 (tree hole) to 7 (Neesia) years and proficiency even only around the age of 10 years (Meulman et al., 2013). Furthermore, the main learning mechanisms of sophisticated skills in orangutans were shown to be peering at actions of competent role models and explorative behaviours (Schuppli et al., 2012). Social learning ability, and opportunities for social learning, which requires high social tolerance are essential for the successful acquisition of tool use (e.g. van Schaik & Burkart 2011). Accordingly, significant differences in social interactions between Suaq Balimbing and Tuanan have been found (van Schaik et al., 2009; Schuppli et al., 2012; Schuppli et al., in prep). Hence, solitary object play frequency might not make the difference to achieve a more sophisticated behavioural repertoire. Yet, a prolonged object play trajectory, which we only have evidence for from one analysis, could rather figure as a symptom of the prolonged skill learning phase. Additionally, the late peak of nest practice could hint at the interaction between accomplished skills and play. Hence, play also mirrors the skill level of immatures and might in turn serve as skill practice. Thereby, the

importance of examining the play behaviour of immatures of 4 years and older from Suaq Balimbing is emphasized, of which unfortunately data was lacking for the current study. If object play was related to skill learning, the affinity for certain objects might be reflected in object play. But also qualitative differences in object play, such as more frequent stick or detached object use in Suaq Balimbing than in Tuanan, could not be found. Our findings are inconsistent with the hypothesis by Myowa-Yamakoshi & Yamakoshi (2011) who assigned the increase of play with detached objects with age in chimpanzees to their ability to use tools. In orangutans, the increasing proportion of detached objects with age seems to be a general tendency independently of the degree of tool use complexity of the population. Nevertheless, it cannot be ruled out that immatures in Suaq Balimbing might develop an even stronger preference for play with detached objects with age. Again we emphasize the need to evaluate more data on older immatures in Suaq Balimbing. Moreover, it could be possible that the use of certain objects is rather triggered socially than intrinsically and thus, only when practicing how to use a tool and peering at and exploring tool use, there could also arise an even stronger affinity for detached objects during play in tool using populations such as Suaq Balimbing. Therefore, as it has been found in peering and try-feeding cycles (Schuppli et al., 2012), the assessment of the immediate context, which the object play occurs in, is essential (also see section 4.3.4.1). Possibly, immatures would tend to play more with sticks or detached objects, when the mother or the surrounding individuals are also using tools. Yet, I question this hypothesis, because the data of this study was collected during Neesia season. Thereby, if there was such an immediate tool use effect on object play preferences, it should already have been obvious in the current study. Moreover, no such trend was found concerning other feeding items in a previous study (Jaeggi et al., 2010). It should be noted however that the discrepancy between the two populations might not be as large as previously thought. In 2014, an adolescent female in Tuanan was observed to feed on honey using a stick prepared as a proper tool.

More generally, solitary play decreased around the age of 4 years and nearly ceased at the age of 5-6 years. Weaning in Tuanan was reported to occur around the age of 5.5-7 years, where as in Suaq Balimbing only around the age of 7.9 years (van Noordwijk et al., 2009; Schuppli, pers. comm.). Thereby, the ceasing of solitary play might be linked to weaning. Yet, weaned juveniles rarely still revealed solitary play bouts, but often very short and simple ones, such as swinging arms and legs while resting. Because solitary play nearly quartered from the age of 4 years to the age of 5 years, the decrease of solitary play might rather be attributed to the increasing solid food intake and the time necessary to process the food than to weaning *per se*. Thus, solitary object play seems to be tightly linked to skill acquisition and the additional milk supply by the mother.

# 4.3.3 Combinations of solitary play types

Solitary object and locomotor play occur often in mixed bouts (APO-APM). These mixed forms are not reported in the 2-min scan data, because the protocol follows a hierarchical order in which solitary object play is prioritized. Therefore, I could only assess the mixed forms of solitary play with the all-occurrence data collected during the 7-month period. Nevertheless, a clear peak of APO-APM bouts between the age of 2 – 4 years became apparent, coinciding with the solitary locomotor play peak.

Also the combined form of try-feeding and solitary object play (APO-TF) seemed to be highest during the same ontogenetic period. Though, the linear model with age and the interaction between age and site was the best fitting model and thereby, there was no clear peak. Lois and Cinnamon (Suaq Balimbing) revealed the highest combined APO-TF levels. Accordingly, it could be of interest to further investigate if the site-age interaction found in the current study represents consistently higher try-feeding rates in Suaq Balimbing (Schuppli et al., 2012) or are due to some exceptional individuals.

To our knowledge combined forms of solitary play have not yet been investigated in detail in animals. From the results, we may wrap up that such mixed forms of play only occur if both play types occur at high rates and are relatively frequent in an individual's activity budget.

## **4.3.4 Context of solitary play**

#### 4.3.4.1 Activity of the mother during solitary play

Solitary play occurred at higher frequencies during the time when the mother was resting than expected by the mother's activity budget (fig.47). When the offspring is still dependent on the mother during travel, solitary play was lower than expected when the mother was moving, because the infant was either clinging to the mother or following the mother whose assistance is crucial for the infant. Thus, there is no time to play then. Only as the immatures get older and move largely independent of the mothers' help, around the age of 5-6 years, they can play even if the mother is moving. Even though there would be time to play when the mother is feeding, the play rates were not higher than expected by the mother's activity budget. This bias did not change over age. The reason for the relatively low solitary play frequency during the mothers' feeding bouts might be assigned to different factors at different ages. When immatures are above the age of 4 years, they are capable of processing most feeding items (Dunkel, 2006) and thus, might just be rather feeding than playing when their mother is in a food tree, as play rates also drop at this age. On the contrary, during the first few years, when infants are still learning how to process food, they might be peering at, begging for, tryfeeding or exploring the food of the mother. Meaning, object play would not serve the immediate purpose of learning how to process food (Schuppli et al., 2012) or there are just a lot of additional mechanisms. In the future it could be interesting to investigate the context of solitary play in more detail, especially in respect to qualitative characteristics of solitary play. Are infants more likely to play with similar items after the mother was feeding on them? Jaeggi et al. (2010) found that *practicing* (i.e. goal-directed trial) was significantly more frequent after termite feeding events of the mother, whereas they could not find any enhanced object play rate with termite feeding related objects. This suggests the absence of external stimuli affecting solitary play. In this study, most object play bouts occurred with leaves, twigs, branches and sticks, but not with the most frequently eaten fruits. From personal observations, I would thus also hypothesize that play frequently occurs independently of the mother's specific feeding activity and item. But this remains to be tested in other contexts than termite feeding.

#### **4.3.4.2** Distance to the mother during solitary play

We found that the distance to the mother during solitary play increases with age and does vary with play type. The play types with a social component occurred on average closer to the mother, because the mother often was the target of such solitary play bouts with a social component. Particularly, infants often play with the fur of the mother. The mother is not actively involved, but this kind of play should still be labelled including a social interaction between individuals. We found a positive linear correlation between age and distance to the mother during solitary play. However, it has to be accounted for the fact that we set up distance classes (1 = "0m", 2 = "< 2m", 3 = "<5m", 4 = "<10m", 5 = "<50m"). Previous studies

found that infants only start to move further than 10 metres away from their mothers around the age of 4 years, but a substantial amount of time in a distance more 10 metres from the mother can only be seen by age 6 years (van Noordwijk et al., 2009). The results of the current study suit the previous study. Only individuals older than 8 years reveal an average distance to the mother larger than 4 (corresponds to < 10 m distance) during solitary play. In future studies, not only the absolute distance to the mother, but also the distance to the mother during solitary play in relation to the daily distance values to the mother should be considered. By that, we could see if solitary play happens within the normal distance range to the mother at the specific age of the infant.

### 4.3.4.3 Party size and solitary play

Our findings suggest that there is no effect of party size on the hourly solitary play bout counts when controlling for age. Unfortunately, in the scope of this study, we could not determine if there is an effect of the party members' identities on the solitary play budget. We would expect that a stressful party with flanged males would result in more clinging to the mother and less play behaviour in infants, whereas a party with a potential play partner could even enhance solitary play, because of the positive correlation between solitary and social play. The effect on solitary play by the party of unflanged males could even differ between the two sites (section 4.4.1). However, this remains to be tested.

From another perspective, a tendency of increased nursing and also nursing conflicts has been found when mother-offspring pairs are in association with flanged and unflanged males (Falkner et al., 2015). Following this, parties with males are stressful for the infant and hence, it might lead to less solitary play.

# 4.4 Social play

# 4.4.1 Trajectories – What is crucial for a higher social play frequency?

As expected social play was more prevalent in Suaq Balimbing than in Tuanan. Yet, the two sites did not only differ in absolute social play frequencies, but the social play trajectories of immature individuals differed among the two sites. Whereas in Suaq Balimbing we found a peak of social play between the age of 2 and 4 years, in Tuanan the social play trajectory proceeded rather flatly. Having said that, social play remained constant in Tuanan until after the age of 8 years, while it nearly ceased in Suaq Balimbing after this age. Unfortunately, the very few data points for 4 - 8 year old Suaq Balimbing immatures have to be kept in mind. The current results contrast with social play trajectories found in another study on Sumatran orangutans in Ketambe, where the peak of social play only was around the age of 8 years (van Adrichem et al., 2006). Thus, it will be crucial to assess the social play trajectories again with more data on immatures between 4 and 10 years for Suag Balimbing. For the time being however, we can conclude that social play is generally higher in Suaq Balimbing than in Tuanan. Yet, in Tuanan adolescents (> 10 y) exhibited higher social play frequencies. Yet, to which factors or play partners has the generally higher social play proportion of the orangutans in Suaq Balimbing to be attributed to? To answer this question, we evaluated the play partner composition at the two sites. There was no difference in play amount with the mothers and the sibling across the two sites. Hence, the social play surplus in Suag Balimbing has to be attributed to play with associates. Yet, when considering the play proportion with an associate in relation to the association duration (Play Index), the immatures in Tuanan tended to exhibit even more play (Figure 52). Therefore, it is not the intrinsic play motivation that is different between the two sites, but rather the amount of opportunities immatures receive to play. Consequently, the crucial factor for more social play to occur is the opportunity to play and thus the association frequency. Even in the current data set, which was limited to a few years of data only, the expected higher association frequency among individuals in Suaq Balimbing than in Tuanan emerged. More importantly, the kin-biased associations among females in Tuanan (van Noordwijk et al., 2012) were absent in Suag Balimbing (fig.20). As a result, not only they associate more frequently, but the orangutans of Suaq Balimbing also have more options to associate because of the lack of kin-preference. Moreover, also associations with unflanged males were more frequent in Suaq Balimbing than in Tuanan. Hence, the generally higher degree of sociability offers the immatures more play opportunities. Only the adolescent individuals in Tuanan, ranging independently from their mothers, revealed similar association patterns to the adolescents in Suaq Balimbing, which in turn can explain the relatively higher social play rates of adolescents in Tuanan than in Suaq Balimbing. However, a previous study suggests also an increase of associations during adolescence in Sumatran orangutans (Ketambe) compared to infancy and a peak of social play at 8 years of age (van Adrichem et al., 2006). Moreover, unpublished data from Suaq Balimbing also suggest higher association and play rates in adolescents in Suaq Balimbing than reported in this study (van Noordwijk, pers.comm.). Thus, longterm data are crucial to assess the association and social play patterns of adolescents.

To come back to the hypothesis of associations limiting social play, we would like to point out that even within sites the hypothesis is supported, as the case of Susi illustrates. Susi was the offspring of an orangutan female (Sumi) that was living in an area of the Tuanan forest, which was burnt and thus, faced severe food shortages. Moreover, Sumi's homerange was surrounded by non-related, hostile females, who she did not associate with (van Noordwijk et al., 2012; Ashbury et al., in revision). In our results, Susi's social play frequency was by far the lowest when comparing with Jerry, Milo and Jip. This result is in agreement with the general tendency of lower social play chances for immatures of smaller matrilines (van Noordwijk et al., 2012). Additionally, because the solitary play frequencies were similar to those of the other individuals, the low social play frequency cannot be attributed to a lack of mother milk provisioning. The reason for the low social play frequency could rather be attributed to the lack of relatives to associate with (van Noordwijk et al., 2012). Because the kin-biased associations are only prevalent among adult females (van Noordwijk et al., 2012), there could still have been unrelated adolescents to associate and play with. However, with the many unrelated mother-offspring pairs around Sumi's homerange, a large potential play partner group dropped out.

Nevertheless, we have to emphasize that an association *per se* does not necessarily lead to social play. The associate's age class, kinship and the amount of play within an association (i.e. Play Index) were all related to the probability of play within an association, yet we could not find any significant site difference. Nevertheless, in the current data set, play between unweaned infants and unflanged males was only observed in Suaq Balimbing. Moreover, from scanning the long-term data sets, play of unweaned immatures with unflanged males was very rarely observed in Tuanan. Thereby, we strongly anticipate a significant site difference between the realized opportunities to play with unflanged males, when testing it with a larger data set.

If this was the case, it could be inferred that either in Tuanan unflanged males are perceived rather as a stress factor or as dangerous, whereas in Suaq Balimbing unflanged males are habitually in association and thus, mother-offspring pairs are more relaxed in their presence. As unflanged males are potential role models for social learning in Suaq Balimbing (ongoing study), the higher social play proportion with them might be representative for the higher

social tolerance. Testing a potential relation between social play and social learning mechanisms, such as peering, could be interesting.

Because of the absence of fruit availability effects on social play at both sites (see section 4.2), and our findings of social play being limited by the associations with suitable play partners, we conclude that the higher sociability in Suaq Balimbing is the crucial factor leading to more social play. Of course, on a larger scale fruit abundance and forest productivity have led to a higher degree of gregariousness in Sumatran orangutans (van Schaik, 1999). However, fruit availability does not figure as an immediate cause of more or less play, but the higher sociability does.

From another point of view, we would like to emphasize the importance of social play, not only for the more gregarious population. The fact that the immatures of Tuanan tended to spend more time playing within an association (higher Play Index = "total social play time per total time in association") is evidence for the necessity of social play during ontogeny. Further studies are needed to evaluate if immatures between 4 years of age and weaning are 'dragging' their mothers into associations (or prolonging these) to play (van Noordwijk et al., 2012). Thereby, when immatures are reaching a certain degree of locomotor independence, they might be able to direct travelling routes into the direction of a potentially interesting play partner.

In conclusion, our findings are consistent with the fact that social play is essential for all immatures, regardless of the population's degree of sociability. If associations are rare events, immatures just play more once they are in an association. Yet, the more gregarious population of Suaq Balimbing also realized more social play, which consecutively might enhance social tolerance among individuals. The connection between social play and social tolerance has been found in previous studies on chimpanzees in zoos. The higher rate of chimpanzee play during pre-feeding period is hypothesized to lead to less conflict escalations and peaceful cofeeding (Palagi et al., 2004; Palagi, 2007). Hence, an immediate function of social play might be to relax tensions and enhance social tolerance, also among adult individuals. Alternatively, a comparative study on macaque species found that social play styles among immatures correlate with the species' typical social tolerance. Thus, the less socially tolerant species (Japanese macaques) exhibit less risky play styles than the more tolerant crested macaques (Petit et al., 2008). Therefore, play is representative of species typical social skills and hence, social play possibly assists learning species-specific social tolerance. If we apply this to orangutans, we would expect less restraint during play in Suaq Balimbing than in Tuanan. Alternatively, the higher social tolerance in Suaq Balimbing also results in a wider variety of play partners, such as more frequent play with non-related immatures and unflanged males. In the current study we did not find any evidence for variation in play styles between the two sites, but only in partner composition. As already mentioned beforehand, it will be crucial to assess the timing of social play within an association and if there is a correlation with peering or feeding events, which could potentially enable us to infer a function of immediate social tolerance enhancement.

## **4.4.2** Compensation for social play partner scarcity?

If social play is as indispensable as we hypothesize, could there be a compensation mechanism to counteract a lack of social play? Two such potential processes have already been discussed before. First, adolescents in Tuanan revealed more social play than in Suaq Balimbing, which could hint at delayed compensation for little social play during infancy. However, as mentioned in the previous section, data from earlier study periods in Suaq

Balimbing suggest more social play in adolescents than reported in our results (van Noordwijk, pers.comm.). Thus, in the current study, we could have underestimated the amount of play in adolescents in Suaq Balimbing due to small sample sizes. Nevertheless, when only considering Tuanan, the social play proportion in adolescents even tended to be higher than in dependent immatures, which might allude to a kind of delayed compensation. Second, individuals in Tuanan revealed higher play proportions (Play Index) within an association, which could also serve to fulfil a certain social play demand. Multi-day associations might help to decide upon such a compensation mechanism. The scenario would be, once the offspring has the opportunity to play with a peer after a long time without any association, they play a lot. Gradually the longer the mothers associate over several days, the social play rates decrease resembling a saturation of the social play motivation. A decrease of social play with increasing association length could also resemble an increasing lack of energy due to less feeding and increased physical activity. One option to measure the energetic cost could be to test if there is any ketone excretion in the urine of the two players. Thus, we would be able to decide if play days result in a negative energy balance in players, as well as the mothers. Furthermore, the higher energetic demand of the offspring could also lead to higher mother-offspring conflict rates about nursing. Unfortunately, we did not have data on such multi-day associations in the current study.

A third option to compensate for missing social play opportunities, is to play more with constant associates, such as the mother or during early infancy the older sibling. However, there was a trend towards more mother-offspring play in Suaq Balimbing rather than in Tuanan and no pattern across sites could be seen in sibling play. Therefore, the deficiency of play with associates does not seem to be compensated by the mother or the sibling. Rather these two are the first play partners during infancy and gradually infants start playing with associates, as it was found in earlier studies on orangutans (Rijksen, 1978) and other primates (humans: Pellegrini & Bjorklund, 2004, great apes: Lewis, 2005). Despite that, what if there are no potential associates and play partners around during the entire dependent infancy? The example of Sumi and Susi showed that there was no increased social play frequency with the mother. However Sumi was also weakened due to the low food availability and thus, severe stress might have prevented her from playing with her offspring. More generally, in Tuanan it would be interesting to look at the females that do not belong to the central matriline of the study area who have less association possibilities (van Noordwijk et al., 2012). Do the mothers play more with their offspring or alternatively is there more play between the siblings than between other sibling dyads?

For the time being, I conclude that immatures in Tuanan compensate for the lower social play opportunities by increasing play time once in association with a proper play partner (for more details on play partner preferences see section 4.4.3.1). In contrast, the overall social play frequency is still generally higher in Suaq Balimbing. As previously discussed (section 4.4.1), our hypothesis is that social play is just more important in more gregarious populations to learn and maintain a higher social tolerance. The connection of social play and social tolerance has been found in many species so far (e.g. comparative study: Poirier & Smith, 1974; chimpanzees: Palagi et al., 2004; Palagi, 2007; macaques: Petit et al., 2008; lemurs: Antonacci et al., 2010; also see end of section 4.4.1).

# 4.4.3 Social play – Details

## 4.4.3.1 Motivation to play

The examination of social play should not be limited to play proportions, association opportunities and partner composition, but rather include more details on who is really motivated to play. By deciding upon which individuals are motivated and thus reveal the highest play urge, we might be able to circumscribe the phase or context during ontogeny when social play is crucial and if there is any kind of partner preference. We did not find any indication of sex differences in absolute (social and solitary) play rates in this study, which is inconsistent with findings in more gregarious primates (e.g. gorillas: Maestripieri & Ross, 2004; chimpanzees: Kahlenberg & Wrangham, 2010; Lonsdorf et al., 2014). For this reason and because of the limited data set, the sex of the play partners was not considered. Anyhow, as we will see in the course of this section, orangutan immatures seem to take advantage of any realistic play opportunity they can get. In contrast, Rijksen (1978) reported that play is more prevalent in male orangutans than in females.

Because the motivation to play might be reflected in different manners, we assessed several factors, which could be representative for play motivation.

#### Play Index

The Play Index (proportion of social play per time in association) has already been discussed in the previous sections (4.4.1) as a measure of play urge. The Play Index however could also mirror if a specific dyad is interested in playing with each other.

For example, chimpanzees show a clear preference for age- and size-matched play partners (Palagi & Cordoni, 2011). Yet, because of their higher degree of gregariousness (and the study was conducted with captive chimpanzees, anyways), the chimpanzees can afford to have strong partner preferences. In the current study, there was no significant relation between age difference and Play Index. Hence we can infer that wild orangutans just have to take advantage of the little social play opportunities that they get.

Nevertheless, we did not have data on the whole age difference range of both study sites. Consequently, a difference could arise between the two study sites regarding the partner preference. Particularly in Suaq Balimbing where associations are not only more frequent, but also consist of larger groups, it could be anticipated that immatures rather play with a peer if there is one in association than with any other mismatched party member.

#### Hinde Index for play

One way to infer an individual's level of motivation to play could be to examine its pattern of initiation and termination of play interactions within a specific dyad. For this purpose, we have set up the Hinde Index for play, which ranges from +1 (only play initiations by focal and no termination) to -1 (only play terminations and no initiations by focal). The Index was significantly more positive in mother-offspring and tended to be so in sibling play than in associate play. Because the Hinde Index for play was always from the offspring or the younger sibling's perspective, it indicates that the very young infants are more likely to start play with the mother or the sibling, but the mother or the sibling are more likely to end the play. The fact that mothers are rather passive players has already been suggested by a previous study on zoo-living orangutans (Maple, 1980).

Interestingly, a play bout that was initiated by the older sibling tended to last longer than if the younger sibling initiated play. Thereby, it could be derived if there was motivation also from

the older sibling, play was prone to last longer. Hence, the younger sibling was not able to keep a play bout going if the older sibling was not interested in play. The finding that the younger individuals initiated play more frequently contrasts with findings in bonobos and chimpanzees where adults were more likely to initiate play (Palagi, 2006). Because the Hinde Index for play with an associate was either out of the perspective of the younger or older focal, I tested if there was any age difference component to explain the balance between players. Yet, I could not find such a component. The absence of any age pattern could be attributed to the small sample size. However, even though the sample size was small, there were still a large range of age differences and if there would have been a tendency, it should have stood out by visual inspection of the graph. If the age difference was very large, the younger individual always exhibited a positive Hinde Index for play. Nevertheless, Hinde Indices did not indicate any pattern with age differences of 8 years and less. It must thus be implied that all immature individuals show an interest to play with other immatures, regardless of their age difference. Of course, the different aged individuals might have different reasons to be motivated to play with another individual (e.g baboons: Owens, 1975; review: Poirier & Smith, 1974).

From another point of view, the equilibrium among players (absolute PHI) was not predicted by the amount of play within an association (Play Index). Thus, play initiations might be always by the same individual, but there would still be a lot of play during an association. Unfortunately, the effect of the association initiator and terminator on the Play Hinde Index could not be fully resolved, because of the limited data set. Nonetheless, no tendency at all could be noticed from inspecting the graphs (fig.56). All in all, I cannot conclude if the Hinde Index for play was a good proxy for assessing the motivation to play.

#### Participation score

Though, not only initiation and termination might be indicators of play motivation, but also the level of involvement during play itself. For this purpose, we looked at the participation score differences of individual players in relation to age difference and player composition. The participation score was a measure for how much of the body was involved in play (see methods). We found that the age difference and the partner's age class are crucial for explaining the participation difference between the players. Anyhow, these results might also allude to the older individuals' ability to self-handicap when playing with a younger, smaller individual. Especially the results for the unflanged males who are less involved when the age difference is larger (high participation difference), but exhibit increasing involvement (lower participation difference) as their play partners' age increases. The same evidence for decreasing play intensity of the older individual with increasing age difference was found in chimpanzees (Flack et al., 2004). Hence, our results are consistent with orangutans having an understanding of strength-imbalance and having the capability to self-handicapping if required.

## 4.4.4 Context of social play - Mother

Social play generally took place closer to the mother of the younger player. Nevertheless, this might be seen as an artefact of the typical distance to the mother at a specific age of the immature. Particularly, the distance to the mother was best explained by the offspring's age only and did not alter with the play partner's age class, the age difference between the players, or whether it was a related play partner or not. Furthermore, the distance to the mother also did not differ across the sites. The lack of any other factors than the immature's age affecting

the distance to the mother during social play leads me to assume that social play is generally not perceived a dangerous situation by the mother. This hypothesis is further supported by the absence of any approaching or leaving pattern to the players by the mother. Additionally, there was no inclination towards increased playface probability by the play partner when the mother was closer to the players, as it has been found in chimpanzees (Flack et al., 2004). Unfortunately, it could not be assessed in this study, if the play partner's playface frequency changed with the distance to the mother or other party members, because the videos from previous years could no be matched to the exact play bouts in the data and hence, no context data was available for all the videos. The absence of the correlation between playface presence and distance to the mother is further discussed in the section about playfaces and playful expressions (section 4.5).

Generally, the mother mostly stayed at the same distance to the players, which was also reflected in the high proportion of stationary activities during the offspring's play bouts. The mother mostly fed and rested. In spite of that the activity budget of the mother during play should be normalized by her daily activity budget, as it was done for the solitary play, in order to decide if the proportion of stationary activities really was above expectation. Regardless, the tendency of increased travelling frequency during play with increasing offspring age cannot be attributed to the mothers' activity budget, but rather to the growing independence of the offspring. We could even speculate about the mother's awareness of the offspring's ability to follow her on its own. From another perspective, infants often seemed to forget about the mother when they were playing and when the play bout was finished, they started crying, because the mother had moved on without them (e.g. 4-year old Lois when playing with the unflanged male, Milo).

However, we should be cautious about speculating that the mothers do not change play course and play behaviour of the players. Anecdotal data from Tuanan report mothers being either actively involved in play, watching the offspring play or even interrupting play (van Noordwijk, pers. comm.). Moreover, as discussed previously, orangutans seem to have the ability to restrain themselves if there is an imbalance of strength. This might also be a decisive factor for the mothers' consent to social play with a specific play partner. Hence, we emphasize also here the need for more longterm data. Moreover, detailed analyses are needed of individual cases when the mother interfered during play and what made her intervene.

# 4.5 Playfaces & playful expressions

Playfaces and other playful expressions occurred in the context of all three play types. In this study, only playfaces were looked at quantitatively and more in detail. Vocalisations were very infrequent and varied largely among individuals and sites. Therefore, only descriptive data could be presented in this study. Immatures either produced sounds that were commonly used as playful vocalisations (e.g. "play ooh" in Suaq Balimbing), or used sounds from different contexts during play (e.g. Danum with the "raspberry" sounds). In some cases, it could potentially even be labelled as an innovation, because the vocalisation has not been heard within the population before. Vocalisations were more frequently heard in the context of social play in Suaq Balimbing, but not only during social play, there were also instances of "play ohs" during solitary play. If there were vocalisations in Tuanan then in the solitary play context. No vocalisations were documented in the social play context in Tuanan in the current, relatively small dataset.

In future studies, I suggest that special attention should be paid to vocalisations in the context of play. Not only because of the large variability across sites, but also the seemingly high rate of vocal innovations by immatures, which could shed light on cultural variants of the vocalisation repertoire and if and how such innovations can spread.

During solitary play, playface frequency was lower than in social play and heavily biased towards bouts with combined play types. The same bias of more play faces in social play was also found in chimpanzee infants (Cordoni & Palagi, 2011; Ross et al., 2014). This inclination might be either due to the fact that social play elicits more pleasure and emotions or because of the need to signal playful intentions (Demuru et al., 2014). Yet, these two scenarios are not mutually exclusive.

In the current study, the distance to the mother did not have an effect on playface display of the infants during solitary play. Yet, distances of 0m, <2m and <5m would still allow the mother to see the offsprings' playface (fig.46). Moreover, the solitary play types with a social component did not always exhibit the highest playface occurrence (fig.45). Hence, even though playfaces are more prone to occur in social play, playfaces during solitary play do not seem to correlate with any social components. In order to get more conclusive results, we would have to investigate if the offspring was more likely to display a playface during solitary play, when facing into the direction of the mother or other party members. From personal observations, I would doubt to find such a correlation, but it remains to be assessed quanitatively. The current results related to solitary play, however, are consistent with the hypothesis that playfaces are rather reflecting emotions in orangutans.

Because playfaces are uniformly distributed across a social play bout, it can be implied that playfaces do not primarily function as an initiation signal to the play partner, but rather serve the maintenance of a play bout. Similar findings were also reported in chimpanzees (Cordoni & Palagi, 2011). The fact that play bouts generally last longer if a playface is present, regardless of the visibility, supports the hypothesis that playfaces help to maintain play, which has also been reported in chimpanzees (Waller & Dunbar, 2005). Moreover, not only the mere presence of playfaces, but also the frequency of playfaces predicted play bout duration in this study on orangutans. Thus, our results are consistent with the view that playfaces rather reflect internal states of individuals and hence, would not primarily serve as a mean to communicate playful intent. Furthermore, unlike in chimpanzees (Flack et al., 2004), we could not find any relation between the proximity of the play partners' mothers and playface presence, even when controlling for the age differences of the players. Thus, there does not seem to be a strategic way of using playfaces to convey play as playful to the audience. Nevertheless, within the course of play, there was evidence that playfaces occur more strategically, or at least to convey benevolence and the motivation to play. We found a correlation between playface display and play bites. Nonetheless, this correlation must be taken with caution, because playfaces have been characterized as ritualized mock-biting to signal that play is only play (Bolwig, 1968). Most studies on playfaces (e.g. Ross et al., 2014; Waller et al., 2015) excluded the playfaces that preceded play bites. In the current study, we did not exclude these playfaces. Nevertheless, the correlation would fit the observations in chimpanzees where playfaces occur more frequently in connection with play elements which normally also occur in more aggressive contexts, such as hitting (Ross et al., 2014). Following the same line of argument, I would predict a connection between play checking and pulling each other into falls and playface displays. However, I could not yet analyse the sequences of play elements within play bouts. Thus, from my point of view to decide upon the functional component of playfaces and to characterize its occurrence, it is inevitable to consider the course of a play bout in respect to exact play elements. Moreover, as already studied in bonobos (Demuru et al., 2014), the assessment of visual attention of the play partner towards the playface emitter is essential to determine if there is a communicative function of the playface at all in orangutans. A recent study of rehabilitant orangutans revealed an inclination

of more frequent playface display if the play partner paid visual attention to the playface emitter (Waller et al., 2015). Yet, in the study, there was a near significant correlation with the recipient's facial expression which might infer that also rapid facial mimicries could enhance the correlation of playfaces and visual attention. In fact, a study in the zoo found evidence for rapid facial mimicries in orangutans and that these are more prevalent in similar aged juveniles (Davila-Ross et al., 2008). It would be interesting if we could find the same bias in wild orangutans, where showing playful expressions and emotional contagion could even be of higher importance to maintain rare play opportunities.

Following the same line of argument, playface frequency of the two players was positively correlated and by that play lasted longer. This indicates that either if both players are 'having fun', or if there is a better communication about playful intentions and to maintain play, play lasts longer. From my point of view, these two options are not mutually exclusive. In geladas a similar relation was found. Namely, Mancini et al. (2013) attribute longer play durations to rapid facial mimicries and take this as an indicator for better communication. In our study, the temporal delay or the general chronological order of playface displays by the two players was not analysed. Thereby we cannot yet imply a causal relation between playface displays by the both players because of the necessity to first assess visual attention and the sequence of play elements.

From another point of view, playface frequency did not vary significantly with play partner regardless of the age difference, except for mother-offspring play. Mother-offspring play is often one-sided with an inactive mother and very active, motivated infants trying to involve mothers in play, and thus the duration of such play bouts also tends to be shorter. Not only exhibit mothers hardly any playfaces, but also the offspring's playface rates are significantly lower than when playing with other play partners. However, since there is no significant age effect on playface rates I infer that playfaces arise more frequently in play bouts where both partners are involved actively. Unfortunately, I could not find any relation between the participation scores, which represented how much of the body is involved in the playful interaction, and playface frequency. This leads me to suggest the evaluation of play complexity and pace, such as play element rates in a given time, rather than an overall score for participation in relation to playface display. Counter to my prediction, the study on rehabilitant orangutans found a trend to higher playface frequencies at lower play intensities (Waller et al., 2015).

Furthermore, in the current study, during play bouts with higher playface frequency the individual was also more likely to exhibit a higher active holding rate. Thus, active maintenance of body contact and playfaces are interlinked. The same bias of increasing playface rates with increasing physical contact was also found in bonobos (Demuru et al., 2014).

Another point to mention is the similar playface rates at the two study sites. On the one hand, we would have expected more playful signals in a more socially tolerant population, such as Suaq Balimbing, because the individuals might be more proficient communicators, if playfaces served communicative purposes. On the other hand, there might have been a higher demand for communicating playful intentions in a less gregarious population to signal benevolent intentions. Leading to the conclusion that either playfaces must be regarded as simple emotional state representations in orangutans, or the similar playface rates across the different populations might be due to different reasons. Additionally, it is important to mention that the higher prevalence of playful vocalisations during social play in Suaq Balimbing might also be evidence for more social and more proficient social interactions.

All in all, our results suggest that playfaces are rather representations of the internal state reflecting a high motivation to play. With this, however, we do not negate that the play

partner or surrounding individuals perceive the playface as a benevolent or motivational signal.

# 4.6 Synthesis

Solitary locomotor, solitary object and social play follow different developmental trajectories in both Bornean and Sumatran orangutans. Accordingly, the literature broadly suggests these three play types exhibit different trajectories (humans: Pellegrini & Smith, 1998b; antelopes: Thompson: 1998; vervet monkeys: Fairbanks, 2000; gorillas: Maestripieri & Ross, 2004; meerkats: Sharpe, 2005a; chimpanzees: Cordoni & Palagi, 2011). Nevertheless, the course of each play type varies greatly between different species. We found the highest solitary object play rates already at very young ages, which then is followed by a peak in solitary locomotor play. Social play tends to be lower in the first few months of life and then remains around the same rates throughout dependent infancy. In gorillas, however, the solitary locomotor play peak preceded the peak in object play, as opposed to our findings. In the chimpanzee, no distinction between solitary locomotor and solitary object play was made. Though for social play, they neither found a clear quantitative peak, but an increase in complexity with age (Cordoni & Palagi, 2011). More distantly related primates revealed different patterns with a consistent object play trajectory, but an early peak of locomotor play that is then replaced by social play (Fairbanks, 2000).

In conclusion, play probably varies with the more general behavioural repertoire of a species and might even be linked to neural development (Fairbanks, 2000). Hence, a relation with skill development and play might even be an important mechanism to assist skill acquisition. This hypothesis is further supported by the fact that at least solitary object and locomotor play seem to be ontogenetically fixed and do not vary with fruit availability. The case of social play is more complicated, even though this play type was not found to be affected by fruit availability, the degree of gregariousness turned out to be the crucial limitation to social play.

# **5** Conclusion

The study investigated which factors limit play frequencies and if there are qualitative differences in play across different contexts. We found distinct ontogenetic play trajectories with solitary object play being high during early infancy (0 - 3.5 years), a peak of solitary locomotor play around 2-4 years of age and social play being rather constant during dependent infancy and decreasing during adolescence. Furthermore, social play was characterized by an early onset of play with the mother and the older sibling and only gradually around the age of 2 years play with associates started. The two sites, Tuanan and Suaq Balimbing, not only varied in absolute social play frequency, but also in play partner composition and association patterns (play opportunities). Nonetheless, we could not find any difference in play motivation between the two populations and in the less gregarious population of Tuanan, immatures even tended to play more within an association than in Suaq Balimbing. We can thus explain the higher social play frequency in the more gregarious population of Suaq Balimbing by the higher degree of sociability and the resulting increase of social play opportunities. More abundant fruit availability has been made responsible to the more sociable Sumatran orangutans. However on a smaller scale, none of the three play type frequencies altered with varying fruit availability at either site.

All in all, we can conclude that play happens irrespective of the ecological and social circumstances and details, and thus is apparently crucial during the ontogeny of orangutans.



"Play is vital... Play for your life!"

**Figure 84:** Hypotheses-Network-Scheme with the connections found to correlate with play quantity/quality (black arrows) and the factors which were not affecting play behaviour (grey arrows with red crosses).

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## Appendix

## Activity budget with different data sets

This section is set up in addition to the result section 3.1 "Play activity budget" to show model outputs from different data sets according to how selected observers were. All model outputs for the very selected observers are included in the result section of thesis. Hereby, we report the results on average daily solitary object, solitary locomotor and social play from data sets containing i) all observers and ii) selected observers for young individuals (<7y). We report always the complete output table and the comparison to the 0 model. The reason for the smaller sample size in the complete model is that FAIs are not available for all data points.

#### Solitary object play - All observers

#### Best fitting model

	Value	SE	DF	t	р
Intercept	0.6094	0.0589	19	10.3377	0.0000
Site Tuanan	0.0902	0.0852	19	1.0587	0.3030
Age	-0.0039	0.0007	14	-6.0642	0.0000
Site Tuanan:Age	-0.0023	0.0011	14	-2.1051	0.0538

(χ<sup>2</sup>(6)= 44.23, p<0.0001, AIC=-57, N=59 of 24 individuals

#### *Complete model*

-	Value	SE	DF	t	р
Intercept	0.9113	0.1322	29	6.8945	0.0000
Age	-0.0050	0.0007	29	-7.1598	0.0000
SiteTuanan	-0.2010	0.0937	20	-2.1441	0.0445
Sexm	-0.0776	0.0457	20	-1.6989	0.1048
av.FAI	-0.0181	0.0111	29	-1.6285	0.1142
Age:Site Tuanan	-0.0004	0.0009	29	-0.4479	0.6576

#### Solitary object play - Selected observers for young individuals

#### Best fitting model

<b>v</b> 0						
	Value	SE	DF	t	р	
Intercept	0.6077	0.0571	20	10.6492	0.0000	
Site Tuanan	0.0972	0.0816	20	1.1917	0.2473	
Age	-0.0038	0.0006	20	-6.5566	0.0000	
Site Tuanan:Age	-0.0025	0.0010	20	-2.5587	0.0187	
						-

χ<sup>2</sup>(6)=48.32, p<0.0001, AIC=-50.51, N=44 of 22 individuals

Complete model

1						
	Value	SE	DF	t	р	
Intercept	0.6859	0.1454	18	4.7181	0.0002	
Age	-0.0041	0.0008	16	-5.0199	0.0001	
Site Tuanan	0.0397	0.1159	18	0.3425	0.7360	
Sex m	0.0029	0.0665	18	0.0432	0.9660	
av.FAI	-0.0058	0.0116	16	-0.5032	0.6217	
Age:Site Tuanan	-0.0023	0.0011	16	-2.0528	0.0568	
120 00 01 12 1	<b>a a t</b>					

AIC= -39.31, N=40, gr=21

## Solitary locomotor play - All observers

## Best fitting model

<b>V</b> U					
	Value	SE	DF	t	р
Intercept	0.6422	0.1278	33	5.0249	0.0000
SiteTuanan	0.2744	0.1695	22	1.6193	0.1196
Age	-0.0041	0.0013	33	-3.0852	0.0041
Age:Site Tuanan	-0.0048	0.0021	33	-2.3085	0.0274

 $\chi^{2}(6)$ = 32.48, p< 0.0001, AIC= 27.89, N=59 of 24 individuals

#### Complete model

	Value	SE	DF	t	р
Intercept	0.7870	0.2887	29	2.7263	0.0107
Age	-0.0049	0.0018	29	-2.7590	0.0099
Site Tuanan	0.1875	0.2206	20	0.8502	0.4053
Sexm	-0.0440	0.1378	20	-0.3193	0.7528
av.FAI	-0.0057	0.0217	29	-0.2637	0.7939
Age:SiteTuanan	-0.0042	0.0023	29	-1.8297	0.0776

AIC=32.9, N=55, gr=23

## Solitary locomotor play – selected observers for young individuals

## Best fitting model

						_
	Value	SE	DF	t	р	
Intercept	0.6256	0.0551	21	11.3467	0.0000	
Age	-0.0046	0.0006	21	-7.3693	0.0000	
$y^{2}(4) = 22.50$	n < 0.0001 AIC - 2	40  N = 44  of  22	individuala			

 $\chi^{2}(4)=33.59$ , p<0.0001, AIC=-3.49, N=44 of 22 individuals

#### *Complete model*

	Value	SE	DF	t	р	
Intercept	0.7086	0.2916	16	2.4300	0.0272	
Age	-0.0048	0.0014	12	-3.4189	0.0051	
Site Tuanan	-0.0179	0.2201	16	-0.0815	0.9360	
Sexm	-0.0325	0.1018	16	-0.3196	0.7534	
av.FAI	0.0008	0.0261	12	0.0297	0.9768	
Age:Site Tuanan	-0.0012	0.0019	12	-0.6240	0.5443	
	0.1					Ì

AIC=3.64, N=40, gr=21

#### Social play- all observers

Desi jiiing mouel	2				
	Value	SE	DF	t	р
Intercept	0.3633	0.0507	33	7.1673	0.0000
Age	-0.0022	0.0005	33	-4.1489	0.0002
Site Tuanan	-0.2130	0.0673	22	-3.1657	0.0045
Age:Site Tuanan	0.0027	0.0008	33	3.3146	0.0022
$\chi^2(6) = 16.52, p < 6$	0.001, AIC = -	49.16			

## Best fitting model

#### Complete model

1					
	Value	SE	DF	t	р
Intercept	0.3324	0.1837	28	1.8090	0.0812
Age	-0.0026	0.0008	28	-3.3779	0.0022
SiteTuanan	-0.1480	0.1899	20	-0.7792	0.4450
Sexm	-0.0205	0.0504	20	-0.4067	0.6885
av.FAI	0.0099	0.0175	28	0.5640	0.5772
SiteTuanan:av.FAI	-0.0144	0.0241	28	-0.5954	0.5564
Age:SiteTuanan	0.0030	0.0009	28	3.1774	0.0036

#### Social play - selected observers for young individuals

#### Best fitting model

	Value	SE	DF	t	р	
Intercept	0.3733	0.0482	20	7.7446	0.0000	
Age	-0.0023	0.0005	20	-4.6044	0.0002	
SiteTuanan	-0.2616	0.0707	20	-3.7010	0.0014	
Age:SiteTuanan	0.0028	0.0008	20	3.5050	0.0022	
						_

 $\chi^{2}(6) = 19.86$ , p < 0.001, AIC=-42.93, N = 44 of 22 individuals

#### Complete model

	Value	SE	DF	t	р
Intercept	0.3985	0.1766	18	2.2561	0.0367
Age	-0.0028	0.0007	15	-3.9311	0.0013
Site Tuanan	-0.1886	0.1863	18	-1.0124	0.3247
Sex m	-0.0393	0.0531	18	-0.7393	0.4692
av.FAI	0.0062	0.0162	15	0.3843	0.7062
Site Tuanan:av.FAI	-0.0276	0.0261	15	-1.0560	0.3077
Age:Site Tuanan	0.0033	0.0009	15	3.6655	0.0023

## Play activity budget with additional data from Suaq Balimbing

Because there was additional data for Suaq Balimbing, the play activity budget analyses were repeated in order to have more data on immatures in th eage range 4 - 10 years from Suaq Balimbing. However, the additional data only contained few additional data points for these ages. Here we report the results when only taking data collected by selected observers. Moreover, due to time constrains, the FAI has not been added to the analyses. However, because of all the results reported in the thesis, including longterm data from Tuanan, and FAI effects on play were generally absent, we can assume that FAI would not change the current results.

Quadratic and cubic functions were also tested. However, only models with linear age effects were significant.

#### Social play

Best fitting mod	el				
	Value	SE	DF	t	р
(Intercept)	0.3621	0.0473	20	7.6547	0.0000
Age	-0.0022	0.0005	20	-4.0379	0.0006
SiteTuanan	-0.2226	0.0755	20	-2.9507	0.0079
Age:Site Tuanan	0.0020	0.0010	20	2.0299	0.0559
2					

 $\chi^{2}(6) = \overline{17.98}, p<0.0001, AIC=-35.41, N=44 \text{ of } 22 \text{ individuals}$ 

#### *Complete model*

	Value	SE	DF	t	р
Intercept	0.3845	0.0778	20	4.9445	0.0001
Age	-0.0024	0.0007	20	-3.3820	0.0030
Site Tuanan	-0.2284	0.0779	19	-2.9313	0.0086
Sex m	-0.0214	0.0589	19	-0.3640	0.7198
Age:Site Tuanan	0.0021	0.0010	20	2.0404	0.0547

 $\chi^2(7) = 18.13$ , p<0.01, AIC=-33.56, N=44 of 22 individuals

### Solitary object play

#### Best fitting model

2001 June 8					
	Value	SE	DF	t	р
Intercept	0.6752	0.0454	21	14.8827	0.0000
Age	-0.0081	0.0015	20	-5.5463	0.0000
Age <sup>2</sup>	0.0000	0.0000	20	2.6040	0.0170
2(5) 11.00	0.0001 110	44.00 31 44	6.00 1 1 1 1		

 $\chi^{2}(5)=41.80$ , p<0.0001, AIC=-44.08, N=44 of 22 individuals

#### Complete model

	Value	SE	DF	t	р
Intercept	0.6006	0.0857	19	7.0059	0.0000
Age	-0.0060	0.0020	19	-3.0600	0.0064
Site Tuanan	0.1269	0.0837	19	1.5171	0.1457
Sex m	0.0044	0.0627	19	0.0708	0.9443
Age <sup>2</sup>	0.0000	0.0000	19	1.3414	0.1956
Age:Site	-0.0020	0.0012	19	-1.6397	0.1175
Tuanan					

 $\chi^{2}(8) = 44.56$ , p<0.0001, AIC=-40.84, N=44 of 22 individuals

## Solitary locomotor play

	Value	SE	DF	t	р	
Intercept	0.6410	0.0525	21	12.2029	0.0000	
Age	-0.0047	0.0007	21	-7.0851	0.0000	
2(1) 22.01	0.0001 110	1.01 31 14	6 8 8 1 1 1 1			Ĩ

χ<sup>2</sup>(4)= 33.81, p<0.0001, AIC=-4.31, N=44 of 22 individuals

## Complete model

	Value	SE	DF	t	р
Intercept	0.6688	0.1131	20	5.9158	0.0000
Age	-0.0045	0.0010	20	-4.4042	0.0003
Site Tuanan	0.0142	0.1133	19	0.1257	0.9013
Sex m	-0.0194	0.0856	19	-0.2267	0.8231
Age:Site	-0.0014	0.0015	20	-0.9318	0.3625
Tuanan					

 $\chi^{2}(7)$ = 36.12, p<0.0001, AIC=-0.62, N=44 of 22 individuals