Master Thesis

Mother-Offspring Conflict in Orangutans

Disentangling different contexts of mother-offspring conflict in Sumatran and Bornean orangutans

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Summary

Parent-offspring conflict arises when parents and offspring disagree over the amount of parental investment. So far, most studies have focused on weaning conflict. However, in various species more sources of conflict are known or predicted. Slow life histories and very long inter-birth intervals make orangutans a particularly suitable study species to disentangle different sources of conflict. These traits have the advantage that each phase of infancy is more prolonged and thus different kinds of conflict which would coincide in species with faster life histories can be teased apart. In this study we examined mother-offspring conflict in Sumatran (*P.abelii*) and Bornean orangutans (*P. pygmaeus wurmbii*). The aim was to describe and distinguish different contexts of conflict in relation to the factors: offspring age, food availability, offspring sex, maternal age, number of individuals in association and site. Simultaneous mother and offspring data was collected during nest-to-nest follows, using 2-min interval focal sampling and detailed *ad libitum* sampling of conflicts and potential conflict situations. In total, 558 hours of detailed data at the field site Suaq Balimbing, Sumatra and 933 hours of data at Tuanan, Borneo of 17 immatures ranging from 4 to 113 months of age were collected. We could distinguish three main contexts of behavioral conflict: nutrition, locomotion and proximity, which themselves could be teased apart even further into fourteen different fine-grained conflict 'problems'. Hourly conflict frequencies were predicted most commonly by offspring age, but the number of individuals in association and the study site also had an influence. In relation to the opportunities for a specific conflict to occur, conflict frequencies increased with offspring age, as well as during periods of food shortages. Moreover, mother-offspring pairs with ancient mothers had fewer conflicts, corresponding with the 'terminal investment hypothesis'. The lack of rejections during final weaning indicates that milk provisioning gradually declines without active behavioral inhibition on the mother's part. During periods of food shortages, nutrition and locomotion conflicts tend to increase in frequency and overall conflict intensity was elevated. The increased conflict frequencies, in combination with low distress intensities, when in association, suggest that offspring might be intimidated by strangers. In addition, variation between the two study sites was explained by the differences in forest structure and productivity. In conclusion, we found that there are indeed different contexts of conflict that peak according to the competence of the offspring, but are also driven by social and ecological conditions.

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1 Introduction

1.1 Research background and study objective

Parent-offspring interactions are one of the most widespread social behaviors, not only important in humans, but also shown by many animals and even plants (Godfray 1995a). As a result of female pregnancy and, in mammals, lactation, especially mother-offspring interactions are crucial for offspring survival and therefore also for female reproductive success (Hrdy 1999). Given the long offspring dependency on the mother, orangutan mothers invest more time in each offspring than any other known mammal, including other apes (Galdikas & Wood 1990, van Noordwijk et al. 2009).

Generally, mother-offspring interactions are cooperative, because mother and offspring share a common interest for the offspring to survive and later reproduce but, especially in primates, also for the mother to survive and provide postweaning care (van Noordwijk 2012). Nonetheless, conflicts over the rate and termination of investment can arise because of a trade-off for the mother between investing in her current offspring and the chances of survival and investing in future offspring (Williams 1966, Trivers 1974). Mother-offspring conflict is thought to be based on an underlying genetic conflict of interest. Fitness can be seen as the success of spreading own genes. Thus, to maximize fitness, each individual should promote all genes that are identical to its own genes, respectively support the individuals carrying those genes. On average, a mother shares fifty percent of her genes with each of her offspring, whereas the current offspring is fully related to itself but only to fifty percent to its full-siblings or for twenty-five percent to its half-siblings. Since a mother is equally related to all of her offspring but the current offspring is fully related to itself and at most only half to its siblings, the offspring's benefits from investment are twice as large as those of its mother. As a result the mother and her offspring have different optima of investment, which potentially leads to a conflict (Hamilton 1964, Trivers 1974).

Mother-offspring conflicts can arise in different contexts varying with the offspring's needs and competence (Simpson et al. 1986), as well as maternal condition and other ecological factors (Clutton-Brock 1991, Hauser & Fairbanks 1988). In this study, I aim to disentangle different contexts of mother-offspring conflicts, examine its timing during offspring development and identify factors that influence conflict, amongst others by comparing two species of wild orangutans.

1.1.1 Parental investment vs parental care

Most parent-offspring interactions concern expenditure of parental resources on the offspring (Clutton-Brock 1991). This resource expenditure enhances both the parent's and the offspring's fitness, by reducing the chances of offspring death from care-dependent factors (Barrett et al. 2006) and indirectly increasing the reproductive success of the parents (Trivers 1972).

Different forms of parental expenditure can be hierarchically divided into parental care and parental investment. Parental care is a broad term, which includes any parental behavior that increases offspring's fitness. Care behaviors can start as soon as the preparation of nesting sites up to postnatal care (Clutton-Brock 1991). Parental investment, on the other hand, is defined as any behavior by a parent that increases the offspring's chance of survival but at the same time decreases the parent's ability to invest in other offspring. Investment is costly because it is provided in the form of time- or energy-consuming behavior patterns or somatic expenditures (Trivers 1972). Alternatively, it can also lead to an increased mortality risk such as an increased predation risk due to lack of attentiveness to predators or offspring solicitations that attract predators (Altmann 1980, Maestripieri 2002).

Forms of parental investment

In all sexually reproducing species, parental investment starts already with the metabolic investment in primary sex cells (Trivers 1972). Investment continues during development of the embryo and fetus in the uterus of viviparous species (Haig 1993, Crespi & Semeniuk 2004, Moore 2012) and also though care of fertilized eggs in some oviparous species (Clutton-Brock 1991). Continued investment after birth is maintained by at least one parent in all mammals as wells as most birds (Farmer 2000) and some other species such as scorpions (Benton 1992) or poison dart frogs (Weygoldt 1987).

In mammals, parental investment is provided almost exclusively by the mother (Trivers 1972, Clutton-Brock 1991). In comparison to males, females invest more resources into large eggs than male into tiny sperm (Bateman 1948, Trivers 1972). Mammalian females continue investing in the offspring by carrying it to term (Williams 1966, Trivers 1972) and herewith supply it with nutrients and protection as well as thermoregulation. Since females are responsible for the internal investment, they are certain that the infant is truly their own offspring, whereas males rarely have complete paternity certainty. Thus males not only have the option, but also have a greater incentive than females, to desert the offspring and pursue other mating opportunities (Trivers 1972, Clutton-Brock 1991). Considering that females already put a lot of time and energy into the offspring from conception until birth, it is in their interest to continue investing even more into the offspring to ensure its survival so that the previous investment pays off. Subsequently, even though mammalian species with paternal investment or helpers exist, the extended period of postnatal investment is also provided for the most part by mothers (Trivers 1972, Gross 2005). Female lactation is considered the most energetically costly stage of reproduction (Gittleman & Thompson 1988). In orangutans, females require up to twenty-five percent more energy during lactation (van Noordwijk et al. 2013a). Other maternal postnatal investment includes protection against infanticide and predators, thermoregulation and in primates also carrying of the offspring and tolerance such as food sharing to provide opportunities for social learning (van Noordwijk 2012). Especially in great apes, maternal investment is high and crucial for the survival of the offspring (Delgado & van Schaik 2000). Since females almost exclusively provide all parental investment in mammals, the focus will be set on mammalian female parental investment in this study.

Generally, a mother and her offspring share a common interest in investing into the offspring to ensure its survival and later reproduction. This contributes to the offspring's fitness and indirectly to the mother's fitness, since the prospects that her genes are transferred into future generations are increased (Haig 1993). Moreover, mother and offspring share a common interest for the mother to survive. Through future reproduction of the mother, the mother's fitness and indirectly also the offspring's fitness increase, and the offspring profits from continued investment and, in primates, even post-weaning care (van Noordwijk 2012). However, investment in the current offspring leaves the mother with fewer resources to invest into future offspring. Consequently, there are situations in which the mother and her offspring disagree over the amount and termination of parental investment, which can potentially lead to a conflict (Trivers 1974).

1.1.2 Existing hypotheses explaining parent-offspring conflict

The presence of parent-offspring conflict has been shown in many species in theoretical models (i.e. birds: Clark & Ydenberg 1990, herbivorous insects: Roitberg & Mangel 1993, plants: Zhang & Jiang 1998, 2000) as well as empirical studies of behavioral conflict (i.e. birds: Stamps et al. 1985, primates: Maestripieri 2002, marine mammals: Trillmich & Wolf 2008, turtles: Janzen & Warner 2009). In primates, phases of parent-offspring conflict are characterized by high levels of maternal rejections and infant distress (Hinde 1974, Nash 1978, Lee 1987). However, the underlying basis of the conflict is still debated. At the moment there are two main hypotheses explaining the mechanisms of parent-offspring conflict. The 'Parent-Offspring Conflict Theory' proposed by Trivers (1974) assumes an underlying genetic conflict about the amount and termination of investment whereas the 'Timing Hypothesis' proposed by Altmann (1980) describes parent-offspring conflict as a behavioral conflict over the timing of investment.

1.1.2.1 Parent-Offspring Conflict Theory

Trivers' (1974) 'Parent-Offspring Conflict Theory' proposes that genetic conflicts of interests are present in all parent-offspring relationships in which parents and their offspring are not genetically identical. Genetic conflicts arise because of the different *degrees of relatedness (r_0)* between the competing parties (Trivers 1974). In mammals a mother's probability of sharing a gene with any of her offspring is fifty percent *(r=0.5)*, so she is equally related to all of her offspring. Therefore, to her every offspring has the same amount of benefits and costs. Benefits correspond to the reproductive success of the offspring whereas costs are measured as the reproductive success of the mother's future offspring or the offspring's siblings respectively. Each offspring however is fully related to itself *(r=1)* but on average only fifty percent to its full-siblings *(r=0.5)* or twenty-five percent to its half-siblings *(r=0.25)* (Hamilton 1964). This results in a twice as large benefit for the current offspring when the mother invests in it as when the mother would invest in one of its full-siblings. Thus, the mother and her offspring differ in their optima of investment in the current offspring and conflicts over the rate and the termination of investment can arise. This genetic conflict of interest can result in a behavioral conflict between mother and offspring. Whenever the mother's optima of investment is exceeded but the offspring's optima is not reached yet, offspring should take maternal resources directly or deceive the mother into exceeding her optimal investment for example through excessive begging (Trivers 1974).

Conflict over the rate of investment

Each individual should try to maximize its total benefit by maximizing the difference between costs and benefits at any given moment during the period of maternal investment. The net benefit an individual exploit from investment, as given by the benefit to cost ratio, depends on the relatedness between two individuals *($^b/_c$*r)*. This means that the benefits of investment to an individual are increased, respectively the costs decreased, according to the amount of shared genes. Since the offspring is fully related to itself but the mother is only related to fifty percent to her offspring, the benefits to the offspring are twice as high, respectively the costs only half of those to the mother. This leads to the situation that an offspring is selected to favor more maternal investment than its mother is selected to give at any given time (Trivers 1974).

Conflict over the termination of investment

According to theory, maternal investment should be provided up to the point at which the benefits equal the costs *($^b/_c$*r = 1)*. It is assumed that the benefits of investment to the offspring decrease with increasing age and the costs to the parents increase or remain the same, so that the benefit to cost ratio declines progressively. As the benefit to cost ratio depends on the relatedness between two individuals, the offspring is selected to favor maternal investment until the costs to the mother are twice as high as those to itself. As the optimal amount of maternal investment does not fully coincide between a mother and her current offspring *($^1/_2 < {}^b/_c < 1$)*, a potential period of conflict over the termination of investment exists when the mother's optimum of investment has been exceeded, but the offspring's optimum is not reached yet (Trivers 1974).

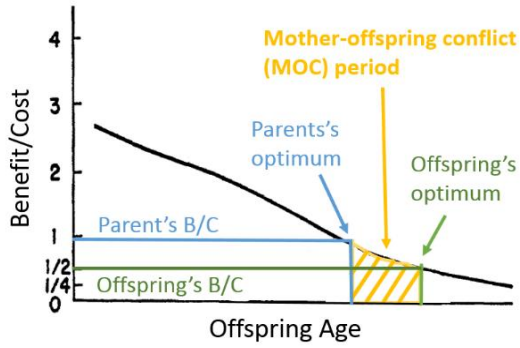

Figure 1. **Conflict about the termination of investment.**
Benefit to cost ratio (B/C) of the mother in relation to offspring age. The mother's optimum for the end of investment in the current offspring is when B/C=1. The offspring's optimum for the end of investment is when costs to the mother are twice as high as her benefits, assuming that future siblings are full-siblings (1/2 B/C of the mother). Disagreement over the termination of investment arises between the parent's and the offspring's optimum (modified from Trivers 1974).

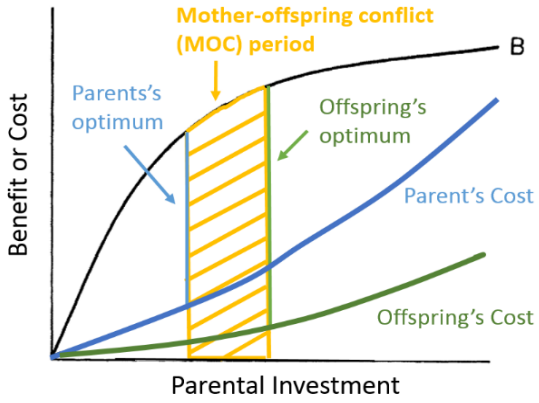

Figure 2. **Conflict about the rate of investment.**
Benefits or costs in relation to the rate of parental investment. B represents the benefit to parent and offspring. The offspring's cost (OC) is half of that of the parent (PC). Fitness is maximized when B-PC, respectively B-OC is largest. Disagreement over the rate of investment occurs between the parent's and the offspring's optimum (modified from Trivers 1974.)

1.1.2.2 Timing Hypothesis

The alternative 'Timing Hypothesis' claims that behavioral conflict is not over the rate and termination of investment, but rather over the coordination of the timing of investment. It proposes that behavioral conflict occurs because the mother tries to train the infant not to solicit investment at inconvenient times when investing, when in the infant interferes with other activities such as foraging (Altmann 1980, Dunbar & Dunbar 1988). Yet, the conflicts about the timing of maternal investment could be the proximate result of the differences in the long-term genetic interests between a mother and her offspring (Schino & Troisi 1998). Thus 'Parent-Offspring Conflict Theory' and the 'Timing Hypothesis' are not mutually exclusive (Barrett et al. 1995) and both can result in behavioral conflict.

1.2 Why study mother-offspring conflict in orangutans?

Long offspring dependency

Orangutans are a particularly interesting species to study mother-offspring conflict because they have slow life histories and very long inter-birth intervals of more than six years (van Noordwijk & van Schaik 2005, van Noordwijk et al. 2009, Wich et al. 2009, van Noordwijk et al. 2013a). The slow life histories have the advantage that each phase of life is more prolonged so that different kinds of conflicts -which would coincide in species with faster development and shorter inter-birth intervals- can be teased apart. Consequently, the termination of different forms of investment are more spread across infancy and thus conflict over the termination of different contexts of investment can be examined separately. Given the long inter-birth intervals, mother-infant bonds in orangutans are close and long-lasting (van Schaik 2001). Thus, we find an elongated period of time during which potential conflict over the rate of investment might occur.

Single offspring and semi-solitary

In broods of more than one offspring, conflict over maternal investment between siblings can occur and thus be interwoven with parent-offspring conflict (Macnair & Parker 1979, Parker et al 1989). This is not the case in orangutans, which usually give birth only to one infant at a time (Markham 1995, Goossens et al. 2011). In addition, orangutans have a tendency towards individual-based fission-fusion grouping with parties staying small and the mother and her offspring often ranging alone (van Schaik 1999). This minimizes the effects of other individuals on the relationship between a mother and her offspring. However, associations do occur and hence influence of association partners can be analyzed as well, amongst others by comparing Sumatran and Bornean orangutans. Sumatran and Bornean orangutans diverged about 1.1 -2.3 million years ago (Ryder & Chemnick 1993, Warren et al. 2001, Zhang et al. 2001) and today Sumatran orangutans live at higher densities and are more gregarious than Bornean orangutans (van Schaik 1999).

Close human relatives

As orangutans are one of the closest living human relatives (Glazko & Nei 2003), the study of orangutan mother-offspring conflict could shed light on probable human mother-offspring conflicts, which are not easily distinguished in humans. Like orangutans, humans nurse their infants for several years, but despite their slow life histories, infants are weaned quite early around the age of 2.5 years before a new sibling is born (Kennedy 2005). Therefore potential blurring factors that are present in humans are reduced in orangutans, which might help us to better understand mother-offspring conflict at its basics.

1.3 Contexts and factors influencing mother-offspring conflict

Contexts of mother offspring conflict

One aim of the present study is to disentangle different contexts of conflict. To our knowledge, nutrition is the best studied context of conflict so far (i.e. gulls: Mathevon & Charrier 2004, burying beetles: Leigh & Smitheth 2012, dogs: Manabi et al. 2013) and also Trivers based his 'Parent Offspring Conflict Theory' on nutrition conflicts. However, especially in primates, more contexts of conflict have been suggested or found (Simpson et al. 1986, Altmann & Samuels 1992, Jurke, & Pryce 1994). We predict that there are at least three main contexts of interactions, which can be split into more fine grained contexts. First of all, we expect nutrition conflicts, which can be about milk or tolerated food taking. In addition, we predict conflicts concerning locomotion and proximity. Mother-offspring conflict can arise in all of these contexts because they involve maternal investment, in the form of the mother investing energy or time into the offspring, which could otherwise be used to acquire energy for herself. A more detailed description of each predicted context will be presented in the following sections.

Factors influencing Mother-Offspring Conflict

For each context separately, we examine different factors that might have an influence on mother-offspring conflict. The focus was set on offspring age (Simpson et al. 1986) to assess mother-offspring conflict about termination of investment. Furthermore, food availability (Lee 1987, Hauser & Fairbanks 1988, Fairbanks & McGuire 1995, Lycett et al. 1998) was taken as a proxy of the energy available, but also other factors such as offspring sex (Trivers 1974, Trillmich 1986, Nguyen et al. 2012), maternal age (Pugesek 1981, Clutton-Brock 1991) and social environment (Wolfheim et al. 1970) in form of number of associates were analyzed to assess their impact on conflict about the rate and, if possible, termination of investment. The mother's reproductive state (DeVore 1963, Worlein et al. 1988, Gomendio 1991, Berman et al. 1993), her activity (Altman 1980, Maestripieri 1995), the offspring's activity and individual differences (Fairbanks 1996) are also factors that possibly influence mother-offspring conflict, but they could not be taken into account during the course of this project due to time and data constraints. In addition, a comparison between two orangutan study populations was made to evaluate the possible influences of ecological and population differences.

1.3.1 Offspring age

Offspring age is closely linked to the development and needs of an infant. With increasing age the offspring's needs change. It continuously learns new skills and develops independence at different ages for distinct aspects of life (van Noordwijk et al. 2009). Therefore mother-offspring conflict might occur at various stages of an infant's life due to different sources of conflict (Simpson et al. 1986).

1.3.1.1 Nutrition

The first context we examined was nutrition. Even though orangutans start to feed on solid food around the age of one year, they are nursed for more than six years and therefore have the longest nutritional dependence of all non-human primates (Wich et al. 2009, van Noordwijk et al. 2013a).

Milk

The best known context of mother offspring conflict is the weaning conflict. It has been examined in many primates such as baboons (DeVore 1963, Altmann 1980, Barrett et al. 1995) or vervets (Hauser 1988), but also other mammals for example seals (Trillmich 1986), bison (Green 1993), pigs (Bøe 1991), dogs (Malm & Jensen 1997), guinea pigs (Rehling & Trillmich 2007, 2008) and elephants (Lee & Moss 2011). Weaning is the period of maternal investment in which the rate of milk transfer from mother to offspring drops most sharply (Martin 1984, van Noordwijk et al. 2013a), whereas we refer to final weaning as the time point when the offspring was last seen suckling. Seasonal breeders with short

inter-birth intervals can take advantage of seasonal periods of high food availability either by timing the maximal lactation effort to a peak in food abundance or, if peaks are unpredictable due to mast fruiting, by conceiving during high fruit availability (Brockman & van Schaik 2005, van Noordwijk et al. 2013b). Mothers pursuing the first tactic profit from high fruit abundance by being able to feed enough to produce a maximal amount of milk. The second tactic leads to births after a peak in food abundance. These mothers build up fat stores during peaks of food availability, which is then transferred to the offspring through lactation. In these single-year lactators, the start of weaning usually coincides with the onset of solid food eating. For slow developing multi-year lactators like orangutans however, it is neither possible to time the period of highest offspring needs to a peak of food abundance, nor to build up large enough energy stores to sustain them through many years of varying food availability. Therefore, mothers lactating over multiple years provide the offspring with a rather low but fairly stable amount of milk. Consequently, the offspring has to start feeding on solid food sooner than at the onset of weaning because at some point the milk supply cannot meet its energy needs anymore. Thus, there is a prolonged period after the milk insufficiency point in which the mother supplies the offspring with a stable amount of milk but the offspring also has to start eating solid food (van Noordwijk et al. 2013a, 2013b). According to the 'Parent-Offspring Conflict Theory', this leads to a potential period of conflict over the rate of milk investment starting already at the milk insufficiency point, before the actual weaning period, until final weaning.

The classical weaning conflict refers to a period of conflict during weaning, which should peak at final weaning. In orangutans final weaning takes places between the ages of 5.5 to 6.5 years in Bornean orangutans and a little later in Sumatran orangutans between the ages of 6 to 7.5 years (van Noordwijk et al. 2009, 2013a). The optimal timing within these ranges depend on the offspring's physiological development and skill competence (van Noordwijk 2012). However, in multi-year lactators, there might be a second peak of conflict over milk gift, namely at the milk insufficiency point. The milk insufficiency point is reached in orangutans at the age between 1 and 1.5 years (van Noordwijk et al. 2013b). This conflict might also be present in single-year lactators, but it is not evident since the two events of milk insufficiency and final weaning more or less coincide, whereas in orangutans we can disentangle the two potential conflicts.

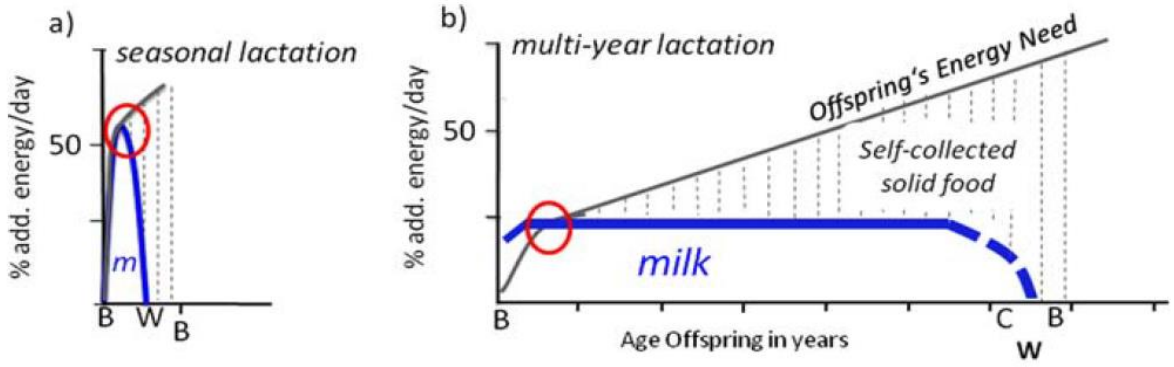

Figure 3. **Offspring's energetic needs (black) and energy supplied by the mother (blue) in relation to offspring age for a) single-year lactators and b) multi-year lactators.**
In multi-year lactators the proposed final weaning (W) conflict and the conflict at the milk insufficiency point (red circle) can be disentangled. B indicates the birth of an offspring (van Noordwijk et al. 2013a).

Solid food

Even though an orangutan infant starts eating solid food around the age of one year (van Noordwijk and van Schaik 2005), it still does not yet have the ecological competence to provide all food for itself and often begs the food from its mother. Food-taking, sharing or provisioning is found in many animals, including mammals (i.e. Killer whales: Hoelzel 1991, Meerkats: Doolan & Macdonald 1999, Tamarins: Feistner & Price 1990, 2000, Hyenas: Holekamp & Smale 1990). The amount of food offspring receives in the form of milk or solid food, is positively correlated with its survival and growth rate. In mammals, breeding success is often related to adult size, which again is usually well correlated with early growth. Thus, additional caloric input usually leads to greater overall fitness of the offspring (Clutton-Brock 1991). For the mother however, investing extra resources to the current offspring reduces her future reproductive success (Godfray 1995b) and therefore decreases her fitness. According to Trivers (1974), this can lead to a conflict over the rate and termination of tolerated food-taking.

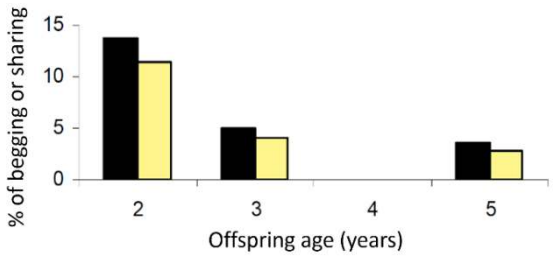

Figure 4. **Begging and 'sharing' rate in relation to offspring age.**
Begging rate (Begging bouts/feeding bouts; indicated by black bars) and 'sharing' rate (bouts with the offspring acquiring food/feeding bouts; indicated by yellow bars) decline with increasing offspring age (Jaeggi 2006).

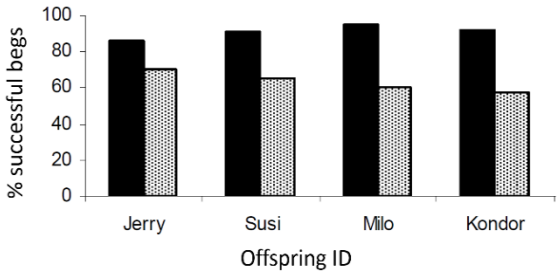

Figure 5. **Begging success rates for difficult and easy to process food items.**
The percentage of successful begging events decreases only for easy-to-process items (grey bars), but not for difficult-to-process items (back bars). Offspring are listed according to their age, starting with the youngest offspring: Jerry (2y), Susi (2y), Milo (3y), Kondor (5y), (Jaeggi 2006).

Most of the time orangutan mothers are rather tolerant towards their offspring. However, they do not share food actively, but only when begging preceded (Jaeggi 2006). Infants beg by holding a hand to their mother's mouth or by trying to take the food directly from their mother's hand (van Noordwijk et al. 2009). Begging can be persistent and accompanied by whining and screaming, which indicates some sort of a conflict of interest. Another indication of potential conflict situations is, that begging success rates of hard to process food items are constantly high for infants of all ages, but success rates for easy to process items decline as the infant ages (Jaeggi 2006). Moreover sometimes weaned offspring were chased away when they tried to feed on the same branch as their mother (van Noordwijk and van Schaik 2005). In addition, there has been one observation of mother-offspring conflict over the termination of tolerated food-taking when the offspring was about six years old (Jaeggi et al. 2008). The decline in number of different kinds of foods begged for as well as the decrease in the amount of tolerated food-taking with increasing offspring age (Jaeggi 2006, Jaeggi et al. 2008) suggest potential mother-offspring conflict over tolerated food-taking.

1.3.1.2 Locomotion

The second context of mother-offspring conflict I intend to examine is travel. Orangutans are the largest arboreal primates. They have a variety of skills to move in the forest canopy which need to be learned, in particular crossing gaps between trees (Bard 1995, Philipps 2011). Infants are carried by their mothers for at least the first two years of their lives up to four years of age. Once they are able to move independently, they still need help crossing gaps between trees until they fully reach locomotory independence around six years of age (van Noordwijk et al. 2009).

Carrying

Carrying is the most costly form of primate parental investment apart from lactation, especially for species that need to travel in order to forage (Altmann & Samuels 1992). Carrying conflicts have been reported in several primate species such as callimicos (Jurke & Pryce 1994), baboons (Altmann 1980) and chimpanzees (Goodall 1986). Moving independently is energetically more costly for the offspring than being carried. Therefore it is in the offspring's interest to be carried sometimes, even though it would be able to move on its own (Altmann 1980). The mother however increases her energy expenditure if she has to carry the extra weight of her infant. This additional energy cost increases as the offspring gets older and heavier (Altmann & Samuels 1992, van Noordwijk et al. 2013a). Indeed, in orangutans there is a continuous decline in the time an offspring is carried when the offspring is between two and four years of age (van Noordwijk et al. 2009). Consequently, there is a period of potential conflict over carrying starting at the point of independent locomotion of the offspring until the termination of carrying.

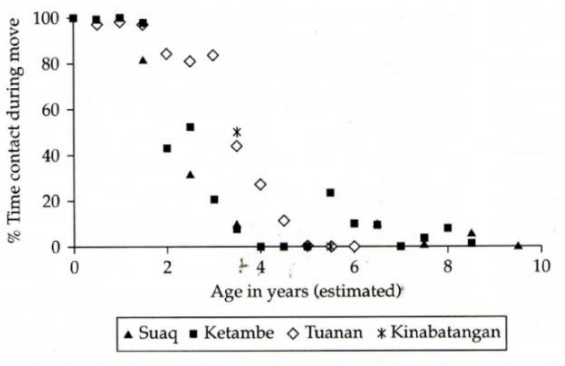

Figure 6. **Amount of carrying in relation to offspring age.**
The percentage of time the offspring is clinging to its mother while she moves decreases with increasing offspring age (van Noordwijk et al. 2009).

Assisted crossings

Once an offspring is not carried anymore, it still not able to move fully independently in the forest canopy, because it is not yet able to cross larger gaps between trees (van Noordwijk et al. 2009).

An infant can benefit from riding in the same tree as its mother as her weight sways one tree closer to another or by using the back-swing after its mother has crossed (Bard 1995). Furthermore, mothers can actively assist their offspring by hanging themselves between two trees and acting as a bridge for their offspring (MacKinnon 1974) or by bending two trees close together so that the infant can cross on its own (van Noordwijk & van Schaik 2005). An offspring is sometimes able to cross between trees without any help from its mother, but with a detour which makes travel more costly (van Noordwijk et al. 2009). Therefore it is in the offspring's interest to receive help rather than taking the more difficult way. The mother on the other hand would be much more efficient if she did not have to help and wait for her offspring, because she loses foraging time and energy. With increasing age, the amount of help an offspring receives from its mother declines (Philipps 2011), but gap crossing skills are not fully mastered until the offspring's sixth birthday (Chappell et al., subm.). This decline, in relation to the different interests of mother and offspring, bears potential for conflict over assisted-crossings between offspring ages of two to six years old.

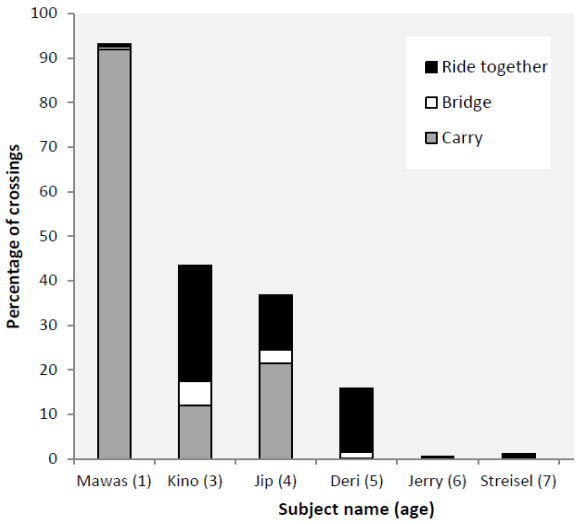

Figure 7. **Percentage of crossings assisted crossings in relation to offspring age.**
Assistance with crossing can be given by carrying the offspring (grey), making a body bridge (white) or the infant riding the same tree as its mother (black), (Philipps 2011).

1.3.1.3 Proximity

Offspring collects

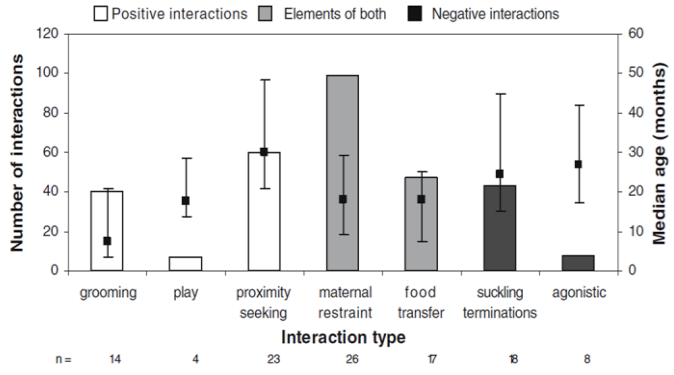

Figure 8. **Mother-offspring interactions in gorillas.** Number of interactions (histogram bars) and median age of the offspring (square with interquartile range) of different interaction types (Nowell & Fletcher 2007).

The third context I intend to examine is proximity. Even though orangutan mothers occasionally reject suckling, food-taking or clinging attempts, they are rather tolerant towards proximity of their dependent offspring, only (almost) weaned offspring have occasionally been observed to be displaced (van Noordwijk pers. comm.). However, there might be conflicts, not about the mother increasing distance, but rather keeping the offspring close to ensure for its safety. It is also in the mother's interest to protect her infant to make sure that not all her previous investment is lost. Maternal restriction in primates has been reported for example in rhesus macaques as to protect their infants from intragroup aggression (Hinde & Simpson 1975, Bardi & Huffman 2002, Maestripieri 2002) and Yunnan snub-nosed monkeys as to reduce the risk of injury and accidents (Li et al. 2013). A study of Nowell and Fletcher (2007) showed that in gorillas *(Gorilla gorilla gorilla)* there are a great number of mother-offspring interactions in which the mother restrains her offspring. These restraints occurred mostly when the offspring was between ten and thirty month of age. This time period of maternal restraint coincides with the transition from being carried almost all the time to independent locomotion, which happens in gorillas around the age of one to three years. A similar finding was made already made by Hansen (1966) in rhesus macaques. Maternal restraints and retrieves increased during the first forty days of an infant's live and then decreased again sharply. These restraining and retrieving behaviors coincide with the period during which the offspring's locomotor abilities mature. Infant restraints were classified as the mother interfering with the infant's attempts to leave her presence whereas retrieves are signals for the infant to return and restore contact with the mother.

In orangutans, the transition of being carried to independent locomotion occurs between the ages of two to four years (van Noordwijk et al. 2009). Even though orangutans are not group-living and therefore do not often need protection from intragroup aggression, this might still be a critical period of infant development. From that time on, infants can actively approach playmates if they encounter other orangutans. They might not pay so much attention to their movement and surroundings when they are absorbed in play, so possible dangers are not noticed as quickly. In addition, already one-year old offspring spend more than half of their time out of body contact to their mother (van Noordwijk and van Schaik 2005) and start leaving close proximity (<2m) and are thus out of the mothers reach. For large and heavy arboreal primates such as orangutans, falls off trees can cause serious injuries or even death as observed in chimpanzees (Goodall 1986). Therefore the transition from being carried to independent locomotion could be a critical period. Therefore it might be in the mother's interest to protect her offspring through restriction or retrieves, especially during encounters with other individuals. During encounters with other mother-offspring pairs, there have been observations of the infants pulling towards each other to play, while their mothers restrained them (van Noordwijk, pers. comm.). When a mother attempts to retrieve or restrains her offspring, the offspring can resist, which is energy and time consuming for both individuals. Thus potential conflicts about maintaining close proximity can occur.

1.3.2 Food availability

Fluctuations in food availability affect the biology and behavior of a variety of different species including primates (Copepods: Huntley & Brooks 1982, Frogs: Anholt & Werner 1995, Dolphins: Heithaus & Dill 2002, Macaques: Albert et al. 2013, Birds: Vincenzi et al. 2013). The most favored food of orangutans is fruit (Galdikas 1988, Morrogh-Bernard 2009). The Southeast Asian rainforest, the habitat of orangutans, is characterized by substantial intra- and interannual fluctuations in fruit abundance due to irregular and unpredictable supraannual mast-fruitings and annual fruit peaks (Ashton et al. 1988, Knott 1998). In orangutans, food availability has been shown to affect diet composition (Galdikas 1988), feeding time and distance travelled per day (van Noordwijk et al. 2013a), as well as female ovarian functioning (Knott 2001) and sociality (Utami Atmoko et al. 1997, Knott 1998), although the last mentioned effect has been debated. No effect of fruit abundance on sociality was found in an orangutan population in Suaq Balimbing, Sumatra. Therefore differences between populations have been suggested (van Schaik 1999). The influence of food availability on mother-offspring conflict has not yet been examined in orangutans, but studies of other primate species show an effect on the intensity of mother-offspring conflict, although with differential results (Hauser & Fairbanks 1988, Fairbanks & McGuire 1995, Lycett et al. 1998).

1.3.2.1 Nutrition

Nutrition is directly related to food availability. Food, as an energy resource, influences maternal and infant condition directly and influences offspring condition as well indirectly through milk availably. As an offspring ages, it continuously needs more energy for maintenance and growth. At first, all energy is provided by the mother and gradually the offspring starts to contribute more and more to its increasing needs (van Noordwijk et al. 2009, van Noordwijk 2012).

Milk

Non-seasonal, large bodied mammals have a threshold weaning weight which is about thirty percent of maternal weight (Ross 2003). If a mother cannot give enough milk to her offspring, weaning is delayed because more time is needed to reach the weaning weight, resulting in prolonged inter-birth intervals (Lee 1996). Extended periods of low food availability can result in a poor nutritional condition of the mother, giving her less energy sources available to produce milk, which in turn results in reduced energy resources for the offspring as well. Since the offspring's energy need stays the same, but less milk is available, the milk insufficiency point is reached earlier. This means offspring has to start providing energy for itself earlier by eating solid food, even though it might not be fully capable of doing so yet (van Noordwijk, pers. comm.). In this situation the mother is not able to produce more milk for her offspring without endangering her survival, but for the offspring it is easier to obtain its energy from milk rather than feeding on solid food.

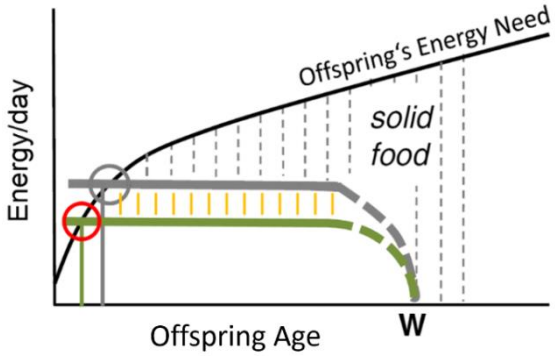

Figure 9. **The effect of low food availability on the offspring's energy budget.**
During periods of food shortages, the amount of an offspring's daily energy needs provided by the mother is reduces (green). Thus the point at which the offspring has to start eating solid food (red circle) is shifted to a younger age.

Solid food

The conflict over food sharing is expected to be greater if food availability is low because both, mother and offspring, struggle to keep up their energy balance, especially as the offspring needs to provide more food for itself. Giving away food results in a drop of the already low energy resource for the mother but would increase the offspring's energy. In orangutans, begging success is lower during periods of low food availability (Jaeggi 2006). Therefore we expect mother-offspring conflict about solid food to be elevated during periods of food scarcity.

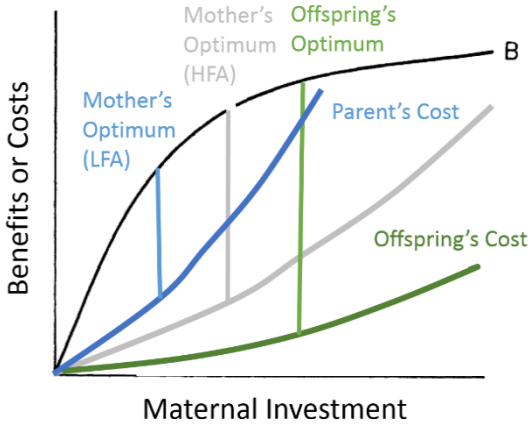

Figure 10. **Effect of food availability on mother-offspring conflict.**
During periods of food shortages (LFA), investment is predicted to be more costly (blue) than during periods with high food availability (HFA, grey). The offspring's cost (green) are expected to increase only slightly.

1.3.2.2 Locomotion

A similar logic as for the impact of food availability on nutrition applies for the effect of food availability on locomotion. During periods of food shortages, orangutans tend to travel shorter distances than during periods with high food availability (van Noordwijk et al. 2013a), probably to reduce travelling costs and save energy. Another way for the offspring to reduce traveling costs is to be carried. However, mother and offspring do not necessarily disagree on carrying. The mother needs to provide the infant with energy through lactation to refill its energy deposits, which it lost during independent locomotion. If this expenditure through lactation is greater, than what she would expend by carrying her infant, it is also in the mother's interest to carry her offspring (Altmann & Samuels 1992, van Noordwijk 2013a). Nonetheless, unless the infant's locomotion is still very inefficient, the mother not only increases her energy expenditure by carrying her offspring but also loses time for foraging, because travel is slower with the additional weight of the offspring. Furthermore, the mother also incurs costs from assisting her offspring in crossing gaps between trees, due to lost foraging time. The offspring however can save energy by being carried or not having to make a detour to cross a gap. During low food availability, both, mother and offspring, should try to minimize their expenditure even more and lost foraging time is more costly. Thus, mother-offspring conflict over locomotion should increase during low food availability.

1.3.2.3 Proximity

So far, no studies to our knowledge have been conducted that explicitly examine the influence of food abundance on restrain-retrieve behaviors. As orangutan mothers reduce their travelling time during low food availability, it suggests that they are trying to save energy (van Noordwijk et al. 2013a). The same might be true for the offspring, so that it does not venture too far away, because it also incurs costs from moving around. Therefore we hypothesize that mother-offspring conflicts concerning retrieve-restraint behavior will not increase due to low food availability.

1.3.3 Offspring sex

Another factor which can influence mother-offspring conflict is offspring sex. Evidence for effects of offspring sex on the amount of parental investment has been found for example in fur seals (Trillmich 1986), African elephants (Lee & Moss 1986) and Seychelles warblers (Komdeur 1995, Komdeur et al. 1997). The mother should invest more in the sex that provides a greater return in form of maternal fitness. This can be achieved through higher survival probabilities, greater reproductive success, less

competition or lower reproductive and rearing costs for the mother. Orangutans neither differ significantly in inter-birth intervals, weaning age or offspring survival (van Noordwijk et al. 2009, unpubl. data), nor size at weaning in captivity (Leigh & Shea 1995) between the sexes, therefore we assume that rearing costs are similar for males and females. However, the mating system of orangutans has a background of intense male-male competition. In orangutans, male reproductive success is much more variable than that of females (Trivers 1972). Thus a high quality male might have a much greater reproductive success than a female, whereas low quality males might sire no offspring at all. As the mother also increases her fitness through indirect fitness of the reproduction by her offspring, the mother might benefit more by investing in a male offspring to raise males of good condition. Therefore mother-offspring conflict might be less pronounced in males than in females.

1.3.4 Maternal age

Mother-offspring conflict can be influenced by the age of the mother in species that reproduce more than once (Clutton-Brock 1991). The 'Terminal Investment Theory' is based on predictions of the life-history theory, which states that there is a trade-off between reproduction and future survival. Due to the basic assumption of limited resources, resources invested in reproduction are not available for growth and maintenance anymore. With increasing age the chances of survival and reproduction of an individual decline and thus fewer resources should be directed towards growth and maintenance, but more towards reproduction (Williams 1966). This should lead to an increase in maternal investment and as a result the optimum of investment of mother and that of offspring approximate. The studies on terminal investment have been very inconclusive, or even contradictory. In barbary and rhesus macaques evidence for terminal investment was found (Paul et al. 1993, Hoffman et al. 2010), whereas another study on rhesus macaques (Berman 1884) the terminal investment hypothesis was rejected. Studies in long-lived birds have found also both, support (Pugesek 1981, Part et al. 1992, Pugesek 1995) or rejection (Sæther et al. 1993), of this hypothesis. On the basis of the terminal investment hypothesis, we predict that mother-offspring conflict should decrease in very old mothers.

1.3.5 Association partners

Mother-offspring conflict may also be influenced by the social environment. An influence on restrictive behavior could be found for example in macaques (Wolfheim et al. 1970), squirrel monkeys (Kaplan 1972) and vervets (Fairbanks & McGuire 1993). In all cases, mothers became more restrictive towards their infant in a potentially dangerous environment. The effect of the social environment on nutritional or locomotory mother-offspring conflict has not yet been studied explicitly.

Orangutans have a semi-solitary lifestyle with a tendency to individual-based fission-fusion grouping and association rates are quite low because of the high costs grouping which are likely to be a result of nutrition poor habitats (van Schaik 1999). Other individuals are food competitors and due to low encounter rates, they are possible also not very familiar (if not from the same matriline). Therefore orangutans might be stressed when in association with other individuals, especially not familiar ones. Consequently we predict that mother-offspring conflict about nutrition and travel is increased due to energetic costs, whereas restrain-retrieve conflicts will probably depend on the identity of the individual in association.

1.3.6 Other factors influencing mother offspring conflict

1.3.6.1 Mother's reproductive state

Many studies have shown that mother-offspring conflict can depend on the mother's reproductive state (i.e. baboons: DeVore 1963, long-tailed macaques: Gore 1986, Japanese macaques: Worlein et al. 1988, rhesus macaques: Gomendio 1991, Berman et al. 1993). In seasonal breeders, maternal rejections and the probability of conception during the next mating season are correlated and seem to be based on both the mother's and the infant's condition (Simpson et al. 1981, Lee 1987). Gomendio (1991) observed high rejection rates during infant suckling attempts and distress before and during

the mother's first estrus in rhesus macaques. Infant distress also remained increased after the mother's estrus if the mother had conceived. A similar finding was made by Berman et al. (1993). Even though orangutans have no mating season, earlier weaning can result in shortened inter-birth intervals, which can increase the mother's lifetime reproductive success. In fact, there have been observations of infants interfering with the mother's mating, but it mother-offspring conflict in relation to the mother's reproductive state has not yet been measured explicitly (van Noordwijk, pers. comm.).

1.3.6.2 Activity of the mother

Altmann (1980) argued that mother-offspring conflicts do not have a genetic basis and in return proposed the "Timing Hypothesis" which states that behavioral conflicts between mothers and their infants are not about the amount of investment, but rather about the timing of investment in relation to maternal activity. Theory predicts that conflicts occur when infants solicit investment at inconvenient times, such as soliciting nipple access when the mother is feeding. Evidence for this hypothesis has been found for example in baboons (Altmann 1980, Altmann & Samuels 1992, Barrett et al. 1995) and long-tailed macaques (Karssemeijer et al. 1990, van Noordwijk 2012). A study of orangutans showed that contact time between mother and offspring decreases earlier when the mother is foraging than when she is travelling or resting (van Schaik & van Noordwijk 2005, van Noordwijk 2012). Nevertheless, the coordination conflict proposed by Altmann (1980) and the investment conflict proposed by Trivers (1974) do not necessarily exclude each other (Barrett et al. 1995), therefore maternal activity can be looked at as another factor influencing mother-offspring conflict.

1.3.6.3 Activity of the offspring

In addition, the activity of the offspring could also have an influence on the timing and rate of mother-offspring conflict. If an offspring is absorbed in play it probably does not solicit resources from its mother. The effect of play on the offspring's energy balances has not been examined so far. However, assuming that play influences the offspring's energy balance negatively, the infant should solicit more investment from the mother after play. Therefore, we would expect increased mother-offspring conflict over nutrition and locomotion after intense play bouts.

1.3.6.4 Individual differences

Probably, mother-offspring conflict will also differ between the different mother-offspring pairs, since each mother might have her individual maternal style as found for example in guinea pigs (Albers et al. 1999), pigs (Pitts et al. 2002), bottlenose dolphins (Hill et al. 2007) and primates (Fairbanks 1996).

1.4 Comparison between Suaq Balimbing, Sumatra and Tuanan, Borneo

An interesting aspect of this study is the comparison between the orangutans at Suaq Balimbing, Sumatra and Tuanan, Borneo. Sumatran and Bornean orangutans are similar in their development of independence, but Bornean orangutans are weaned earlier than Sumatran orangutans (van Noordwijk et al. 2009, 2013b). Therefore the age of the offspring at which we find final weaning conflict should be different for the two sites, namely later at Suaq Balimbing than at Tuanan.

Moreover, the habitat of orangutans in Sumatra is more productive than in Borneo. Forests in Sumatra have more periods of high fruit availability with more stems on fruit and the density and productivity of key orangutan trees is higher, resulting in generally higher food availability on Sumatra than on Borneo (Marshall et al. 2009). The difference in the general level food availability could lead to differences in mother-offspring conflict in respect to changing food availability between the two sites. An increase in food availability is expected to yield more evident changes in behavior in Tuanan than in Suaq Balimbing, because of the higher year-round food availability in Sumatra. In addition conflicts concerning nutrition and locomotion are predicted to be more pronounced at Tuanan as the energy level of orangutans is generally lower (Marshall et al. 2009)

Additionally, Suaq Balimbing consists mostly of primary forest whereas the forest at Tuanan had been subject to selective logging in the past. As the forest at Tuanan has been selectively logged in the past, it consists of more emergent and smaller trees, which result in a dense lower canopy that is not present at the primary forest at Suaq Balimbing. These ecological differences could have an influence on the travelling behavior of the orangutans, since the dense lower canopy at Tuanan offers a greater number of support structures than the widely spaced canopy at Suaq Balimbing (Vogel et al., 2009). Thus we predict that gap crossing conflicts are more common at Suaq Balimbing than at Tuanan.

Finally, Sumatran orangutans are generally more gregarious, associate more often and live at higher densities than Bornean orangutans (van Schaik 1999, Delgado & van Schaik 2000). The population density in Suaq Balimbing, Sumatra is almost twice as high as in Tuanan, Borneo (Husson et al. 2009). Suaq Balimbing has the highest known orangutan density of seven individuals per square kilometer (Singleton and van Schaik 2001) whereas Tuanan has a density of 4.5 individuals per square kilometer (van Schaik et al., 2005). These circumstances could lead to very different reactions to association partners between the two sites including differences in mother-offspring interactions. We predict that mother-offspring conflict rate in all contexts will be higher at Tuanan than at Suaq Balimbing, because of increased food competition and more unfamiliar association partners due to the lower population density at Tuanan.

1.5 Questions and hypotheses

The aim of this project was to disentangle different contexts of mother-offspring conflict, examine its timing during offspring development and identify factors that influence mother-offspring conflicts in Sumatran and Bornean orangutans. Focus was set on three main potential conflict contexts of nutrition, locomotion and proximity in relation to different factors, mainly offspring age and food availability. Furthermore the influence of offspring sex, maternal age and sociality on mother-offspring conflict will be considered as well as a comparison between the two study sites.

For this purpose, the following questions and hypotheses have been formulated:

1) In what *contexts* does mother-offspring conflict occur?

- Conflicts occur in three main contexts: Nutrition, locomotion and proximity.
- The subjects of nutrition conflicts can be milk and solid food.
- The subjects of locomotion conflicts can be carrying and assisted gap crossing.
- The subjects of proximity conflicts can be retrieves and restrains.

2) What are the *age trajectories* of mother-offspring conflict during offspring development?

Nutrition

- There is a first peak of mother-offspring conflict at the milk insufficiency point when the offspring is one year old and a second peak of conflict during weaning when the offspring is between 5.5 and 7.5 years old.
- Food sharing conflicts increase as the offspring ages, with solicitations for easy to process foods being rejected earlier than difficult to process food items.

Locomotion

- Carrying conflicts are present when the offspring is between the ages of zero to two years old and will increase with age in relation to carrying time.
- Assisted-crossing conflicts peak when the offspring is between two and four years old.

Proximity

- Restriction starts with the beginning of independent locomotion of the offspring and decreases as the offspring ages.

3) Which *factors* influence mother-offspring conflict and how?

Food availability

- Nutrition and locomotion conflicts increase with decreasing food availability.
- Proximity conflicts are not influenced by low food availability.

Offspring sex

- All conflicts are more pronounced in female than in male offspring due to greater variation in reproductive success in males.

Age of the mother

- All conflicts are less pronounced in very old mothers as proposed by the 'Terminal Investment Hypothesis'.

Association partners

- All conflicts increase with increasing numbers of association partners, but proximity conflicts will also depend on the identity of the associated individual.

4) Are there differences in mother-offspring conflict between the Sumatran and Bornean study sites?

- Final weaning conflicts occur later during offspring development at Suaq Balimbing than at Tuanan.
- Due to general lower food availability, nutrition and locomotion conflicts are more frequent at Tuanan.
- Carrying conflicts are similar at both sites, but gap conflicts are more pronounced at Suaq Balimbing than at Tuanan due to differences in forest structure.
- Proximity conflicts are more common at Suaq Balimbing because the frequency of associations with other individuals is higher

2 Material and Methods

2.1 Study sites and study period

This study was conducted in two study areas during a period of six months. At Suaq Balimbing (3° 04´N, 97° 26´ E, Gunung Leuser National Park, Aceh Selatan, Sumatra, Indonesia) data was collected from February to June 2014. At Tuanan (2° 09´ S, 114° 26´E, Mawas Reserve, Central Kalimantan, Borneo, Indonesia) data collection took place between March and August 2014. The research area at Suaq Balimbing consists of 500 ha primary peat swamp forest with adjacent areas of mixed dipterocarp hill forest, seasonally flooded freshwater swamp and some riverine forest. The research at area Tuanan consists of 750 ha recovering peat swamp forest, in which there had been selective logging in the past. At both sites long-term research projects are run by the Anthropological Institute of University of Zurich in collaboration with Fakultas Biologi of Universitas Nasional (UNAS), Borneo Orangutan Survival (BOS) Foundation in Tuanan and Sumatran Orangutan Conservation Program (SOCP) and Paneco in Suaq Balimbing. Behavioral observations on wild orangutans have been carried out from 1992 to 1999 and 2007 to date in Suaq Balimbing and 2003 to date in Tuanan. Most of the high quality conflict and infant data used in this study was collected by myself at Suaq Balimbing and by Julia Kunz at Tuanan. In addition, data of trusted fellow students and volunteers was incorporated. Most of the context data on the mothers was collected by well-trained assistants at both sites.

2.2 Study subjects and amount of data

To assess the development of mother-offspring conflict, behavioral data was collected simultaneously on differently aged immatures and their mothers. All of the study pairs were well known and habituated individuals. At Suaq Balimbing, birth month of immatures were known at least within a timespan of three months while the ages of older offspring were estimated according to absolute and relative size (Schuppli, pers.comm.). At Tuanan birth dates or at least birth months were known (van Noordwijk, pers.comm.). High quality data focusing on mother-offspring conflict could be collected on four different mother-offspring pairs at Suaq Balimbing and eleven different mother-offspring pairs at Tuanan (Table 1). In total, 1480h of follow data could be obtained from dependent offspring and juveniles ranging from four to 113 months of age, consisting of 547 hours in 57 follow days at Suaq Balimbing and 933 hours in 84 follow days at Tuanan. However, all data of the offspring Sony at age 52 months had to be excluded, since his mother had been lethally injured during a fight. Total follow days consisted of 11 found-to-nest, 40 nest-to-nest and 6 nest-to-lost at Suaq Balimbing and of 11 found-to-nest, 69 nest-to-nest and 4 nest-to-lost at Tuanan, ranging from 51 min to 13 h and 2 min.

Table 1 **Amount of data collect.**
Amount high quality follow data for each mother-offspring pair collected within a time span of six months, showing name, age and sex of the offspring, the name and age of the mother, the number of follow hours and the site where the data was collected.

Offspring	Offspring age (months)	Offspring sex	Mother	Mother age	Follow hours (hh:mm)	Site
Ivan	4	Male	Inul	Ancient	46:16:00	Tuanan
Ivan	7	Male	Inul	Ancient	84:25:00	Tuanan
Rendang	8	Male	Raffi	Young	63:58:00	Suaq Balimbing
Rendang	10	Male	Raffi	Young	73:50:00	Suaq Balimbing
Jane	11	Female	Juni	Young	11:12:00	Tuanan
Jane	12	Female	Juni	Young	56:26:00	Tuanan
Jane	14	Female	Juni	Young	08:45:00	Tuanan
Frankie	20	Male	Friska	Ancient	48:30:00	Suaq Balimbing
Frankie	21	Male	Friska	Ancient	51:23:00	Suaq Balimbing
Cinnamon	24	Female	Cissy	Ancient	24:41:00	Suaq Balimbing
Kahiyu	26	Female	Kondor	Young	59:26:00	Tuanan
Joya	35	Male	Jinak	Ancient	18:10:00	Tuanan
Joya	38	Male	Jinak	Ancient	43:29:00	Tuanan
Lois	44	Male	Lisa	Young	98:01:00	Suaq Balimbing
Lois	46	Male	Lisa	Young	45:19:00	Suaq Balimbing
Danum	47	Male	Desy	Young	63:00:00	Tuanan
Sony	49	Male	Sidony	Young	94:11:00	Tuanan
Sony	52	Male	Sidony	Young	63:00:00	Tuanan
Charlie	61	Male	Cikipos	Young	23:18:00	Tuanan
Mawas	70	Female	Mindy	Young	73:34:00	Tuanan
Mawas	72	Female	Mindy	Young	11:46:00	Tuanan
Ipsy	84	Female	Inul	Ancient	11:06:00	Tuanan
Ipsy	87	Female	Inul	Ancient	77:45:00	Tuanan
Kino	88	Male	Kerry	Young	52:10:00	Tuanan
Kino	91	Male	Kerry	Young	71:27:00	Tuanan
Jip	99	Male	Juni	Young	11:12:00	Tuanan
Jip	100	Male	Juni	Young	18:08:00	Tuanan
Ronaldo	100	Male	Raffi	Young	52:32:00	Suaq Balimbing
Jip	103	Male	Juni	Young	33:53:00	Tuanan
Fredy	111	Male	Friska	Ancient	46:09:00	Suaq Balimbing
Fredy	113	Male	Friska	Ancient	42:29:00	Suaq Balimbing

2.3 Data collection and analysis

Data was collected simultaneously by two observers on mother and offspring during focal follows. When found, a focal mother-offspring pair was followed to their evening nest, then full day follows from morning to evening nest were conducted ranging from five to ten consecutive days or until the focal animals were lost. For behavioral data collection, standardized methods of focal animal sampling including instantaneous scan sampling with two minutes intervals and ad libitum focal animal sampling following an established protocol for orangutan data collection (www.aim.uzh.ch/Research/orangutan-network.html) were used. In the two minute scan samples, the activity of the focal animal and its distance to all party members was recorded as contextual data. In this project, special attention was given to indicators of conflict between mother and offspring. These behaviors as well as the corresponding controls for baselines were documented ad libitum to get a complete record.

2.3.1 Behavioral measures

All occurrences of distinct behavioral measures were recorded ad libitum to detect mother-offspring conflict. When any of the behavioral elements was observed, the reaction of both the mother and the offspring was recorded as well.

Indicators of conflict

Offspring distress vocalizations: The context, kind and duration of distress vocalizations such as mips, whimpers, cries, screams or tantrums.

Rejection by the mother: The context, kind and quantity of rejections such as turning away, biting or chasing the offspring.

Offspring collect by the mother: The context, kind and quantity of a restraint or retrieve, including throat scrapes which are considered as offspring collect calls uttered by the mother (van Schaik et al. 2006)

An event was labeled as a conflict, if at least one of the conflict indicators was present and if it was evident that this conflict indicating behavior was caused by a behavior or state of the other individual of the mother-offspring pair.

Control data for baselines

Suckling and begging bouts: The quantity and duration of suckling and begging bouts. One bout is equal to one suckling or begging attempt. A bout can be successful or unsuccessful independent of conflict.

Offspring collects: All offspring restraints or retrieves as well as throat scrapes uttered by the mother. An offspring collect can be successful or unsuccessful, independent of conflict.

2.3.2 Components of conflict

We calculated the intensity of a conflict according to its components and total duration:

$$\text{Conflict intensity} = \text{Frequency of offspring collects} * \text{Maximal degree of intensity of offspring collects} + \text{Frequency of rejections} * \text{Maximal degree of intensity of rejections} + \text{Duration of distress} * \text{Maximal degree of intensity of distress vocalization} + \text{Total duration of conflict}$$

The duration of the conflict was added to the equation as an addition and not a multiplication, because the multiplying stratified the values too much. The frequency of rejections and collection was counted as the number of rejections per conflict or the number of collection cries whereas the duration of distress vocalizations was measured in intervals of two minutes.

To assess conflict intensity, each conflict indicator was scored according to the degree of intensity of distress, rejection or infant collects (Table 2). The frequency of rejections and offspring collects were measured in counts per conflict. The durations were categorized into classes, because exact duration was difficult to obtain.

Table 2 **Indicators of conflict.**
The kind of distress vocalization, rejection, offspring collect and reaction to distress determined the degree of intensity of each conflict indicator. The degree of intensity was scaled from one to four.

Degree of intensity	0	1	2	3	4
Vocal distress by infant	Other vocalization	Mip / Whimper	Cry	Scream	Tantrum
Examples[1]	Squeak, play oh, etc.	Short calls, roughly evenly pitched/ Soft whimmering sound	Cries, louder, higher pitched than whimper, sometimes with sobbing	Loud, high pitched, piercing sound, voice breaks	Crying, screaming accompanied by throwing or shaking branches
Rejection by mother	**Ignore**	**Passive**	**Active**	**Interactive**	**Agonistic**
Examples	Mother does not change behaviour	Mother shifts position, starts moving, keeps moving, move her hand away, taps offspring	Mother moves away, brushes offspring's hand away hand of offspring	Mother pushes, displaces offspring	Mother bites, chases offspring
Infant Collect	**Passive**	**Active**	**Interactive**		
Examples	Mother collects offspring- offspring cooperates	Offspring moves away, or hold on to something when mother tries to collect it	Offspring actively resists when mother tries to collect it		
Reaction to distress	**Ignore**	**Passive**	**Active**		
Examples	Mother does not change behavior	Mother stops moving until infant has caught up, lets infant nurse, take food	Mother returns, assists offspring		

[1] Examples of the different vocalizations are available on the Orangutan Network Homepage (http://www.aim.uzh.ch/research/orangutan-network/orangutancallrepertoires.html)

Table 3 **Duration of conflict.**
Conflicts were classified into one of five duration classes. Separate duration classes were made for the duration of distress vocalizations and the total duration of conflict

Duration Class	0	1	2	3	4	5
Distress vocalization	0s	1s-10s	11s-30s	30s-1min	1min-3min	>3min
Total Conflict	0s	1s-29s	30s-2min	2min-4min	4min-8min	>8min

2.3.3 Levels of conflict context

To tease apart different sources of conflict, all conflict events were divided into three main 'contexts' of conflict. Once labeled as in one context, the events then were split according the 'subject' of desire, which were again separated into different potential 'problems' (Table 4).

Table 4 **Levels of conflict context.**
The most general context level 'context' is subdivided into different 'subjects' of desire which are split into different 'problems'. Criteria for the classification of the different 'contexts', 'subjects' or 'problems' are listed for each level. At the level of 'problems', an event was labeled as a conflict if the criteria as indicated in brackets are met.

Context	Subject	Problem
Nutrition Caloric input	**Milk** Nipple access	**Suckle** Offspring tries to get/has nipple access (but is rejected/ignored and utters distress vocalizations)
	Solid Food Edible item	**Food solicit** Offspring tries to get/has solid food item (but is rejected/ignored or utters distress vocalizations).
		Theft Mother takes food from offspring (then offspring utters distress vocalizations).
Locomotion Offspring getting from one place to another	**Gap** Space between branches of different trees	**Independent cross** Offspring tries to cross a gap (and utters distress vocalizations).
		Gap collect Mother makes a body bridge across a gap and collects offspring (but offspring resists/utters distress vocalizations).
	Carry Offspring clinging to mother when mother moves	**No cling** Offspring tries to cling/or is clinging to the mother when the mother starts/is moving (but is rejected/ignored or utters distress vocalizations).
		Carry collect Mother collects offspring before/during moving (but offspring resists/utters distress vocalizations).
Proximity Distance between mother and offspring	**Distance** Offspring and mother are separated, no cling	**Too far** Offspring approaching/following mother (and utters distress vocalizations) after mother or offspring had increased distance to the other.
		Too close Mother or offspring approaches the other (then mother displaces offspring).
		Stay close Mother throat scrapes or restrains offspring to stay close but not in cling (but offspring does not react/resists/utters distress vocalizations).

Proximity Distance between mother and offspring	**Cling** Offspring clings to mother's body	**No cling** Offspring tries to cling/or is clinging to the mother (but is rejected/ignored and utters distress vocalizations)
		Cling collect Mother collects offspring and does not move (but offspring resists/utters distress vocalizations).
	Other	**Nest** Offspring tries enter nest of the mother (but mother displaces offspring).
		Baby Offspring tries to interact with younger sibling (but mother displaces offspring).
Other	**Other/Social/Special**	**Cry/Mip** Any distress vocalization caused by something else than mother-offspring conflict.
Unknown	**Distress**	**Cry/Mip** Any distress vocalization, for which it is unknown if it is due to mother-offspring conflict.

2.3.4 Variables of interest

For analyses on a daily basis variables of interest were mainly offspring age, food availability, offspring sex, mother age, number of party members and site. In brackets are the abbreviation as used in the results of the statistical analyses.

Offspring age (AgeO): Since exact birth dates are only known for a few individuals and follow days within one month were considered as one follow period, offspring age was used in (estimated) month and was set to be consistent within a follow period.

Sometimes it was necessary to use age classes. Four different age classes were defined according to locomotor development (van Noordwijk et al 2009) and sibling birth. The latter is the time by which an offspring is usually weaned: 0-2 years (offspring is in cling most of the time during travel), 2-4 years (transition between cling and independent travelling), 4 years-sibling birth (independently travelling until birth of sibling) and juvenile (younger sibling is present).

Normalized food availability (FA): A food availability index (FAI) had been measured once every mid-month. These FAIs had to be classified, because of the cemengang *(Neesia sp.)* season at Suaq Balimbing. During cemengang season, orangutans at Suaq Balimbing moved to the hills and almost exclusively fed on the highly nutritious cemengang seeds. Since cemengang trees are included in the phenology data used for the calculation of the FAI, FAI was classified by rounding them to the nearest 0.5, and assigning cemengang season months a food availability class (FAC) of plus one to the highest measured FAI. If a follow period was split over two months, average of the two FACs was calculated. This resulted in FACs of 5.5 to 8.5 at Suaq Balimbing and 2 to 4 at Tuanan. Since there was no overlap of the FAC between the two sites, FAC were normalized by calculating the mean FAC of every site during the study period. Then the mean of each site was set as the zero value and the remaining values were ordered in steps of one around zero, resulting in changes from -3 to 3 at Suaq Balimbing and -2 to 2 at Tuanan. Like this trends in the changes of food availability are still evident, but food availability is not dependent to site anymore. Effects of overall food availability should still be evident in the variable site. When referring to food availability, during the rest of the thesis normalized food availability is meant. If we refer to the non-normalized food availability, the term 'total food availability' will be used.

Offspring sex (Sex): Offspring sex was included in the analysis, but only one out of the four individuals at Suaq Balimbing was female, therefore no site-specific sex difference could be included in the analyses.

Mother age (AgeM): For the analyses, mothers were split into two age classes, which are roughly evenly distributed across the other factors, according to the lifetime number of known offspring. All mothers known to be very old had four or more known infants and were considered as “ancient”, the others as “young”.

Number of party members (NPM): The number of party members per day was measured as association partners in addition to the focal mother-offspring pair added up during the whole day. If there was a sibling present, it was also not taken into account, because of the dependency of sibling presence on age. Based on van Schaik (1999) and van Noordwijk and van Schaik (2005), other individuals were considered to be in association if there were within 50m of the mother-offspring pair. Since the number of party members in orangutans is usually low, I divided them into three classes consisting of no association partners, one to two association partners, and three or more association partners. This way, a party with another mother-offspring pair fits into the same class. For some analyses, only a one-zero indication, whether any party member was present or not, was used due to lack of data on party sizes of three or more association partners (indicated as PM in analyses). Number of party members per day and not only during an event was taken as a measure because it is very likely that orangutans are aware of the presence of others much earlier than we observers are.

Site (Site): Site was included as a factor to see population or ecological difference between the sites at Suaq Balimbing, Sumatra and Tuanan, Borneo.

2.4 Inter-observer reliability

The data used for this project was collected over a period of 6 months at two different sites by several observers. The high quality infant data used in this study was mainly collected by myself and Julia Kunz or volunteers trained by Caroline or me. In addition, mother data collected by volunteers or field staff was used to complement the data.

Starting February to March 2014 Julia Kunz and I were trained together in obtaining data by Caroline Schuppli at Suaq Balimbing. In addition to obtaining first data, we worked out detailed data collection methods and went on multiple follows together to assure that reliable and consistent data was taken at both sites. From March to July 2014 I collected data at Suaq Balimbing while Julia did the same at Tuanan. Finally, from July to August 2014 both Julia and I took data at Tuanan and went on multiple follows together again, to discuss the way the data had been collected and verify that data collected by either of us from both sites can be reliably used for analysis.

Inter-observer reliability was assured by the joint training, as well as by conducting inter-observer reliability tests between Caroline, Julia and me during the first month at Suaq Balimbing. Inter-observer reliability was calculated as Indices of Concordance and Spearman Correlations from full day follows during which both observers were taking data on the same individual without verbal exchange. Inter-Observer Reliability of Visibility, Cling and Activity resulted in a Spearman Correlation of 0.89 across the three observers (Table 5). In addition, Hannes Wiese, who was trained by me, and Anna Marzec, who was instructed by Julia, contributed a few follows to the data set.

Moreover, daily totals of frequencies independently collected ad libitum data of the same focal animal were compared for a measure of similarity of data between the different observers. Since there was not enough data from follows where two or more observers were following the same individual, inter-observer reliability was calculated from average hourly conflict rates of successive follows of the same individual using paired Wilcoxon Signed Rank Tests. Inter-observer reliability of ad libitum data could be calculated for Julia-Sonja (V=0, p=0.10, r=-0.73), Hannes-Sonja (V=2, p=0.79, r=-0.13) and Anna-Julia (V=2, p=1.0, r=0), concluding that there was some variation between the observers or the follow days, but the differences should not significantly affect the hourly conflict rate.

Nevertheless, one major difference in data collection was found during discussions on joint follows and therefore could be directly accounted for in the analyses. Julia did not record all occurrences of what I noted as the lowest intensity milk conflict. Thus I excluded those conflicts from my analyses.

Table 5 **Inter-Observer Reliabilities.**
Mean Index of Concordance for visibility, clinging to the mother and activity of the offspring as exact matches at one two minute scan per day and as matches of the percentage of the total recorded bouts per day, as well as the Spearman Correlation of the total bouts per day between the two observers.

	Type of Comparison	Mean IC - Visibility	Mean IC – Cling	Mean IC- Activity	Spearman Correlation- Total
Julia - Sonja	Exact Match	0.48	0.65	0.54	
	Total Bouts	0.85	0.79	0.96	0.90
Caroline - Sonja	Exact Match	0.54	0.80	0.68	
	Total Bouts	0.87	0.82	0.95	0.92
Caroline - Julia	Exact Match	0.78	0.84	0.67	
	Total Bout	0.84	0.90	0.98	0.84

2.5 Statistical analysis

For frequency analyses, linear mixed models (LMM) were conducted to avoid pseudo replication. Follow period nested in offspring ID nested in mother ID as a random factor was added to the models because a mother can have more than one offspring and data of those two offspring was sometimes taken on the same follow. Consecutive follow days of one individual at a certain age were not averaged before putting into the model to account for variance between follow days, but pseudo replication is taken care of by adding the follow period term to the random factors. Since data is non-orthogonal, best fit models were built by starting out with the maximal model including all parameters of interest and their meaningful two way interactions so that the circular inference due to the order of addition or deletion is reduced. The maximal model was then reduced by removing non-significant interactions until only main effects or significant interactions formed the model (Crawley 2009). Finally, the best-fit model was found by removing insignificant quadratic terms and insignificant main effect until the removal of a main effect did not increase model fit anymore.

To test which conflict indicator was the main component, binomial generalized linear mixed models (GLMM) were conducted and LMM were performed to assess the intensity of conflict and its components. For these analyses the random factors included were mother ID, offspring ID and follow day, because more than one conflict can happen during a follow day.

All statistical analyses were done with R (R Core Team 2014) in R Studio (R Studio 2014) mainly using the packages plyr (Wickham 2011) for summarizing data, nlme (Pinheiro et al. 2015) for conducting LMMs, lme4 (Bates et al. 2014) for building GLMMs and ggplot2 (Wickham 2009) for figures. Reported in tables are the models including all main effects and if present, significant interactions to show the effect of each main effect, even if it's not significant. Values and comparisons in the text are reported from the best-fit model. To remain consistent, all models were estimated using the maximum likelihood method. Residual plots of the best fit model were checked. Data points with standard residuals greater than four were considered as outliers. After investigation, outliers were removed from the dataset and the model was run again without the outlier.

2.5.1 Model setup and limitations

Every model included all six variables of interest as main factors and their meaningful two-way interaction to investigate their influence on mother-offspring conflict in a specific context. For offspring age an additional quadratic term was put in to allow non-linearity. To check for relevance of an interaction term, the two main factors of the interaction were plotted against each other. Interactions were looked at as meaningful if the data was distributed roughly evenly and there were at least three or more sample points for each category of a variable. The interactions NPM-Sex and NPM-Site had to be excluded from all analyses due to biased distribution in collected data. The interactions AgeM-Site and AgeM-NPM were also not included in the analyses due to the link of mother age to offspring age. Since no data on offspring between ages 47 and 99 is available in Suaq and therefore also not enough for large party size, mother age classes between the sites are biased due to offspring age. The interaction AgeO-Site can be included because offspring age is continuous, but has to be treated with caution. Same goes for the interaction NPM-FAIN because no data is available for ancient mothers at high food availability. If included, the interactions NPM-AgeM and Sex-Site have to be treated with caution, because data is limited. For conflict component and intensity analyses, no interactions were added to the model due to sample size limitations. All non-binary output variables were log-transformed for the analysis to approach normal distribution of the model residuals.

2.5.2 Reporting results

All factors contributing to the best fit model are reported in the text, even if not significant. Variables of interest that are not mentioned in the text decreased model fit. Main model outputs of the complete reduced model including all six main factors are given in in a box next to the results. Offspring age squared had always been included in the maximal model but -like insignificant interactions- are not

reported in the complete reduced model if not significant. If chi-squared result are given, the p-value expresses whether the best-fit model was significantly better than the null-model or not, unless mentioned otherwise. For legends that were plotted into a graph, we always very carefully checked not to cover up any data points.

3 Results

3.1 Conflict contexts

Overall, 471 mother-offspring conflicts were recorded. The conflicts can be grouped into three different contexts consisting of eight subjects, which can be split up into 14 different problems (Table 6). 171 of those conflicts were documented at Suaq Balimbing and 300 at Tuanan.

Table 6 **Total number of conflicts**.
All observed conflicts categorized into context, subject and problem.

Context		**Subject**		**Problem**	
Nutrition	103	Milk	32	Suckle	32
		Solid food	71	Food solicit	70
				Theft	1
Travel	100	Carry	27	No carry	11
				Carry collect	16
		Gap	73	Independent cross	54
				Gap collect	19
Proximity	268	Cling	7	No cling	4
				Stay cling	3
		Distance	248	Too far	226
				Too close	20
				Stay close	2
		Other	13	Baby	8
				Nest	5

3.2 Pre-analysis

The influence of visibility and follow time on mother-offspring conflict was examined, before examining mother-offspring conflict in relation to the variables of interest.

3.2.1 Visibility

Since, field experience suggested that visibility of the offspring might differ according to its age and site, we plotted visibility against offspring age. Visibility per hour was calculated from the 2-minute scan data, as the proportion pf scans per day during which the offspring was visible in relation to the total amount of 2-minute scans. Figure 11 shows that younger offspring were generally less visible per day than older offspring. As visibilities were not available for all follow days, I calculated the average visibility per age and site, by averaging the available data and fitting a curve which gives a theoretical visibility per age and site. For all following analyses, frequency per hour was corrected by the theoretical visibility per age and site.

3.2.2 Follow days, follow type and follow duration

To see if short follow periods yielded different conflict frequencies than longer periods, I examined the effect of total follow duration of a follow period on conflicts per hour. According to Figure 12 total follow duration only has a slight effect on conflict frequency (Figure 12), but it was mostly the longest follow periods that differed from the rest. If the three follow periods that were longer than five days are excluded, no effect of follow period duration on conflict frequency is present ($\chi^2(1)=0.06$ $p=0.800$) Since it would be expected that longer follow periods lead to better results, especially as the average daily conflict frequency had a large variance within a follow period, all data was thus used for the analyses.

Visual inspection of plots also showed that neither follow type ($\chi^2(2)=0.68$, $p=0.710$, Figure 13), nor follow duration ($\chi^2(1)=1.33$ $p=0.250$, Figure 14) had a major influence on conflict frequency. Therefore all data irrespectively of follow type or follow duration was included in the analyses.

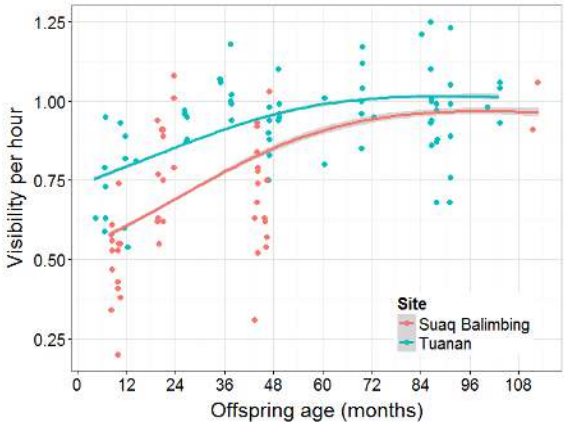

Figure 11. **Offspring visibility in relation to age and site.**
Visibility from two-minute scans per active hour across offspring age. Red stands for the site Suaq Balimbing, blue to Tuanan. N=230.

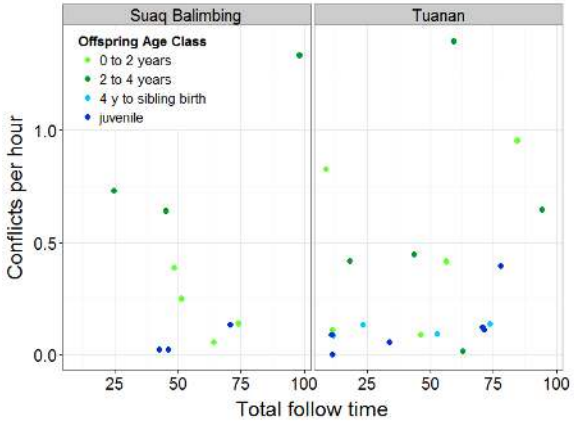

Figure 12. **Influence of total follow time on conflict frequency.**
Number of conflicts per active hour against total follow hours of an individual during one follow period. A follow period is equal to one offspring age in months and consist all follows not more than two weeks apart. Light green dots refer to 0-2 year-old offspring, dark green to 2-4 year-olds, light blue to 4 year-olds until a sibling is born, dark blue to offspring with a younger sibling. N=30.

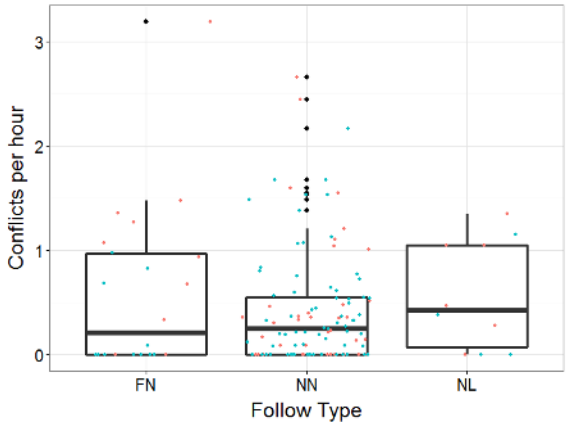

Figure 13. **Influence of follow type on conflict frequency.**
Number of conflicts per active hour against follow type. Follow types are found-to-nest (FN), nest-to-nest (NN) and nest-to-lost (NL). Follow types can have any duration, but generally NN are longer. Red stands for the site Suaq Balimbing, blue to Tuanan. N=115

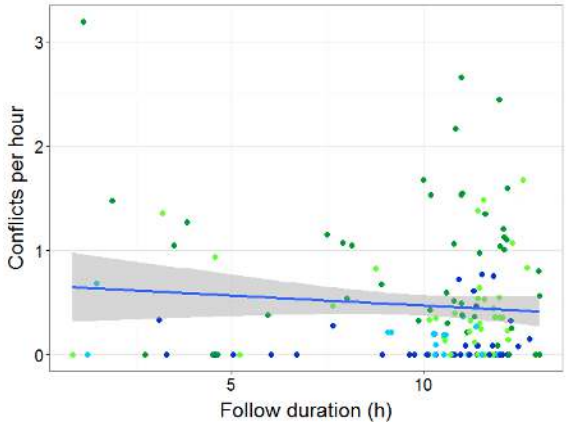

Figure 14. **Influence of follow duration on conflict frequency.**
Number of conflicts per active hour in relation to the total number of hours the offspring was followed during one day. Light green dots refer to 0-2 year-old offspring, dark green to 2-4 year-olds, light blue to 4 year-olds until a sibling is born, dark blue to offspring with a younger sibling. N=115.

3.2.3 Time of day effect

To examine whether the time of day had an influence on the number of observed conflicts, I plotted the mean number observed conflicts per 'day block' across the different 'problems' and age classes. 'Day blocks' were categorized by the hour of day: 5.00-8.00, 9.00-11.00, 12.00-14.00 and 14.00-18.00. The first and the last day blocks consist of four instead of three hours because waking time and sleeping time varied from day to day. Since the sun rises one hour earlier at Tuanan than at Suaq Balimbing, orangutans at Tuanan awaken approximately one hour earlier than those at Suaq Balimbing. Therefore I adjusted Tuanan time to Suaq Balimbing time by adding one hour, before fitting the 'day blocks'.

The time of day, did not seem to affect conflict frequency of most 'problems' (Figure 15). There could be a time of day effect in begging conflicts for offspring up to two years of age and in suckling conflicts in offspring between four years of age to weaning. In addition, juveniles seemed to have more conflicts towards the end of the day. However, I still used all of the data because the number of times an offspring was observed during a particular 'day block' was similar. Offspring aged zero to two years were sampled 113.5±3.7 times per day block, two to four year olds 258.5±6.0 times, four year old to offspring with younger sibling 16.25±0.5 times and offspring with a younger sibling 47.25±0.5 times. Therefore the time of day effect, particularly on juveniles, should not bias the results even if not only full day follows were used. However, day time effects should be kept in mind if there are any results that might be caused by time of day effects.

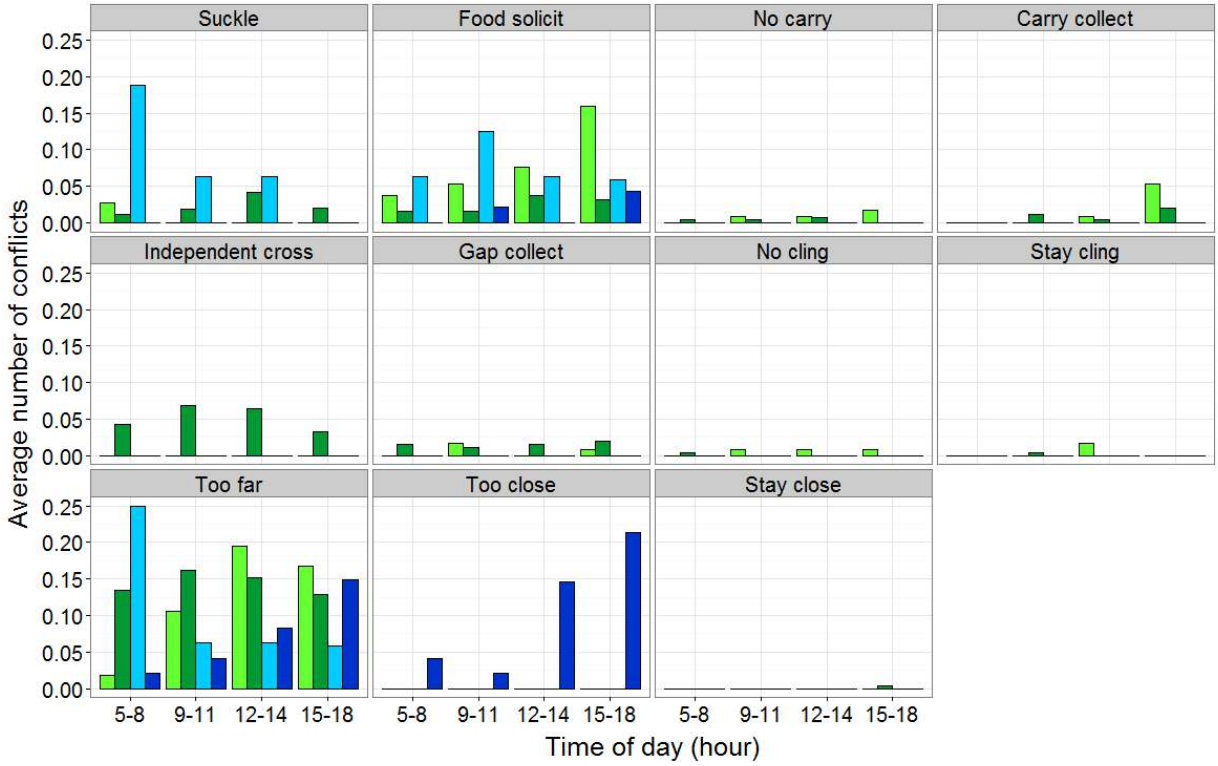

Figure 15. **Influence of the time of day on mother-offspring conflict frequency.**
The average number of conflicts hour in relation to a three to four hour block during one day. Each graph represents one conflict 'problem'. Light green dots refer to 0-2 year-old offspring, dark green to 2-4 year-olds, light blue to 4 year-olds until a sibling is born, dark blue to offspring with a younger sibling. N=141.

3.3 Age trajectories

A main aim of this study was to find out, how the contexts of mother-offspring conflicts change during offspring development. Therefore I examined all hourly conflict frequencies for each conflict 'problem' in relation to offspring age. As we were mainly interested in the age trajectories and whether they differ between the sites, the only interaction included in the following analyses was offspring age*site. Still, all six main factors were included to account for confounding variables. All analyses in this section were conducted using hourly frequencies per day (N=141 in 30 follow periods).

Nutrition

'Suckle' conflict frequency increased with offspring age to peak when the offspring was around four years of age and then decreased again (b=-0.000, t(11)=-3.37, p=0.06, Figure 16a). The peak in conflict at the offspring age of four years was mainly due to the mother-offspring pair Lisa and Lois at Suaq Balimbing. By looking at the figure, we see that conflict frequency at Tuanan stays rather low and tends to increase slightly until the offspring reaches the age of seven. A trend to a site difference was evident with mother-offspring pairs at Suaq Balimbing having slightly more 'suckle' conflicts per hour than those at Tuanan (b=-0.023, t(11)=-1.92, P=0.081), but there was no significant interaction between offspring age and site. However, the main factor influencing hourly conflict frequency of 'suckle' conflicts was the number of association partners present per day. Conflict frequency increased significantly during days with three or more individuals in association (b=0.123, t(109)=6.57, p<0.0001).

Offspring age was also the best factor out of these six to explain the frequency of 'food solicit' conflicts. 'Food solicit' conflict frequency tended to decrease with increasing offspring age, but the effect was only marginal (b=0.0001, t(12)=-1.82, 0.094, Figure 16b). Only one conflict resulted from the mother stealing a food item from its four-year old offspring.

Locomotion

Carrying conflicts decreased with age. Both, 'no carry' (b=0.000, t(12)=-2.16, p=0.051, Figure 16c) and 'carry collect' frequencies (b=-0.000, t(12)=-2.32, p=0.039, Figure 16d) were elevated until the offspring was four years of age and was highest in one year-olds, respectively zero year-olds. The most significant effect on conflict frequency for 'carry collect' conflicts was the number of association partners present per day. Conflict rate increased significantly if three or more individuals were in association (b=0.056, t(109)=3.61, p=0.0003). However the number of observed conflicts was low for both conflict 'problems'.

'Independent crossing' conflict frequency peaked in four-year old offspring (b=0.000, t(11)=-3.20, p=0.008, Figure 16e) and tended to differ between the sites (b=0.043, t(11)=-1.86, p=0.089). A site difference was also found in 'gap collect' conflicts, as they only occurred at Suaq Balimbing (b=-0.033, t(11)=-2.78, p=0.018). No age effect on 'gap collect' conflict frequency was found (Figure 16f). Yet, from the plot it was evident that they only occurred up to the offspring age of four.

Proximity

A significant effect of age on conflict frequency was neither found for 'no cling' (Figure 16g) nor for 'stay cling' conflicts (Figure 16h). However, age was still the best explanatory factor.

'Too far' conflicts were the most frequent conflicts to occur in offspring of almost all ages. 'Too far' conflict frequency decreased with offspring age and was highest when the offspring was about two years old (b=-0.002, t(12)=-2.81, p=0.016). By looking at Figure 16i, we might expect a site difference, but no significant effect of site was found. However, if three or more individuals were in association, 'too far conflict frequency was significantly elevated (b=0.144, t(109)=2.54, p=0.012). The mother only displaced her offspring when it was older than seven years of age and already had a younger sibling (b=0.000, t(12)=3.35, p=0.006, Figure 16k). A mother restricting an offspring not to leave her close proximity was observed only once in a mother-offspring pair at Tuanan with a four-year old offspring.

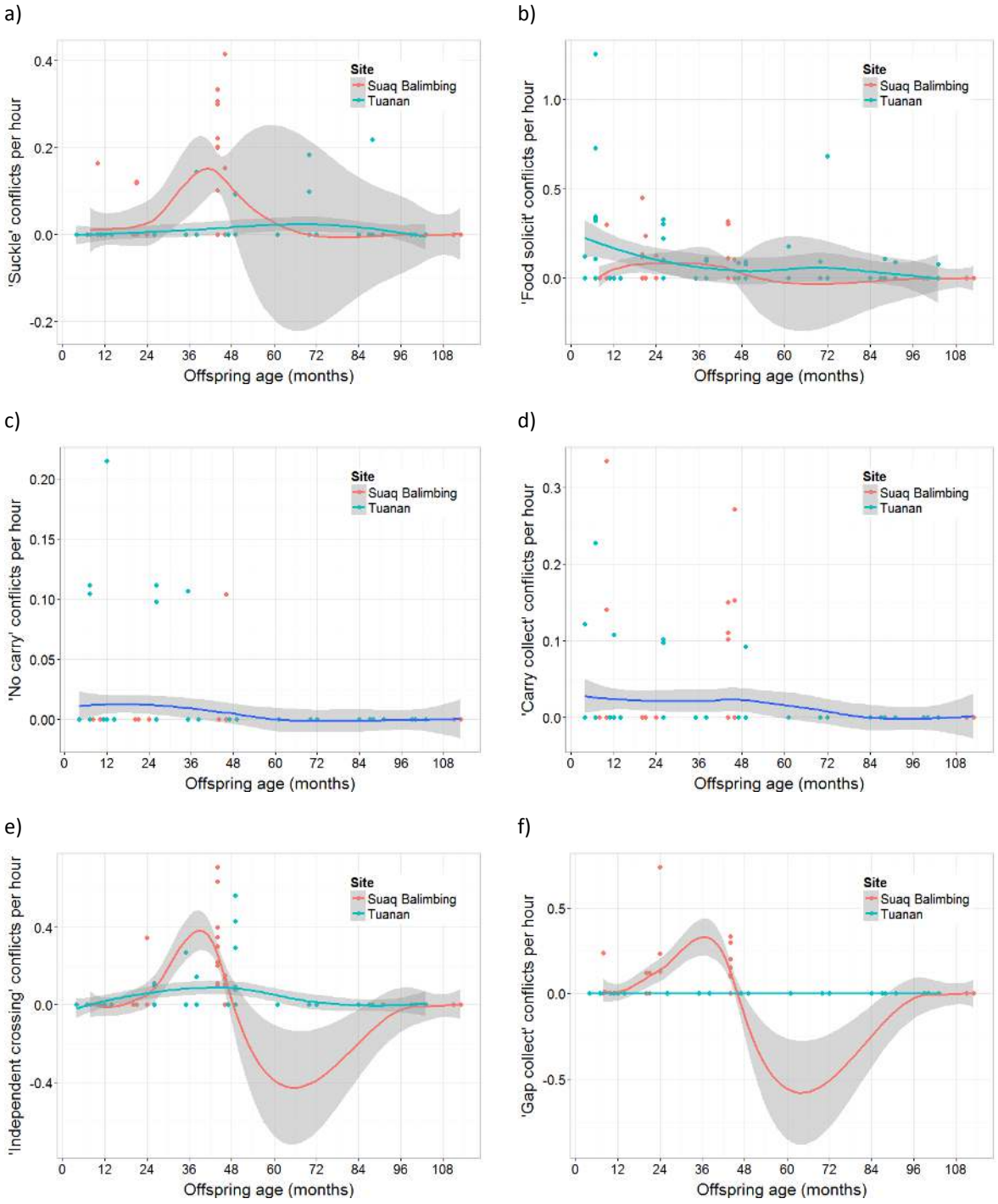

Figure 16. **Conflict frequencies per hour (1).**
Conflict frequencies per active hour in relation to offspring age. Conflict context 'problems' are a) 'suckle', b) 'food solicit', c) 'no carry', d) 'carry collect, e) 'independent crossing', f) 'gap collect'. Red stands for the site Suaq Balimbing, blue for Tuanan. N=141

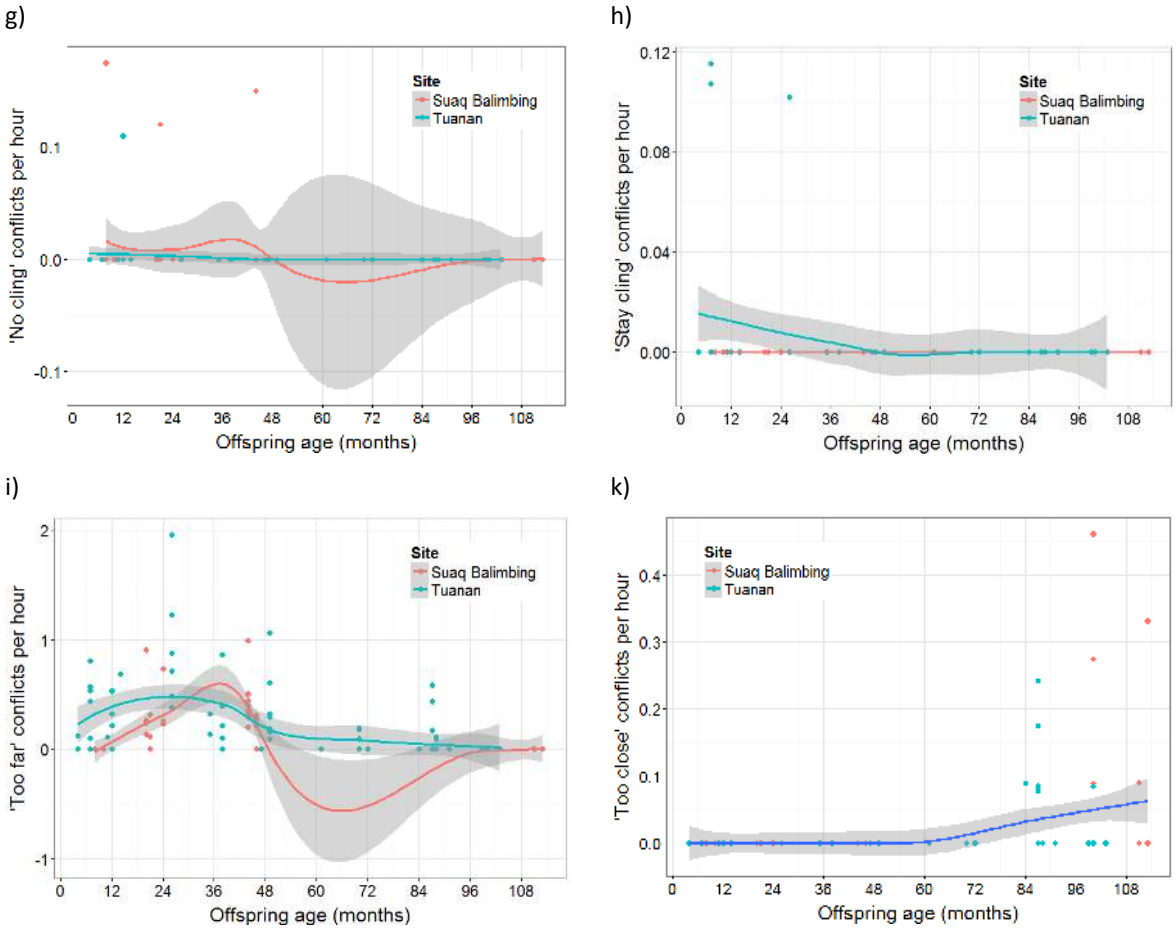

Figure 17 **Conflict frequencies per hour (2).**
Conflict frequencies per active hour in relation to offspring age. Conflict context 'problems' are g) 'no cling', h) 'cling collect', i) 'too far' and k) 'too close'. Red stands for the site Suaq Balimbing, blue for Tuanan. N=141

3.4 Overall conflict

To get an overview of conflict in general, I pooled all of the conflicts for first analyses. As the opportunities for each conflict 'problem' are not all expressed best by the same baseline, overall conflict frequency was measured in relation to the duration of the active period per day. Therefore the following results indicate the conflicts or intensities observed per day irrelative of opportunities.

These analyses showed that general hourly conflict frequencies were mainly affected by party members present per day and offspring age. Conflict rate increased by 86% if three or more party members were present that day (b=0.248, t(101)=3.38, p=0.001, r=1.000, Figure 18a) and generally decreased with offspring age (b= -0.003, t(12)=-2.86, p=0.014). Yet from the plot it was evident that conflict rate was lower in the youngest offspring and seemed to peak in three year olds (Figure 18b).

Box 1
Overall conflict frequency per hour
Best fit model: $\chi^2(3)=18.74$, p=0.0003
Full model: $\chi^2(7)=21.76$, p=0.003
Nr. Observations: 141
Groups: Mother 13/Name 17/Period 30
Table 7 **Overall conflict frequency.** Model output from linear mixed model testing conflicts per hour.

	Value	DF	t	p
(Intercept)	0.512	101	4.29	0.00
AgeO	-0.003	11	-2.65	0.02
FAIN	-0.144	3	-1.57	0.21
Sex (m)	-0.003	11	-0.11	0.91
AgeM (y)	-0.024	10	-0.29	0.78
NPM (1-2)	-0.006	101	-0.14	0.89
NPM (3+)	0.253	101	3.37	0.00
Site (T)	-0.010	10	-0.12	0.91

Most conflicts were characterized by offspring distress vocalization (80%), followed by rejections by the mother (27%) and resisted offspring collects (9%). This adds up to more than 100% because a rejection or an offspring collect could be accompanied by offspring distress.

Whether an offspring uttered distress vocalizations ($\chi^2(3)=29.24$, p<0.0001), was rejected ($\chi^2(3)=33.08$, p<0.0001)or resisted when collected ($\chi^2(2)=19.85$ p<0.0001) during a conflict depended mostly on offspring age and site. An offspring was rejected more frequently when it was older (b=0.752, z=4.67, p<0.0001, Figure 19a) and at Suaq Balimbing (b=-0.073, z=--3.14, p=0.002). Resistance or distress vocalizations as a response to offspring collects was found more frequently when the offspring was younger (-0.029, z=-2.72, p=0.007, Figure 19b) as well as four times more per conflict at Suaq Balimbing than at Tuanan (b=-2.002, z=5.05, p=<0.001). Most conflicts were accompanied by distress vocalizations until the offspring was four years old, then distress rate started to drop (b=0.000, z=-3.79, p<0.001, Figure 19c). Distress vocalizations were heard 1.4 times more per conflict at Tuanan than at Suaq Balimbing. Conflict duration peaked between the offspring's third and fourth birthday (b=-0.000, t(72)=-2.56, p=0.01, Figure 20) and was shorter when more party members were present per day (b=-0.120, t(72)=-2.57, p=0.01). For all analyses in this section N was 468 in 93 follow days.

Conflict intensity increased across age (b=0.003, t(75)=3.87, p=0.0002, N=468 in 93 follow days), which was mainly due to an increase in rejection intensity (b=0.003, t(41)=3.06, p=0.004, N=107 in 57 follow days, Figure 21a). Offspring collect intensity tended to decrease (b=0.059, t(11)=1.97, p=0.07, N=39 in 25 follow days), whereas distress intensity increased slightly (b=-0.042, t(53)=-2.53, p=0.02, N=293 in 68 follow days, Figure 21b) due to the higher degree of intensity but also longer distress bouts if food availability was lower. Intensity was measured in relation to the conflict component of interest.

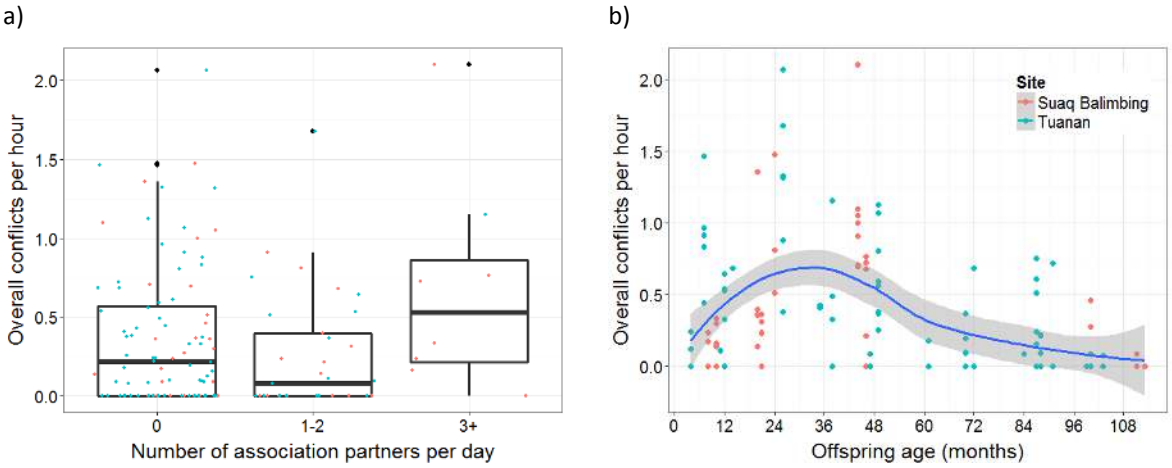

Figure 18. **Overall conflicts per hour.**
Overall conflicts per active hour a) in relation to the number of association partners present during one day and b) in relation to offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=141

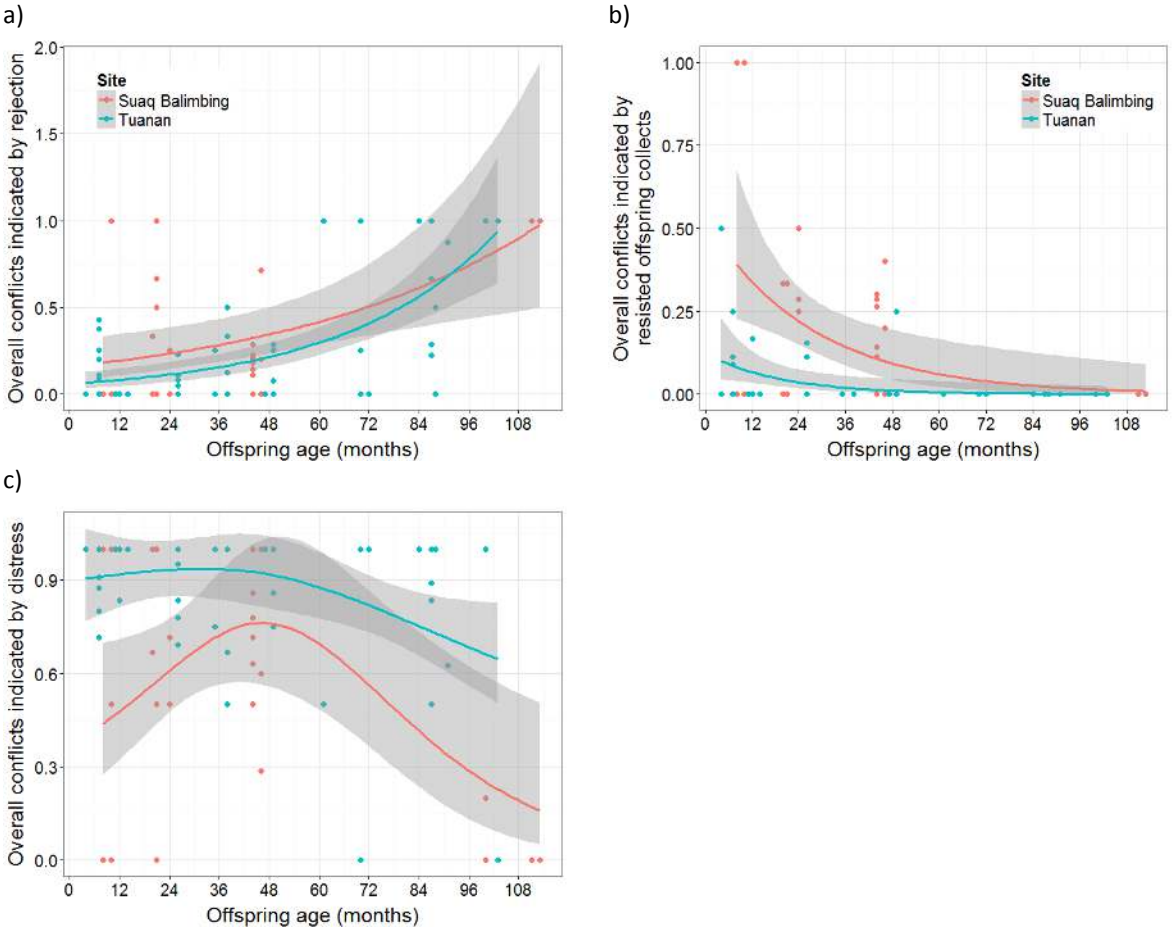

Figure 19. **Conflict components in relation to offspring age.**
The number of times a conflict was indicated by a) rejection by the mother, b) offspring collects which resulted in resistance or distress vocalizations, c) offspring distress vocalizations per day in relation to offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=141

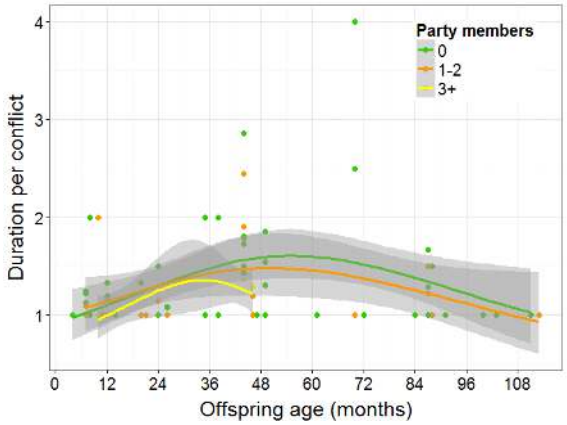

Figure 20. **Conflict duration in relation to offspring age and association partners.**
The average duration of each conflict per day in relation to offspring age. Conflict duration is longest if no other individuals are in association (green) and decreases if one or two (orange) or three or more (yellow) association partners are present during one day. N=141

a) b)

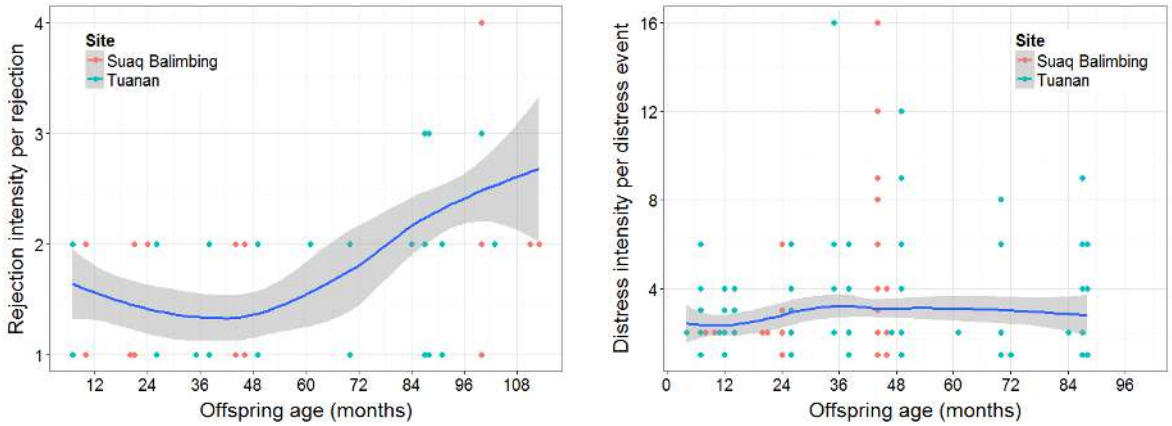

Figure 21. **Intensity of conflict in relation to offspring age.**
a) Rejection intensity (Degree of rejection intensity) (N=106) and b) intensity of distress vocalizations (Degree of distress vocalization intensity*duration of distress vocalization, N=377) per day in relation to offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan.

3.4.1 Distress vocalizations

If each of those components were analyzed separately, we found the amount of distress vocalization per hour decreased with offspring age starting when the offspring is four years old (b=-0.002, t(12)=-2.28, p=0.04).

More distress vocalizations were heard if three or more party members were present during a day (b=0.146, t(109)=2.38, p=0.019).

In addition, there were 332 distress vocalizations heard that could not be attributed to any context (**Error! Reference source not found.**). Since it was unclear if the offspring uttered distress vocalizations due to a mother-offspring conflict or if the reason was something else, these distress vocalizations were not taken into account for the mother-offspring conflict analyses.

Box 2
Offspring distress vocalizations in MOC context per hour
Best fit model: $\chi^2(3)=10.80$, p=0.013.
Full model: $\chi^2(7)=14.64$, p=0.041
Nr. Observations: 141
Groups: Mother 13/Name 17/Period 30
Table 8 **Frequency of distress vocalizations in conflict context.**
Model output from linear mixed model testing the number of distress vocalizations in conflict context per active hour.

	Value	DF	t	p
(Intercept)	0.317	109	3.12	0.00
AgeO	-0.002	11	-2.25	0.05
FAIN	-0.002	11	-0.07	0.95
Sex (m)	-0.109	3	-1.40	0.26
AgeM (y)	-0.011	10	-0.15	0.88
NPM (1-2)	0.034	109	1.01	0.31
NPM (3+)	0.157	109	2.52	0.01
Site (T)	0.062	10	0.86	0.41

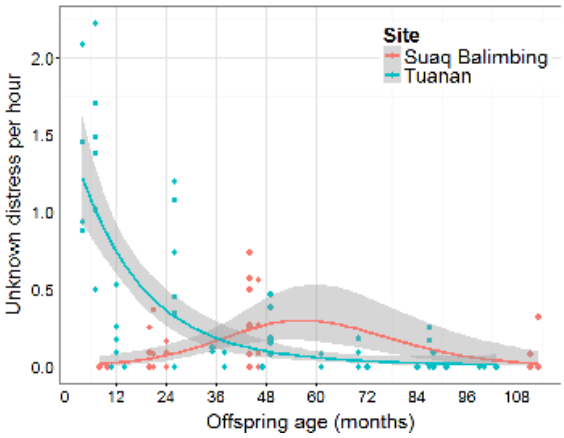

Figure 22 **Unknown distress vocalizations in relation to offspring age.**
The frequency of distress vocalization with unknown context per active hour in a day in relation to offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=141

3.4.2 Rejections

Rejections per hour increased, when daily party size was larger than two additional individuals (b=0.098, t(109)=2.49, p=0.01).

Box 3
Rejections by the mother per hour
Best fit model: $\chi^2(2)=7.16$, p=0.028
Full model: $\chi^2(7)=10.19$, p=0.178
Nr. Observations: 141
Groups: Mother 13/Name 17/Period 30
Table 9 **Rejection conflict frequency.** Model output from linear mixed model testing the number of rejections per active hour.

	Value	DF	t	p
(Intercept)	0.087	109	2.37	0.02
AgeO	0.000	11	0.49	0.64
FAIN	0.010	11	1.36	0.20
Sex (m)	-0.009	3	-0.33	0.76
AgeM (y)	-0.028	10	-1.16	0.27
NPM (1-2)	-0.014	109	-0.66	0.51
NPM (3+)	0.088	109	2.16	0.03
Site (T)	-0.010	10	-0.41	0.69

3.4.3 Offspring collects

Both, all events of offspring collects and offspring collect conflicts per hour were observed more commonly at Suaq Balimbing than at Tuanan (b=-0.081, t(11)=-2.62, p=0.024) and up to the offspring's fourth birthday (b=0.000, t(12)=-2.23, p=0.045). However, the frequency of offspring collect conflicts in relation to all offspring collect events did not vary in relation to any of the factors.

Box 4
Resisted offspring collects per hour
Best fit model: $\chi^2(2)=10.82$, p=0.005
Full model: $\chi^2(7)=18.20$, p=0.011
Nr. Observations: 141
Groups: Mother 13/Name 17/Period 30
Table 10 **Offspring collect conflict frequency.**
Model output from linear mixed model testing the number of offspring collects which resulted in resistance or the uttering of distress vocalizations per active hour.

	Value	DF	t	p
(Intercept)	0.123	109	3.49	0.00
AgeO	0.000	11	-2.13	0.06
FAIN	-0.009	11	-1.41	0.18
Sex (m)	-0.013	3	-0.64	0.57
AgeM (y)	-0.007	10	-0.21	0.83
NPM (1-2)	-0.005	109	-0.31	0.75
NPM (3+)	0.058	109	2.09	0.04
Site (T)	-0.078	10	-2.61	0.03

3.5 Nutrition

3.5.1 Milk

Milk events were indicated by the offspring attempting to initiate nipple contact and were measured as frequency per active hour.

3.5.1.1 Suckle

The number of times an offspring was seen at the nipple or trying to get nipple access per day ('suckle' events), depended mainly on offspring age (b=0.000, t(10)=-3.00, p=0.013, N=140, Figure 23a). Observed suckling frequency started at around four 'suckle' events per active hour in the youngest offspring, increased to eight events in four-year old offspring and then decreased again until the offspring was fully weaned around eight years of age. If there were three or more party members present during a day, suckling frequency increased by 67% (b=0.142, t(108)=2.08, p=0.040, r=1.000, N=140, Figure 23b). Food availability was also included in the best fit model and influenced suckling frequency by decreasing it during higher food availability (b=0.020, t(10)=-1.31, p=0.220, N=140). Since the offspring was usually not visible during rest-in-nest time, I ran the analysis again with frequency per hour of non-nest time. The same pattern was found when rest-in-nest time was excluded. For the analysis one outlier of four-year old Lois was removed. Suckling frequency was three times higher than his average hourly frequency, probably because it was a found-to-nest follow which lasted only about an hour. An unknown individual was in party.

Box 5
Suckle events resulting in conflict per day
Best fit model: $\chi^2(4)=38.99$, $p<0.0001$
Full model: $\chi^2(7)=87.40$, $p<0.0001$
Nr. Observations: 84
Groups: Name 13/Period 20
Table 11 **'Suckle' conflict frequency.** Model output from linear mixed model testing conflicts per 'suckle' event.

	Value	DF	t	p
(Intercept)	-0.007	62	-0.16	0.87
AgeO	0.002	5	3.59	0.02
FAIN	0.004	5	0.45	0.67
Sex (m)	0.006	9	0.19	0.86
AgeM (y)	-0.010	9	-0.35	0.73
NPM (1-2)	0.001	62	0.05	0.96
NPM (3+)	0.192	62	4.90	0.00
Site (T)	-0.042	9	-1.56	0.15

Out of 358 suckle events, 32 resulted in a conflict. The rate of 'suckle' conflicts was measured as 'suckle' events per day which resulted in conflicts per total 'suckle' events that day. 'Suckle' conflict rate increased with offspring age (b=0.002, t(6)=3.48, p=0.008, N=84, Figure 24a). In addition, during days with three or more party member present, conflict rate increased significantly from 1.1 conflicts per day when no party members were present to 7.5 conflicts per day (b=0.197, t(62)=5.22, p<0.0001, r=1.000, N=84, Figure 24b). Additionally, a tendency for a site difference was evident, with more 'suckle' events resulting in conflicts at Suaq Balimbing compared to Tuanan (b=-0.046, t(11)=-1.87, p=0.089, r=1.008). Offspring older than 90 month all had a younger sibling and were not included in the analyses, because they were already weaned so no suckling bouts were observed. Also one outlier was excluded from the analysis, but the results stayed approximately the same as when it was included. The outlier was Mawas, a 70 month old offspring who had two suckle events that day that both resulted in conflict. Both times she cried after she had had nipple access.

Suckling conflicts were characterized by rejections and distress. Of all recorded conflicts, 22 involved a seen rejection and 15 a distress vocalization. The longest conflict lasted five minutes, but generally a suckle conflict lasted less than 30s. For analyses within conflicts only offspring age, food availability and number of party members were taken into account because of unevenly distributed or lacking data of the other factors. The number of conflicts characterized by rejections decreased with offspring age (b=0.002, z=2.92, p=0.003, N=32 in 18 follow days, Figure 25a). Distress rate per conflict decreased with an increasing number of association partners per day (b=-2.18, z=-2.31, p=0.02, N=32 in 18 follow days, Figure 25b).

'Suckle' conflicts increased in distress intensity with increasing offspring age (b=0.046, t(8)=2.85, p=0.022, N=32 in 18 follow days, Figure 26a), but tended to decrease if more party members were present (b=-1.197, t(8)=-2.05, p=0.075, r=1.016, N=32 in 18 follow days, Figure 26b). No factor affected rejection intensity, conflict duration or total conflict intensity.

Even though there were up to seven party members present during one day, when conflicts happened, only one or rarely two party members were present. Out of the 31 suckle events observed while the mother-offspring pair was in association with other individuals, six resulted in a conflict. Conflict rate as well as rejection and distress intensity per conflict did not depend on the identity of the party member (none, mother-offspring pair, unflanged or flanged male) in association during the conflict. However effect sizes were very small.

Box 6
Comfort suckles per hour
Best fit model: $\chi^2(1)=6.17$, p=0.013
Full model: $\chi^2(6)=8,11$, p=0.23
Nr. Observations: 85
Groups: Name 13/Period 20
Table 12 **'Comfort suckle' frequency.**
Model output from linear mixed model testing conflicts per active hour.

	Value	DF	t	p
(Intercept)	-0.012	64	-0.40	0.69
AgeO	0.000	5	0.54	0.61
FAIN	-0.004	5	-0.65	0.54
Sex (m)	0.015	9	0.66	0.53
AgeM (y)	0.019	9	0.88	0.40
PM (yes)	0.037	64	2.30	0.02
Site (T)	-0.009	9	-0.44	0.67

Additionally, it has to be mentioned that not all suckling events seemed to be for milk acquisition, but the offspring also tried to get nipple access for comfort after travel or distance conflicts. These 'comfort suckles' were observed 24 times across all ages at both sites. For the following analysis, I reduced number the classes of association partners from three to two: either party members present or not. When party members were present, the total amount of comfort suckles per hour increased (b=0.038, t(64)=2.545, p=0.013, Figure 27). When the frequency of comfort suckles was set in relation total number of suckle events, there was an interaction effect of party members and site (b=0.016, t(63)=2.65, p=0.010, χ^2=15.38, p=0.002). The number of comfort suckles in relation to total 'suckle' events increased greatly at Tuanan if party members were present, whereas at Suaq they increased only slightly.

Moreover, a behavior, which I called a "nursing snap", only seemed to occur at Suaq, but not at Tuanan. The nursing snap is when the offspring was suckling, or in one case tried to suckle, and then the mother snapped at the offspring. Almost always the offspring stopped suckling as a reaction, but sometimes suckling started again shortly after the snap. This behavior was recorded 13 times in two different mother-offspring pairs. 'Nursing snap' events happened up to three times per day and individual 'nursing snaps' up to four times during a suckle event. This behavior was also scored as a conflict, because the offspring often stopped suckling after a snap and once even cried. Since party size and offspring age were significant explanatory factors in explaining suckle conflicts, I plotted number of snaps per day against offspring age, number of party members per day and type of party member present during the snap, but there was no visible pattern.

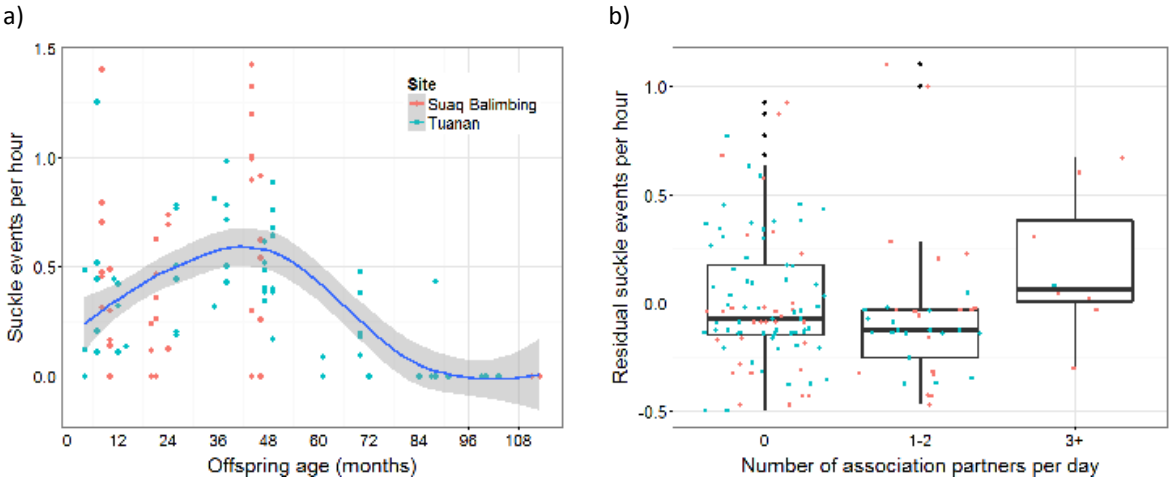

Figure 23. **Suckle events per hour.**
The number of observed suckle events per active hour a) in relation to offspring age and b) in relation to the number of association partners present during one day. Residual events are corrected for offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=141

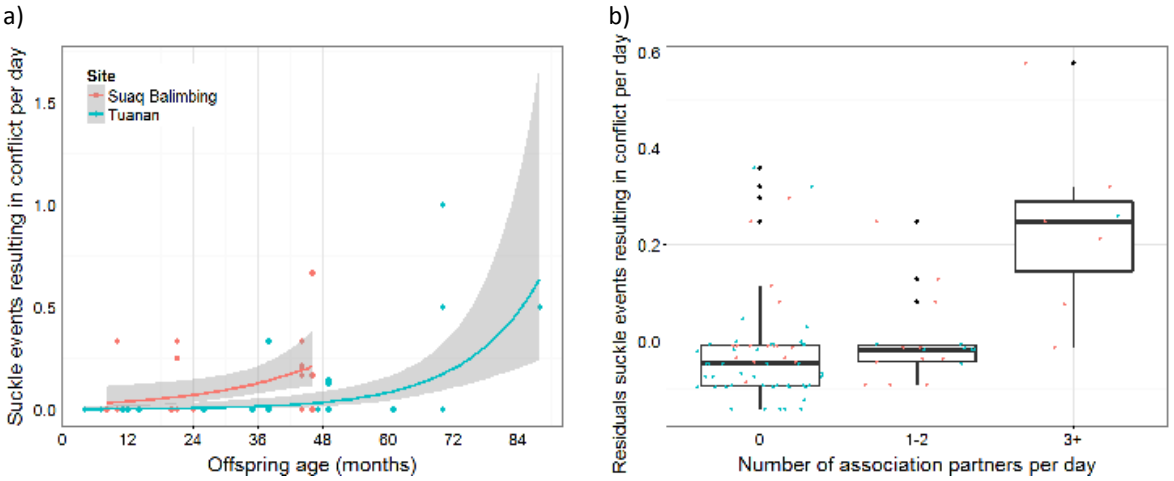

Figure 24. **Suckle conflict rate.**
The number of conflicts per observed suckle event a) in relation to offspring age and b) in relation to the number of association partners present during one day. Residuals event are corrected for offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=141

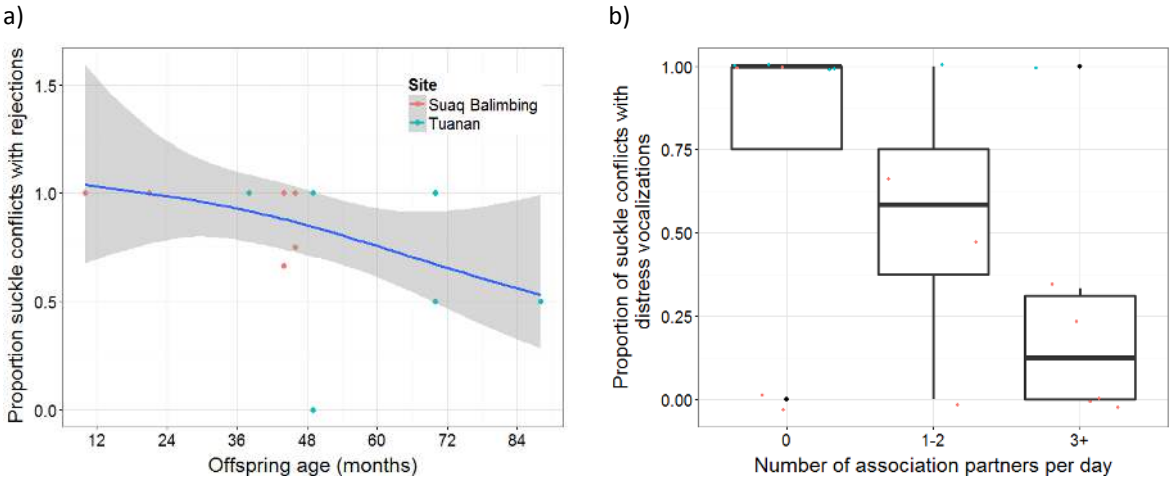

Figure 25. **Conflict components per suckle conflict.**
The number of suckle conflicts indicated by a) rejections in relation to offspring age and b) distress vocalizations in relation to the number of association partners present during one day. Red stands for the site Suaq Balimbing, blue for Tuanan. N=84

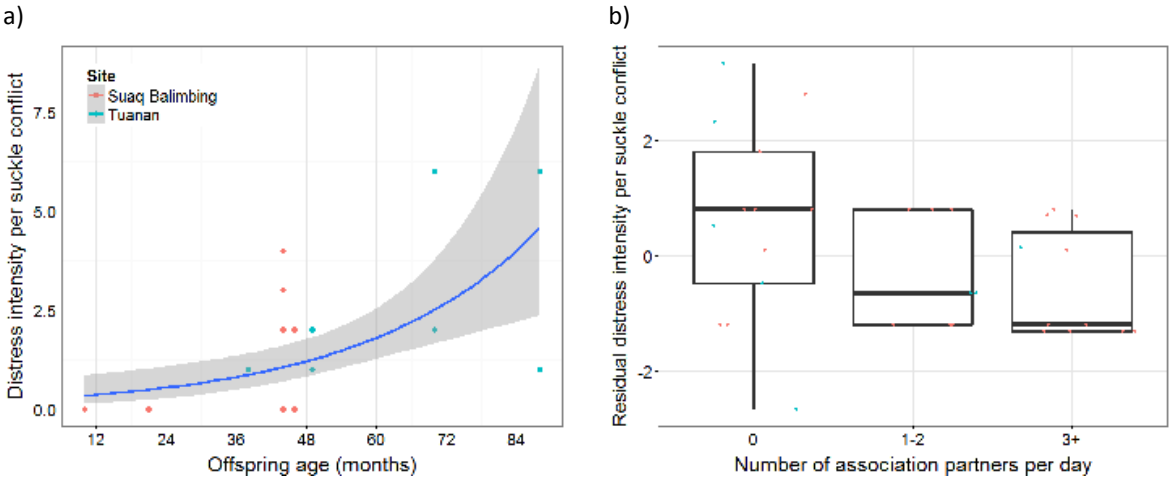

Figure 26. **Distress intensity per suckle conflict.**
Distress intensity (Degree of distress vocalization intensity* distress vocalization duration) per suckle conflict in relation to a) offspring age and b) the number of association partners present per day. . Residuals event are corrected for offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=32

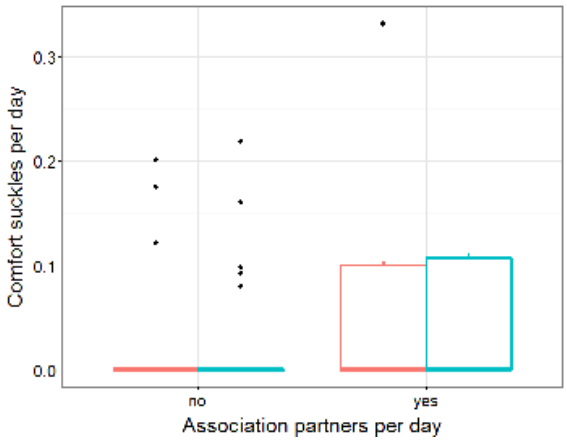

Figure 27. **Influence of association partners on comfort suckles.**
Number of comfort suckle per hour and day in relation to whether association partners are present or not. Red stands for the site Suaq Balimbing, blue for Tuanan. N=141

3.5.2 Solid food

3.5.2.1 Food solicit

The amount of 'food solicit' bouts per feeding hour of the mother decreased with offspring age (b=-0.000, t(11)=-4.92, p=0.0005, Figure 28) and tended to increase with increasing food availability (b=0.003, t(11)=1.86, p=0.090).

The rate of 'food solicit' conflicts was measured as conflicts per observed 'food solicit' bout. 'Food solicit' conflict rate could not be explained by any of the observed six variables of interest. However, there was a strong tendency for higher conflict rates at Tuanan than at Suaq Balimbing (b=0.133, t(11)=2.14, p=0.06, r=0.991). In Tuanan 30% of the 'food solicit' events resulted in a conflict, whereas it was only 11% at Suaq Balimbing. Thus, we replaced the factors 'normalized food availability' and site by the FAI corrected for cemengang season, to examine if total food availability seems to be the main factor responsible for the difference between the two sites. This analysis resulted in a best-fit model including only FAIC ($\chi^2(1)=3.26$, p=0.059), showing that low food availability increases conflict rate significantly (b=-0.026, t(56)=-2.19, p=0.03, Figure 29a).

Box 7
Food solicit conflicts per food solicit event
Best fit model: $\chi^2(1)=4.16$, p=0.042
Full model: $\chi^2(7)=10.69$, p=0.153
Nr. Observations: 81
Groups: Mother 13/Name 15/Period 24
Table 13 **'Food solicit' conflict frequency.** Model output from linear mixed model testing conflicts per 'food solicit' event.

		Value	DF	t	p
(Intercept)		0.061	55	0.60	0.55
AgeO		0.001	7	1.09	0.31
FAIN		0.003	7	0.15	0.89
Sex (m)		0.086	1	1.15	0.46
AgeM (y)		-0.097	10	-1.31	0.22
NPM (1-2)		-0.037	55	-0.54	0.59
NPM (3+)		-0.083	55	-0.75	0.46
Site (T)		0.127	10	1.86	0.09

In addition, we tested separately if the processing difficulty of a food item had an influence on 'food solicit' conflict rate. Processing difficulty was based on the number of steps it took an individual on average to process the food item from picking it until it could be digested. Separate steps were for example: break the item open, peel it, rip of a part of it, bit off tips, scrape it out and spit out parts of it. This procedure was based on Jaeggi (2006) and Forss (2009), but was slightly modified to ensure comparability between the sites. The results of the analysis show that the number of steps involved in the processing of a food item seem to predict whether a 'food solicit' event results in a conflict or not ($\chi^2(3)=-149.72$, p=0.013, Figure 29b). The easier to process the food item, the more likely it was for a 'food solicit' event to result in a conflict.

'Food solicit' conflicts were usually recognized either through a rejection by the mother or a distress vocalization by the offspring. Only ten of the 70 conflicts involved both a rejection and a distress vocalization. A 'food solicit' conflict was more likely to be characterized by a rejection, when the offspring was older (b=0.024, z=1.36, p=0.046, Figure 30a). A tendency towards more rejections per total conflicts was visible at Suaq Balimbing compared to Tuanan (b=-1.548, z=-1.89, p=0.058), whereas more distress vocalizations in relation to 'food solicit' conflicts were recorded at Tuanan (b=2.168, z=2.60, p=0.009, N=71 in 38 follow days, Figure 30b). In contrast to the rejections, conflicts in older offspring tended to be characterized by fewer distress vocalizations than those of younger offspring (b=-0.021, z=-1.74, p=0.083, N=71 in 38 follow days). No factor had an influence on conflict intensity or its components. The factors offspring sex, maternal age and number of party members had to be excluded from the analysis due to unevenly distributed data and processing difficulty had been added to the analyses.

However, 'food solicit' conflict is not identical to an unsuccessful beg. In 14 cases out of the 71 conflicts, a 'food solicit' bout was still successful before or after a conflict. Non-conflict 'food solicit' bouts were successful half of the time on average. During the other half of non-conflict 'food solicit' bouts, the offspring did not get any food but it was neither rejected nor were any distress vocalizations heard.

Whether a food solicit was successful or not varied with offspring age, but also greatly between days within one individual. Success rate tended to increase with offspring age to peak around four years of age and then decreased again (b=-0.000, t(5)=-2.31, p=0.069, N=69 in 22 follow periods). With more party members present per day, success rate of food solicits also tended to increased (b=0.142, t(45)=1.60, p=0.062). Data of the number of processing steps per food item is also available, but it was not possible to include into this analysis during the course of this study.

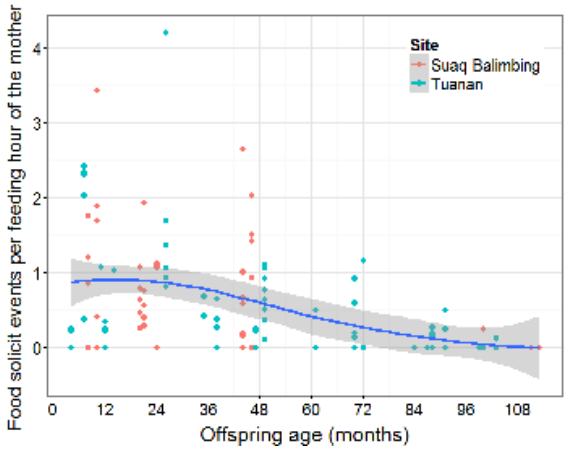

Figure 28. **Food solicit events per feeding hour.**
The number of observed food solicit events hour of the mother feeding in relation to offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=132

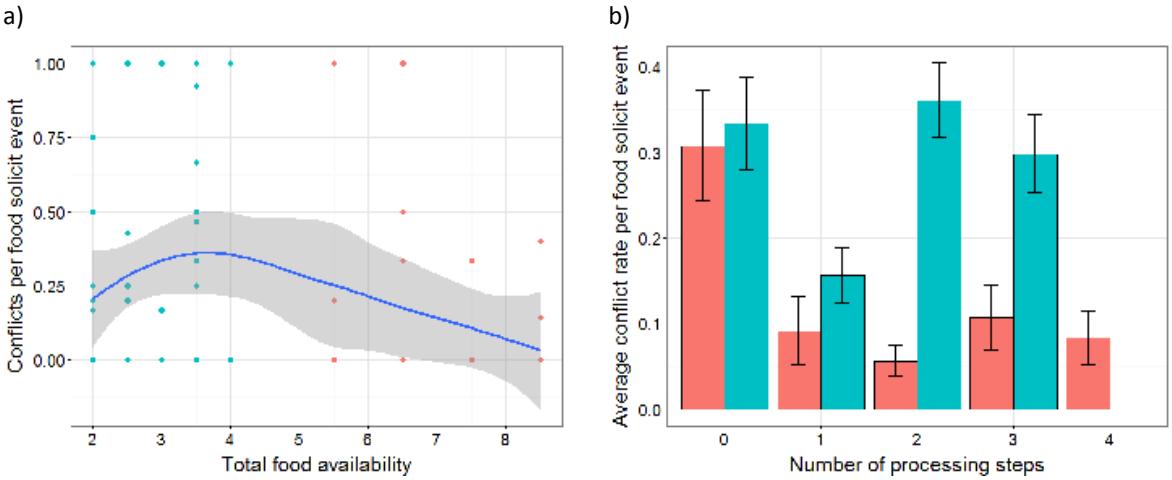

Figure 29. **Food solicit conflict rate.**
The number of conflicts per observed food solicit event in relation to a) the total food availability measured as the food availability index and corrected for cemengang season and b) the number of steps it takes to process a specific food item. Red stands for the site Suaq Balimbing, blue for Tuanan. N=81

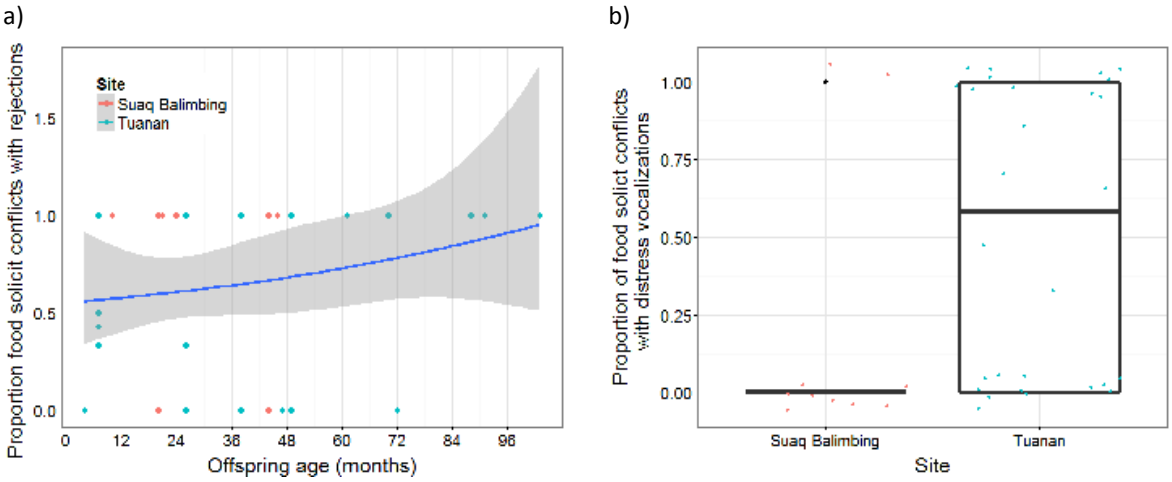

Figure 30. **Conflict components per suckle conflict.**
The number of suckle conflicts indicated by a) rejections in relation to offspring age and b) distress vocalizations in relation to the study site. Red stands for the site Suaq Balimbing, blue for Tuanan. N=71

3.5.2.2 Theft

A mother stealing food from her offspring was observed five times at Suaq Balimbing and seven times at Tuanan during the full study period. Only one of those thefts might have led to a conflict during low food availability at Tuanan. However, it was not clear if the cries of the offspring were a direct result of the theft. There seemed to be no pattern in the food items the mothers took away from her offspring.

3.6 Locomotion

On average mothers at Suaq Balimbing moved more per day (1h53min±8min) than mothers at Tuanan (1h12min±4min), as calculated from the 2-minute scan data. Total movement time per day seemed correlated with food availability. Movement time steadily increased with increasing food availability. The exception were the extremes. If food availability was low, movement time increased again and if food availability was exceptionally high, like during the cemengang season in Suaq Balimbing, movement time decreased again (Figure 31). However the strict site difference and correlation with movement time were not present in the normalized food availability used in the analysis.

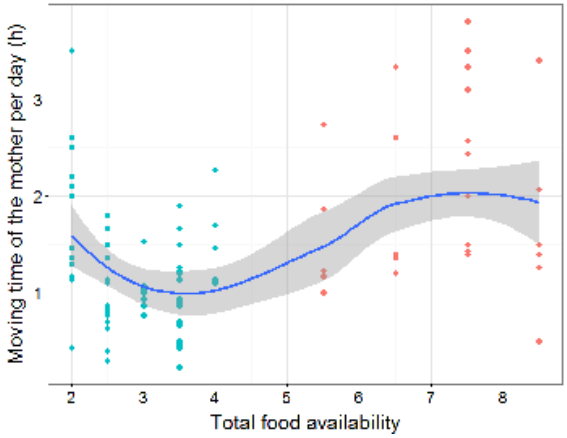

Figure 31. **Time of the mother moving in relation to total food availability.**
Number of hours a mother spends moving per day is influenced by food availability. Total food availability measured as the food availability index and corrected for cemengang season and b) the number of steps it takes to process a specific food item. Red stands for the site Suaq Balimbing, blue for Tuanan. N=132

3.6.1 Carry

3.6.1.1 No carry

Offspring carrying rate decreased with offspring age, in a steep decline, starting at around two years of age when offspring were still carried more than 70% of the time to less than 10% of the time at four years of age (b=0.000, t(11)=7.50, p<0.0001, Figure 32).

In total, eleven 'no carry' conflicts were observed in five different mother-offspring pairs. More 'no carry' conflict per hour move of the mother were recorded at Tuanan than at Suaq Balimbing (b=0.078, t(11)=1.77, p=0.10, r=0.993). Only one of the carry conflicts was observed at Suaq Balimbing, the other ten were observed at Tuanan. Therefore interactions with the factor site were not meaningful and thus excluded from the analysis. However, it is noteworthy that the one event at Suaq Balimbing occurred in an offspring of almost four years of age, whereas at Tuanan 'no carry' conflicts were observed in offspring aged 7 months up to three years of age. Overall conflicts per hour move of the mother decreased with offspring age (b=-0.001, t(12)=-2.31, 0.04, Figure 33). If 'no carry' conflicts were measured per hour the offspring was in cling while the mother moved, none of the six factors explained the variance anymore. We also looked at the number of conflicts per change from the offspring not being in cling to the offspring in cling and the mother moving. This however reduced the data set greatly to only 59 observations and

Box 8
'No carry' conflicts per h move of the mother with offspring in cling
Best fit model: $\chi^2(1)=2.26$, p=0.133
Full model: $\chi^2(7)=6.00$, p=0.539
Nr. Observations: 133
Groups: Mother 13/Name 17/Period 30
Table 14 **'No carry' conflict frequency.** Model output from linear mixed model testing conflicts per hour of the mother moving.

	Value	DF	t	p
(Intercept)	0.039	46	0.15	0.88
AgeO	0.002	5	0.46	0.67
FAI	0.033	5	0.63	0.56
Sex (m)	0.003	7	0.01	0.99
AgeM (y)	-0.165	7	-0.94	0.38
NPM (1-2)	0.039	46	0.24	0.81
NPM (3+)	0.281	46	1.20	0.24
Site (T)	0.275	7	1.75	0.12

five conflicts, because good quality context data was not available for all mother-offspring pairs, so no statistical analysis could be performed. Nevertheless, the highest conflict rates were found in three to four year old offspring, even though older offspring were carried as well sometimes. Changes from not clinging to the mother to clinging while the mother was moving correlated with the total time an offspring clings to the mother when she is travelling (r_s=0.78, Figure 34).

There were two different kinds of 'no carry' conflicts. One was characterized by offspring distress when the mother started moving and the offspring was not yet in cling, the other by mother rejection when the offspring tried to cling. Only two carry conflicts were of the second kind. They occurred in the two oldest offspring with 'no carry' conflicts, but data was too limited for statistical analyses.

All conflicts were short and not intense. However, the different components of conflict intensity varied with offspring age. For this analysis, rejection respectively distress intensities were analyzed in relation to each conflict, because not enough data was available to analyze it per rejection or distress event. Therefore the intensities also reflect also whether the conflict was characterized by a rejection or a distress vocalization. Rejection intensity increased with offspring age ($\chi^2(1)=8.10$, p=0.004, b=0.025, t(5)=4.00, p=0.01, N=8 at 2 Sites, Figure 35a) whereas distress intensity decreased ($\chi^2(1)=7.11$, p=0.008, b=-0.029, t(3)=-3.48, p=0.04, N=6 in 5 follow days, Figure 35b). The models were constructed without the factors site, offspring sex and number of party members, because data was limited. For the rejection analysis, only site was used as a random factor to make the model to work, because each rejection intensity was exactly the same for every point within each individual.

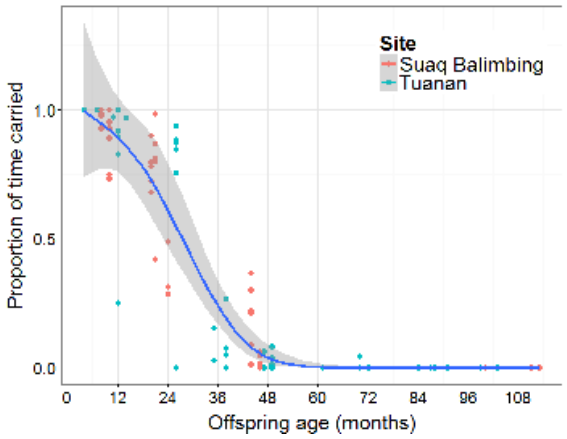

Figure 32. **Proportion of time an offspring is carried in relation to its age.**
Number of 2-min bouts of the offspring was clinging to its mother while the mother was moving/Number of 2-min bouts a mother was moving per day in relation to offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=127

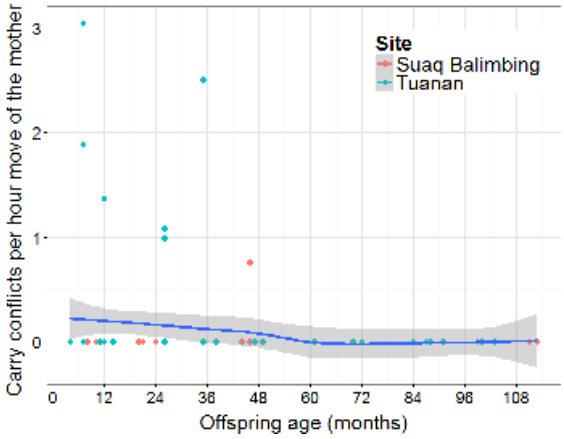

Figure 33. **'No carry' conflicts per hour move of the mother.**
'No carry' conflict frequency per hour the mother spent moving (measured in 2-min bouts) in relation to offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=133

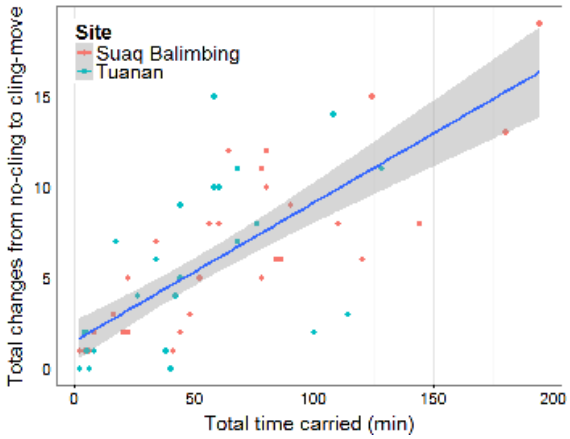

Figure 34. **Changes from no-cling to cling-move in relation to the total time an offspring is carried.**
The number of changes from the offspring not clinging to the mother to clinging to the mother and the mother moving is correlated with the total time an offspring is clinging to the mother's body while she moves. Observations are in 2-min intervals. Red stands for the site Suaq Balimbing, blue for Tuanan. N=133

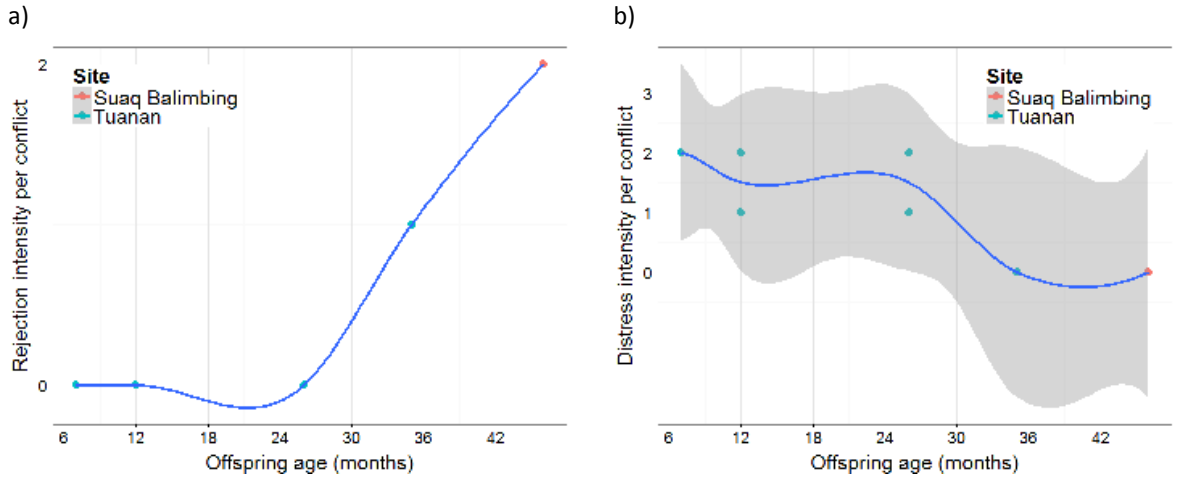

Figure 35. **Intensity per 'no carry' conflict.**
a) Distress intensity (Degree of distress vocalization intensity*distress vocalization duration, N=6) and b) Degree of rejection intensity (N=8) per 'no carry' conflict in relation to offspring age.

3.6.1.2 Carry collect

'Carry collect' events were defined as the mother retrieving or restraining her offspring before or during moving. Due to sample size constraints, the model was constructed without interactions and without the factor sex. 'Carry collect' frequency per hour of the mother moving was highest in young offspring and then gradually decreased until the offspring was around four years of age (b=-0.008, t(11)=2.559, p=0.027, Figure 36). After four year of age, no offspring collects were observed anymore. On average, 'carry collect' frequency at Suaq Balimbing was with 0.46 times/h more than twice as high than at Tuanan with 0.21 times/h (b=-0.006, t(11)=-1.81, p=0.983, r=0.990). Whether an offspring collect event in carry context resulted in a conflict depended mostly on site. 33% of the offspring collects at Tuanan resulted in conflict, compared to 20% at Suaq Balimbing (b=0.258, t(6)=2.69, p=0.04, r=0.965, Figure 37a). If collected, older offspring tended to resist more than younger offspring (b=0.009, t(3)=3.04, p=0.06, Figure 37b). In addition, conflicts seemed to be slightly more common if food availability was higher (b=0060, t(3)=2.31,p=0.10). However, data was very limited and additional removing or adding a few data point might have a large influence on the outcome of the analysis.

Box 9
'Carry collect' conflicts per 'carry collect' event
Best fit model: $\chi^2(3)=12.81$, p=0.005
Full model: $\chi^2(6)=15.81$, p=0.015
Nr. Observations: 39
Groups: Name 8/Period 13
Table 15 **'Carry collect' conflict frequency.**
Model output from linear mixed model testing conflicts per 'carry collect' event.

	Value	DF	t	p
(Intercept)	-0.136	24	-1.41	0.17
AgeO	0.008	3	2.63	0.08
FAI	0.059	3	1.95	0.15
AgeM (y)	-0.031	5	-0.31	0.77
NPM (1-2)	0.114	24	1.19	0.24
NPM (3+)	0.173	24	1.32	0.20
Site (T)	0.292	5	2.85	0.04

All 17 'carry collect' conflicts were characterized by an offspring collect and half of them, resulted in offspring distress. Using statistical analyses and visual inspection of graphs, no factor explaining conflict intensity or any of its components could be found. Offspring sex and maternal age were not considered due to lacking data.

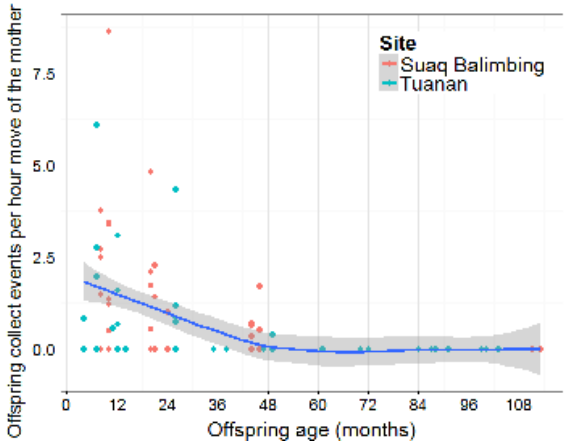

Figure 36. '**Carry collect' events per hour move of the mother.**
The number of observed events of the mother collecting her offspring to move per total hours a mother spent moving. Red stands for the site Suaq Balimbing, blue for Tuanan. N=133

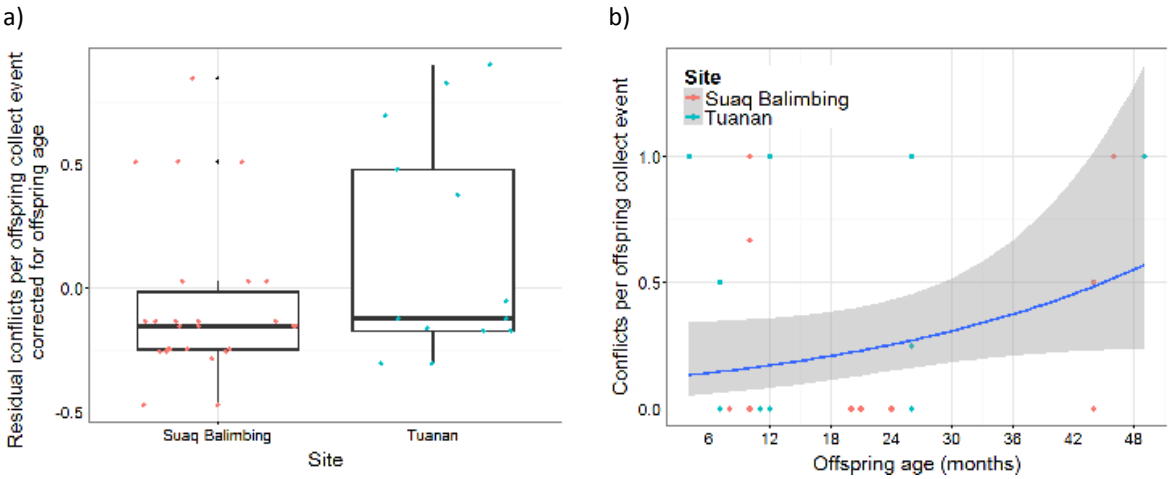

Figure 37. **'Carry collect' conflict rate.**
The number of conflicts per observed 'carry collect' event a) in relation to offspring age and b) in relation to the study site. Residuals event are corrected for offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=39

3.6.2 Gap

3.6.2.1 Independent crossing

Since it was not possible to record all of the gap crosses in the course of this project and thus to analyze gap crossing frequency per gap crossed independently, independent crossing conflicts were measured in relation to different baselines to give a diverse overview. Overall occurrences of 'independent crossing' conflicts per hour peaks at both sites when the offspring is four years old (b=-0.000, t(11)=-3.20, p=0.008), yet there tend to be more conflicts at Suaq Balimbing than at Tuanan (b=-0.043, t(11)=-1.86, p=0.09, r=1.008). Looking at 'independent crossing' conflict frequency per hour of the mother's movement time, we also see that gap crossing conflicts occurred only in mother-offspring pairs with offspring between two and four years of age (b=-0.000, t(10)=-2.90, p=0.02, Figure 38). With increasing food availability, gap crossing conflict frequency tended to decrease (b=-0.048, t(10)=-2.12, p=0.06). Furthermore, site seemed to explain some of the variance in crossing conflict frequency with Suaq having slightly more conflicts than Tuanan (b=-0.136, t(11)=-1.46, p=0.17, r=1.006). However, the model was not significantly better than the null-model ($\chi^2(4)=6.18$, p=0.19). If conflict frequency was tested in relation to the hours a mother spent moving while the offspring was not in cling, the best-fit model included only food availability, in the way that conflict rate tended to decrease with increasing food availability (b=-0.074, t(11)=-1.83, p=0.09).

Box 10
Independent crossing conflicts per h non-cling move h of mother
Best fit model: $\chi^2(1)=3.28$, p=0.070
Full model: $\chi^2(7)=4.48$, p=0.723
Nr. Observations: 109
Groups: Mother 13/Name 16/Period 28
Table 16. **'Independent crossing' conflict frequency.**
Model output from linear mixed model testing conflicts per hour movement of the mother during which the offspring was not in cling.

	Value	DF	t	p
(Intercept)	-0.182	79	-0.76	0.70
AgeO	0.000	4	0.22	0.83
FAIN	-0.079	4	0.84	0.09
Sex (m)	-0.072	10	-0.34	0.77
AgeM (y)	-0.221	10	-0.71	0.50
NPM (1-2)	0.004	79	0.04	0.97
NPM (3+)	0.102	79	0.63	0.53
Site (T)	0.028	10	-0.09	0.93

All 'independent crossing' conflicts were recognized on hearing offspring distress vocalizations. The overall intensity of the conflicts increased with offspring age to a peak around 3.5 years and then decreased again (b=-0.003, t(18)=-2.38, p=0.03, N=54 in 25 follow days). Conflict intensity did not increase due to offspring distress, because offspring of different ages did not differ in their distress intensity. However conflict duration showed a peak at the offspring's age of 3.5 years (b=0.002, t(18)=-2.46, p=0.02, Figure 39a). Conflict duration tended to be higher at Suaq Balimbing compared to Tuanan (b=-0.254, t(3)=-2.69, p=0.07, Figure 39b). However, whether the mother in the end helped her offspring cross or not did not depend on any of the factors. Sex and number of party members had been excluded from the intensity analyses because not enough data was available.

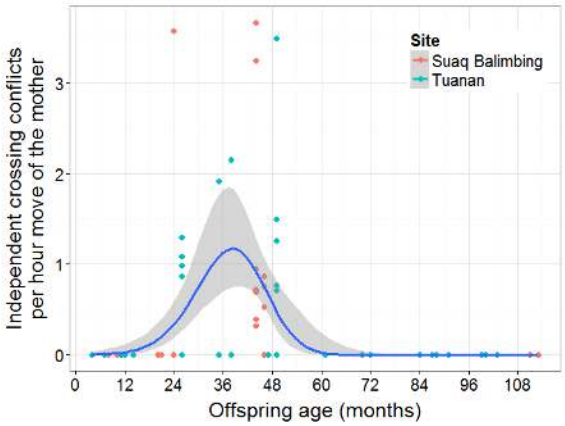

Figure 38. **'Independent crossing' conflicts per hour move of the mother.**
'Independent crossing' conflict frequency per hour the mother spent moving (measured in 2-min bouts) in relation to offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=133

a) b)

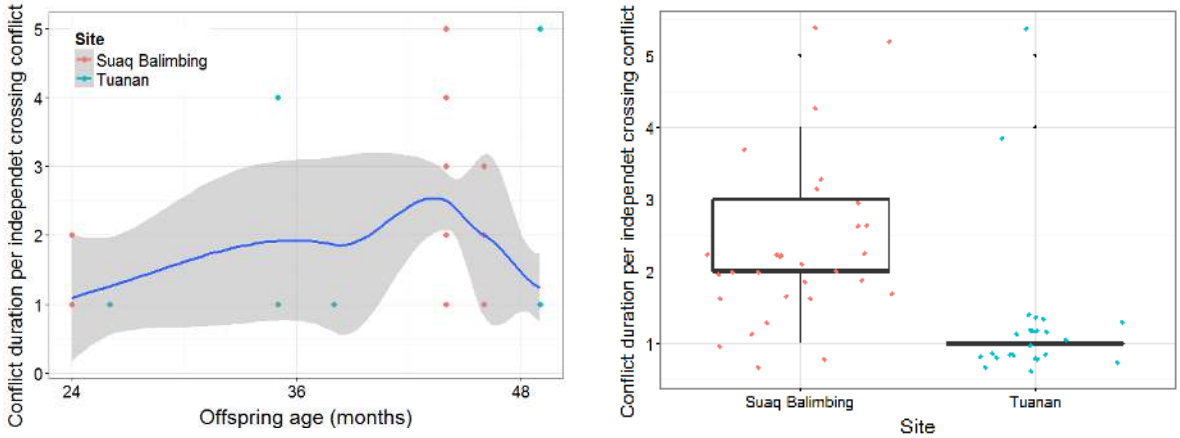

Figure 39. **'Independent crossing' conflict duration.**
The duration of each conflict per day in relation a) to offspring age and b) study site. Red stands for the site Suaq Balimbing, blue for Tuanan. N=54

3.6.2.2 Gap collect

Infant collect events while the mother was hanging between two trees and so forming a body bridge for her offspring across a gap between two trees, were examined per hour move of the mother. These 'gap collect' events only occurred at Suaq Balimbing in our data set. Thus the number of 'gap collects' in relation to the time a mother spent moving also differed greatly between the two sites (b=-0.496, t(11)=-3.74, p=0.003). In addition, offspring older than four years were never collected anymore (b=-0.006, t(11)=--3.07, p=0.01, Figure 40).Therefore only data from Suaq Balimbing was included in the following analyses. However, this reduced sample size by two-thirds and the factor sex had to be removed from the analyses since there was only one female at Suaq Balimbing.

Box 9
Gap collect conflicts per gap collect event
Best fit model: $\chi^2(3)=16.57$, p=0.0009
Full model: $\chi^2(4)=16.84$, p=0.002
Nr. Observations: 19
Groups: Name 4/Period 7
Table 17. **'Gap collect' conflict frequency.**
Model output from linear mixed model testing conflicts per 'gap collect' event.

	Value	DF	t	p
(Intercept)	0.015	9	0.10	0.93
AgeO	0.002	1	0.45	0.73
FAIN	-0.210	1	-3.73	0.17
AgeM (y)	0.767	2	3.07	0.09
NPM (1-2)	-0.172	9	-2.51	0.03
NPM (3+)	-0.235	9	-2.24	0.05

Out of those 30 recorded events, in twelve cases the mother collected her offspring right after she made a bridge and then crossed. In eleven cases the mother waited in the bridge for the infant to cross, and retrieved it after having waited at least 30s. The infant moved away from the mother or resisted the retrieve in seven cases. Since 'gap collects' only occurred at Suaq Balimbing, site was not included in the conflict analysis. Due to limited data, interactions and offspring sex were also excluded from the analysis and results of the intensity of conflict are only descriptive.

The 'gap collect' conflicts decreased during days with parties (1-2: b=-0.163, t(9)=-2.56, p=0.03, r=1.017 and b=-0.225, t(9)=-2.28, p=0.048, r=1.014, Figure 41a if time change, additional data point all). Food availability and mother age class also influenced the outcome of a gap retrieve. During low food availability, conflict rate tended to be higher (b=-0.213, t(2)=-3.81, p=0.062, Figure 41b). In addition young mothers tended to have more frequent as well as more intense gap retrieve conflicts than ancient mothers (b=0.788, t(2)=3.23, p=0.084, r=0.739).

'Gap collect' conflicts were only characterized by retrieves. None of the offspring cried when being retrieved. The duration of the conflicts varied between less than thirty seconds up to three minutes. The intensity of the conflicts mainly differed due to duration differences. Conflicts were usually shorter during low food availability (b=0.095, t(6)=3.23, p=0.017, N=19 in 13 follow days, Figure 42a) and if more than two party members were present during that day (b=-0.443, t(6)=-3.18, p=0.019, r=1.051, N=19 in 13 follow days, Figure 42b).

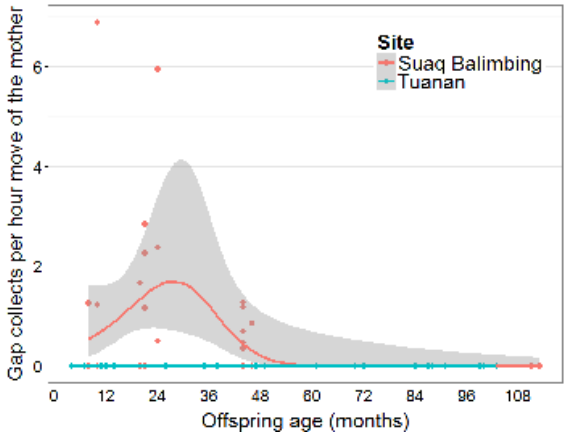

Figure 40. **'Gap collect' events per hour move of the mother.**
The number of observed 'gap collect' events per hour the mother spent moving (measured in 2-min intervals) in relation to offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=109

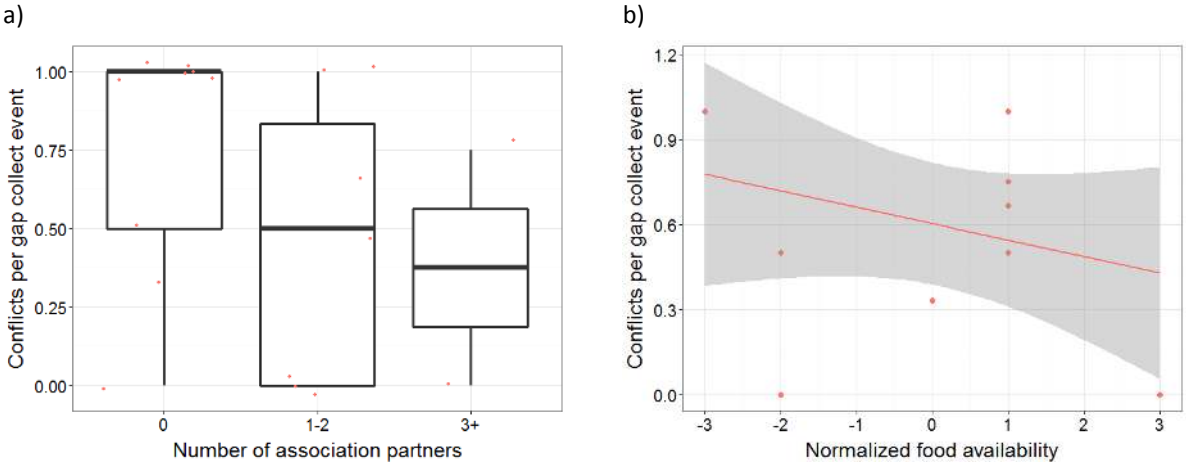

Figure 41. **'Gap collect' conflict rate.**
The number of conflicts per observed 'gap collect' event a) in relation to food availability of each site and b) in relation to the number of association partners present during one day. Residuals event are corrected for offspring age. N=19

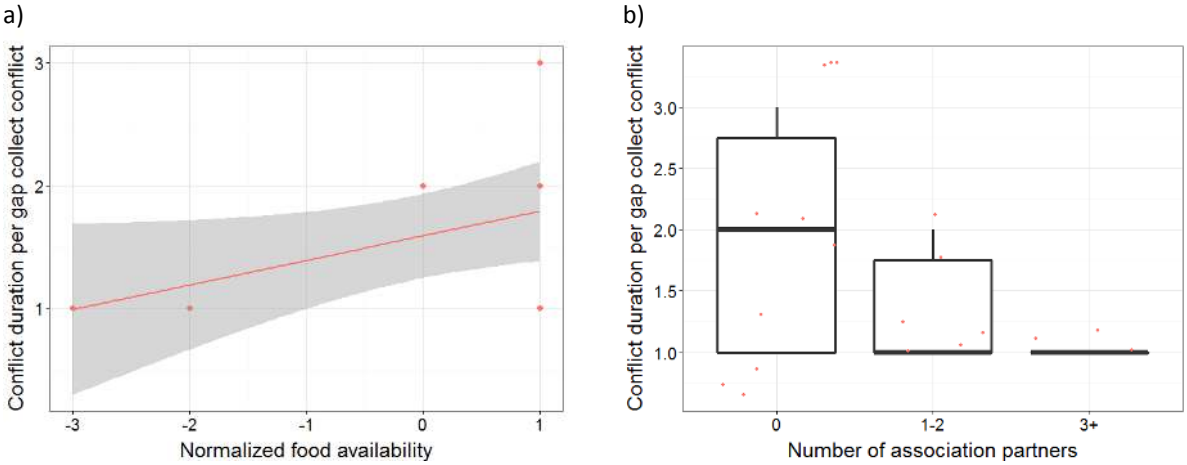

Figure 42. **'Gap collect' conflict duration.**
The average duration of each 'gap collect' conflict in relation to a) food availability of each site and b) the number of association partners present per day. N=19

3.7 Proximity

3.7.1 Cling

3.7.1.1 No cling

The proportion of total time an offspring spent clinging to its mother's body decreased with increasing offspring age (b=-0.017, t(10)=-11.43, p<0.0001, Figure 44). If there were party members present, offspring between two and five year old were carried more often compared to when no party members were present that day (b=0.064, t(873.29, p=0.001). In the first constructed model, interactions between offspring age and sex as well as offspring age and mother age class and mother age class and food availability were found. However, first and the last mentioned were due to unevenly distributed data and hereafter removed for the next analysis, which then only yielded a significant interaction of offspring age and party members present (b=-0.000, t(87)=-2.55, p=0.013). For this analysis we only had two party member classes, whether party members were present or not.

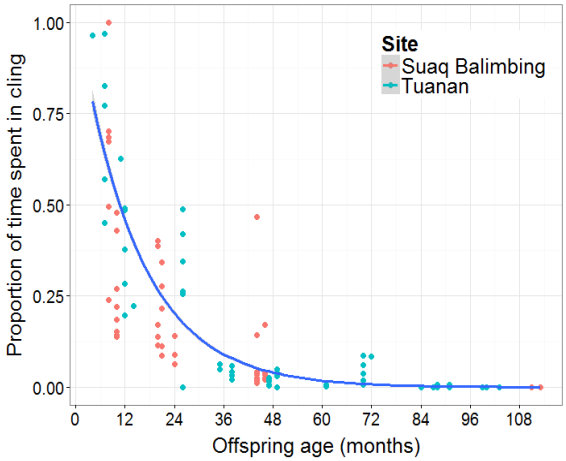

Figure 43. **Proportion of time an offspring is in cling in relation to its age.**
Number of 2-min bouts of the offspring was clinging to its mother/Total 2-min bouts per day in relation to offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=119

Conflicts in which the offspring was not allowed to cling or put out of cling, happened very rarely. We observed 'no cling' conflicts only four times over the full study period, three times at Suaq Balimbing and once at Tuanan in offspring between seven and 44 month of age. Two conflicts were characterized by both rejection and distress vocalizations. For the other two one was recognized through rejection by the mother and the other one by distress vocalizations of the offspring. All four conflict happened at days during which no party members were present. Conflict intensity seemed to increase with offspring age since the two older offspring were the ones that were rejected by the mother. One was shoved off the mother's body and the other mother moved away when her offspring tried to cling. The two younger offspring were not actively rejected and collected again after they had cried.

3.7.1.2 Stay cling

Situations where the offspring wanted to go or stay out of cling were recorded only three times in two different offspring at Tuanan during the full study period. Two year old Kahiyu resisted when she was pulled into the nest and 7 month old Ivan was restrained twice when he wanted to go out of cling. Once it was while an unflanged male was present and Ivan's mother tried to prevent Ivan to go near the male. Both times Ivan cried.

3.7.2 Distance

3.7.2.1 Too far

'Too far' conflicts were measured as conflicts per active hour of the mother, because conflicts about the distance between a mother and her offspring could occur any time during the day. 'Too far' conflicts per active hour were most common in young female infants. Conflict frequency decreased with age for both female and male offspring, with the female offspring conflict rate approaching the one of the males (b=0.006, t(8)=3.32, p=0.011). In addition, the frequency of ''too far' conflicts per hour of the mother's travel time decreased with increasing food availability in mother-offspring pairs with young mothers whereas the rate was increased in pairs with ancient mothers (b=-0.074, t(8)=-2.38, p=0.045). This effect was pronounced at Tuanan and only slightly visible at Suaq Balimbing. Conflict frequency increased with party size and was 62% higher during days with two or more association partners compared to days without associations (b=0.144, t(109)=2.51, p=0.014, r=1.000). As an approximation of number of conflicts in relation to the possibilities for 'too far' conflict to occur, conflicts in relation to the total time an offspring was not in cling, were analyzed. All data points of the youngest offspring Ivan were removed as outliers. As Ivan was still in cling most of the time and was in distress very often as soon as he left body contact with his mother. Thus Ivan had many conflicts about the distance to his mother about leaving very close proximity. This biased the whole data toward his mother's age class, sex and even the site. Consequently, Ivan was not considered in the following analysis, but will be kept in mind for the discussion. Using this data we again found the same interactions between offspring age and sex (b=0.008, t(8)=3.01, p=0.017), food availability and mother age(b=-0.099, t(7)=-2.15, p=0.069) ,as well as a party member effect (b=0.147, t(84)=2.16, p=0.034). Testing the same model including the three-way interactions, we found the interaction AgeO-Sex-PM to be significant (b=-0.006, t(82)=-2.55, p= 0.013, Figure 44a) in addition to the FAIN:AgeO interaction (b=-0.107, t(7)=-2.40, p=0.047, Figure 44b). The best fit model with the three way interaction explained the conflict frequency per non-cling hour of an offspring slightly better than without it ($\chi^2(2)=4.95$, p=0.084).

Box 10
Too far conflicts per hour of no-move and no-nest time of mother without offspring in cling
Best fit model: $\chi^2(11)=55.52$, p<0.0001
Full model: $\chi^2(12)=55.745$, p<0.0001
Nr. Observations: 133
Groups: Mother 13/Name 17/Period 30
Table 18 **'Too far' conflict frequency.** Model output from linear mixed model testing conflicts per no-move and no-nest hour of the mother while the offspring was not in cling.

	Value	DF	t	p
(Intercept)	-0.001	7	-0.16	0.87
AgeO	-0.798	2	-5.16	0.04
FAIN	0.097	7	2.51	0.04
Sex (m)	-0.144	10	-1.90	0.09
AgeM (y)	-0.240	82	-1.96	0.05
NPM (yes)	-0.123	10	-1.44	0.18
Site (T)	0.012	7	4.53	0.00
AgeO^2	0.006	82	2.58	0.01
AgeO:Sex	0.347	82	2.31	0.02
AgeO:NPM	-0.143	7	-2.92	0.02
Sex:NPM	-0.006	82	-2.51	0.01
AgeM:FAIN	-0.001	7	-0.16	0.87
AgeO:Sex:NPM	-0.798	2	-5.16	0.04

All 226 'too far' conflicts were characterized only by offspring distress. Overall conflict intensity did not seem to vary in relation to any factor. Nevertheless, conflict duration showed a non-significant peak in offspring of four to five years of age (b=-0.000, t(51)=-1.86, p=0.069 N=226 in 64 follow days). Distress intensity increased with decreasing food availability (b=-0.056, t(42)=-2.33, p=0.025, Figure 45).

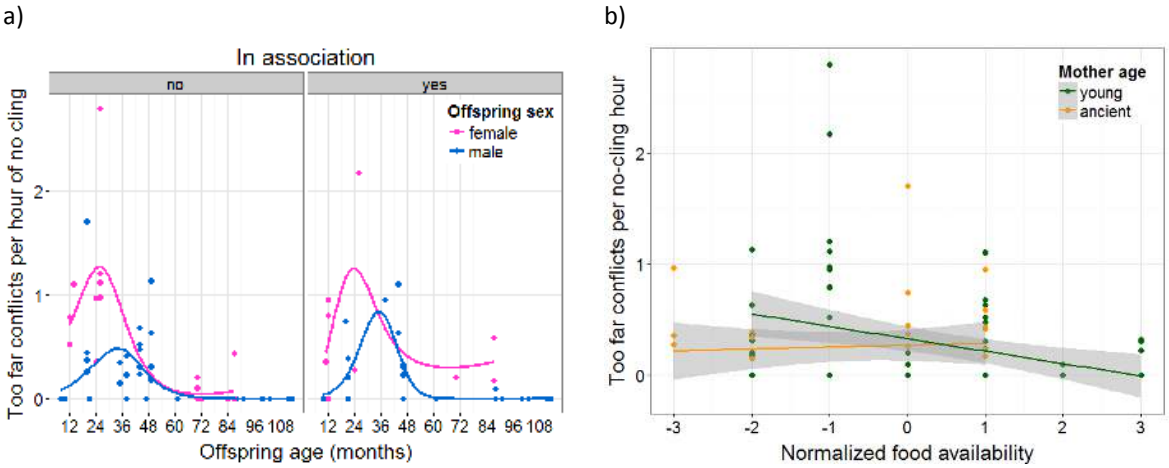

Figure 44. **'Too far' conflicts per no-cling hour.**
'Too far' conflict frequency per hour the offspring did not cling to its mother's body (measured in 2-min bouts) in relation to a) offspring age, sex and whether association partners were present or not and b) food availability per site and maternal age. Pink stands for the female offspring, blue for male offspring. Green stands for young mother, orange for ancient mothers. N=133

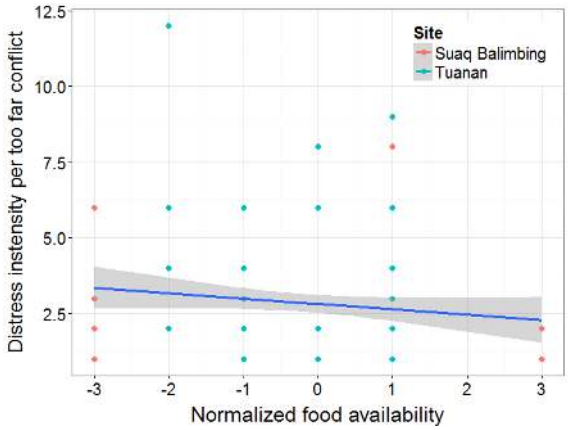

Figure 45. **Distress intensity per 'too far' conflict.**
Distress intensity (Degree of distress vocalization intensity* distress vocalization duration) per 'too far' conflict in relation to food availability per site. N= 226

3.7.2.2 Too close

Conflicts in which the mother tried to increase distance between her and her offspring only happened in the oldest offspring that already had a younger sibling (b=0.001, t(12)=2.43, p=0.03). If only the time during which an offspring was not clinging to the mother was taken as a baseline, conflict rate still increased with offspring age (b=0.000, t(12)=2.29, p=0.04, Figure 46) and there were trends that ancient mothers (-0.018, t(11)=-2.03, p=0.07, r=1.008) respectively female offspring (b=-0.021, t(3)=-2.154, p=0.12, r=1.146) tended to more conflicts than young mothers respectively male offspring. For both model analyses no interactions were taken into account because of the small sample size.

'Too close' conflicts were caused by rejections of the mother and resulted in offspring distress 13times out of the 23 conflicts. Distress vocalizations were more commonly heard at Tuanan than at Suaq Balimbing (b=3.58, z=-2.72, p=0.007, N=20 in 12 follow days, Figure 47). Offspring sex and mother age were not included in the analysis due to unevenly distributed data. Only 20% of the distress vocalizations were heard at Suaq Balimbing compared to 85% at Tuanan.

Box 11
Too close conflicts per no-move and no rest-in-nest h of the mother and no cling time
Best fit model: $\chi^2(3)=9.40$, p=0.024
Full model: $\chi^2(7)=12.37$, p=0. 089
Nr. Observations: 120
Groups: Mother 13/Name 17/Period 30
Table 19 **'Too close' conflict frequency.** Model output from linear mixed model testing conflicts hour of the mother not moving and not in a nest while the offspring was not in cling.

	Value	DF	t	p
(Intercept)	0.020	88	1.62	0.11
AgeO	0.000	11	2.34	0.04
FAIN	0.003	11	1.43	0.18
Sex (m)	-0.022	3	-2.29	0.11
AgeM (y)	-0.022	10	-2.51	0.03
NPM (1-2)	-0.004	88	-0.82	0.42
NPM (3+)	-0.004	88	-0.42	0.68
Site (T)	0.006	10	0.66	0.52

No factor had an influence on overall conflict intensity. By looking at each component separately, no differences could be found in rejection intensity or conflict duration. The average rejection intensity was 2.9 meaning that the offspring was pushed away, but for example Ronaldo had also been chased for several meters by Raffi. The longest conflicts between Ipsy and her mother lasted three and five minutes, because Ipsy tried to approach again and Inul displaced her again. However usually a conflict did not go on for longer than 30s. Distress intensity varied significantly in relation to daily number of party members and offspring age ($\chi^2(2)=20.04$, p<0.0001). Distress intensity was elevated if party members were present (b=1.125, t(3)=6.39, p=0.008, r=0.765) and heading slightly into the same direction when the offspring was older (b=0.016, t(3)=1.93, p=0.129). Sibling age did neither play a role in determining conflict frequency, nor conflict intensity or any components of it.

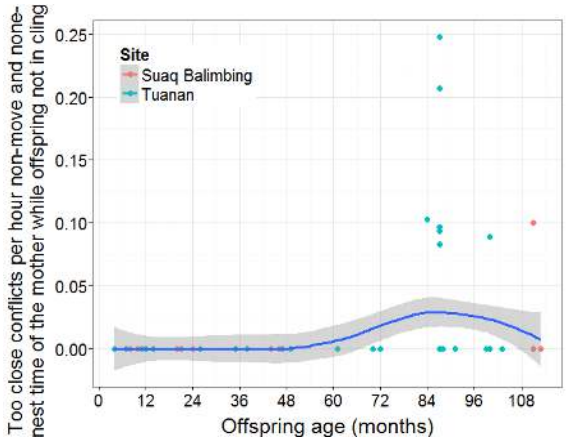

Figure 46. **'Too close' conflicts per none-move and none-nest time.**
'Too close' conflict frequency per hour the offspring did not cling to its mother's body while she was neither moving nor in a nest (measured in 2-min bouts) in relation to offspring age. Red stands for the site Suaq Balimbing, blue for Tuanan. N=120

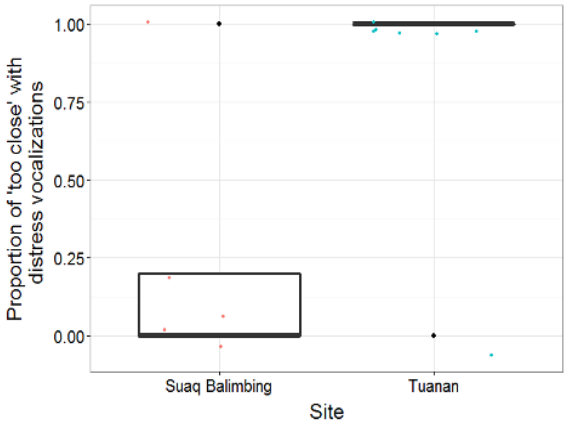

Figure 47. **'Too close' conflicts indicated by distress vocalizations in relation to site.**
The number of 'too far' conflicts indicated by distress vocalizations in relation to the number of association partners present during one day. Red stands for the site Suaq Balimbing, blue for Tuanan. N=13

3.7.2.3 Stay close

The mother sometimes tried to keep her offspring close by throat scraping or restraining it from moving away from her. These offspring collects were considered to be in the context of distance when the mother did not try to put the offspring into cling. Over the whole study period, seven offspring collects in the context of distance were observed: two successive ones in 44 month old Lois and his mother Lisa at Suaq Balimbing and the other seven at Tuanan in offspring ranging from half a year to six years of age. It was neither possible to conduct any meaningful analysis to test what factors had an influence on occurrence of these offspring collect events, nor why they resulted in conflict. 'Stay close' events happened in both male and female offspring, old and young mothers and average food availability. Party members could have an effect on "stay close" events since in 50% a party member was present during the conflict compared to the fact that parties happened only in 44% of the days at Suaq Balimbing and 25% of the days at Tuanan. The only offspring collect event that resulted in a conflict, happened at Suaq Balimbing in the mother offspring pair Lisa-Lois during an association with another mother-offspring pair. Lisa was trying to keep distance to another mother-offspring pair and throat scraped. Lois the first time Lois approached Lisa, but the second time he did not follow. It seemed as if he wanted to stay and interact with the other offspring. The party members that were present at Tuanan during two of 'stay close' events that did not result in conflict were once an unflanged and once a flanged male.

3.8 Summary

3.8.1 Age trajectories

Conflict frequencies varied across offspring age for almost all conflict 'problems'. 'Food solicit', 'no carry', 'carry collect', 'no cling' and 'cling collect' conflicts peaked in between offspring ages of zero to two years. 'Too far', 'gap collect' and 'independent crossing' conflicts peaked between the ages of two to four years. 'Suckle' conflicts peaked in offspring from four years to weaning and 'too close' conflicts peaked after the offspring had been weaned and already had a younger sibling.

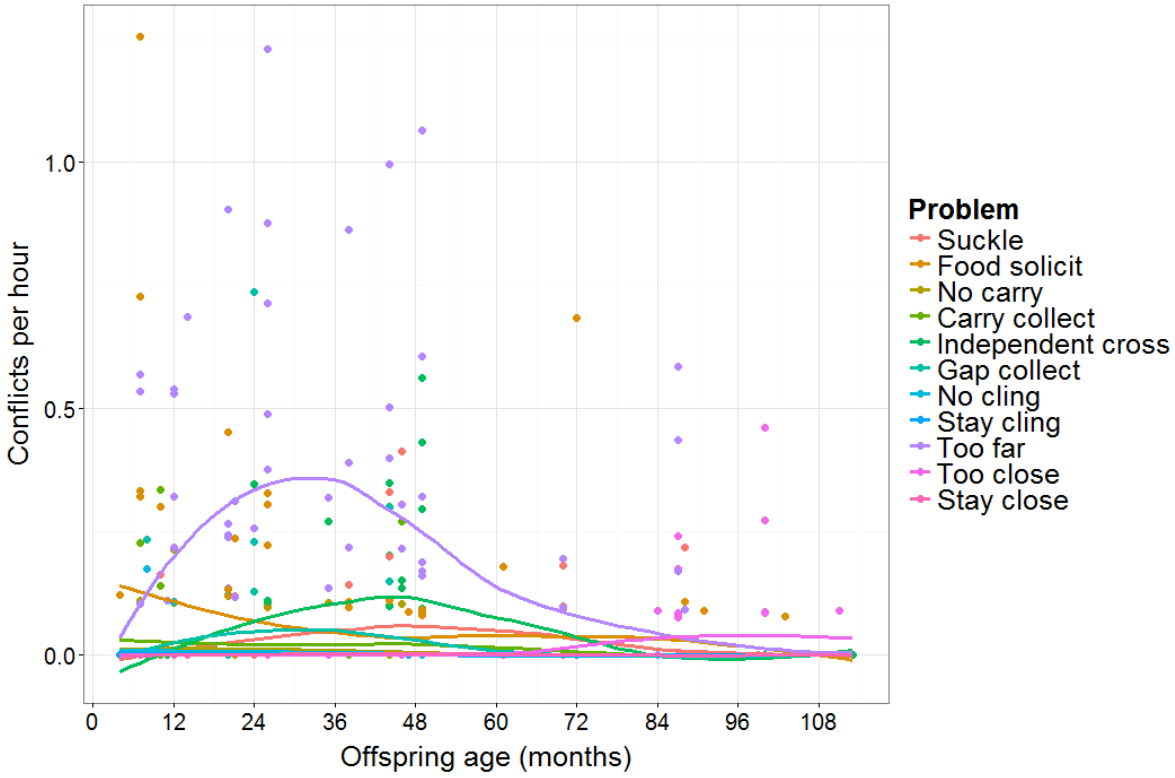

Figure 48. **All conflicts per hour in relation to offspring age.**
All conflicts per active hour classified into 'problems' in relation to offspring age. Different colors indicate different 'problems as indicated by the legend on the right. N=141

3.8.2 Conflict frequencies in relation to different factors

Conflict frequencies generally increased with offspring age and decreasing food availability, according to our predictions. Also according to our predictions, conflict frequencies were lower in old mothers. If a site effect was present, conflict frequencies in Tuanan were higher compared to Suaq Balimbing in the contexts we predicted. The influence of the number of association partners present per day depended on whether the conflict was mother oriented, such as offspring collect conflicts, or offspring oriented such as suckling conflicts. Offspring sex as a main factor did not have an influence on conflict frequencies, but in an interaction with offspring age and party size, females tended to have more conflicts than males if more party members were present.

Table 20 **Summary of conflict frequency of each conflict 'problem' in relation to the opportunities.**
The factors influencing conflict frequency for all conflict 'problems' in relation to opportunities. Green represents main effects and yellow and orange interaction effects. Up arrows indicate increased conflict into the direction indicated in the cell or next to the conflict factor at the top of the table. Stars indicate the significance: 0***0.001**0.01*0.05.0.1.

	AgeO (↑)	FAIN (↑)	Sex	AgeM (old)	NPM (↑)	Site
Milk	↑*	-	-	-	↑***	-
Food	-	FAI ↓*	-	-	-	Tuanan↑.
Theft						
Carry	-	-	-	-	-	-
Move On	↑.	-	-	-	-	Tuanan↑*
Gap	-	↓ .	-	-	-	-
Gap Collect	-	↓ .	-	↓ .	↓*	-
Cling						
Stay Cling						
Too Far	*	*	Female*	↓*	↑*	-
Too Close	↑*	-	Female ↑	↓ .	-	-
Stay Close						
Overall	↓*				↑***	

4 Discussion

The aim of this study was to examine the different aspects and contexts of orangutan mother-offspring conflict in relation to varying factors such as offspring age or food availability as well as the differences between a Sumatran and a Bornean study site. Since orangutans have very slow life histories (van Noordwijk et al. 2009), different contexts of conflict can be teased apart more easily than in other species. Mother-offspring conflicts in orangutans can occur in at least three main contexts: nutrition, travel and proximity. These contexts can be split up even further depending on the subject of interest and the goal to be reached. In this study more than fifteen different potential conflict eliciting problems could be distinguished. In the following sections, each potential conflict subject is going to be discussed in relation to its conflict influencing factors.

4.1 Age trajectories

Offspring age predicted conflict frequency per hour for almost all contexts. The only models that did not show at least a tendency to an age effect were the models for both 'problems' in cling context and 'gap collect' conflicts. However, this is probably mostly due to the great number of days without any conflicts about clinging. Only seven conflicts in cling context were observed during the whole study period. All 'gap collect' events, and thus as well 'gap collect' conflicts, were observed at Suaq Balimbing. Since no data on conflict is available for offspring between four and eight years of age at Suaq Balimbing, it is not clear if 'gap collect' conflicts decrease after the offspring's fourth birthday or if it is a site difference. The lack of data on four to eight year old offspring at Suaq Balimbing makes it difficult to tell apart real differences in trajectories of conflict between the two study sites. An extreme example is the age trajectory of 'suckle' conflicts. From the data we have now, it seems as if 'suckle' conflict frequency would peak around an offspring's fourth birthday. However, it might well be (and we expect) that 'suckle' conflict frequency is still elevated in older offspring at Suaq Balimbing, similar to Tuanan. Yet, from the data that we have so far, it is evident that conflict frequency tends to be higher at Suaq Balimbing than at Tuanan in general.

In addition to the age and site effects, the number of party members seemed to be a good predictor of the number of conflicts per hour in the context of suckling and proximity of mother and offspring. A more detailed discussion is found in the following discussion sections about the specific problem.

4.2 Overall

Offspring Age

Overall conflict frequency per active hour was highest for three-year old immatures and then started to decrease. This is the offspring's age at which the energetic contribution of the mother to her offspring is expected to be highest, because the offspring still needs to be carried frequently and engages in energy consuming play for a large part of the day, but does not yet feed enough to cover its energy needs (van Noordwijk and van Schaik 2005, Kunz 2015). Looking at each conflict component separately we found that distress per conflict stayed relatively stable until the offspring was weaned, and then decreased steeply. In contrast, the number of conflicts characterized by rejections increased with offspring age, starting around the age of four years. This shows that most conflicts up to weaning result in offspring distress. The time of weaning is a major changing point in an orangutan offspring's life. In our data set, as well as in most primates (van Noordwijk 2012), final weaning coincides with the birth of a new sibling. Van Noordwijk and van Schaik 2005 found that weaning also concurs with the stop of mother-offspring play, end of nest-sharing and the start of the offspring spending more and more time in different feeding trees than its mother. As the time in proximity decreases after weaning, fewer conflicts about the distance in travelling or proximity arose. If events, in which the offspring was in distress because it tried to get closer to the mother, were excluded, conflicts characterized by

offspring distress did not decrease anymore with offspring age. Therefore the decrease in distress per conflicts in older offspring is mainly due to a difference in general daily distance from the mother. This highlights the importance for further analyses to take into account distance data, which is available, but could not be taken into account for this study.

The conflicts characterized by offspring collects that were resisted or resulted in of offspring distress vocalization decreased starting at age four. Observed offspring collect conflicts mainly decreased after the offspring's age of four years because the offspring is very rarely collected anymore. In relation to the total time an offspring was observed, conflict rate of course declines, yet in relation to the opportunities of one offspring collect to result in conflict, the number of conflicts stayed the same across ages or even increased, as we will discuss in detail in the following pages. This shows the importance of examining different contexts separately to be able to set the right baseline consisting of the opportunities for a specific conflict to happen.

Food availability

The food availability within site mainly had an effect on the intensity of conflict. With decreasing food availability the offspring collect conflict intensity decreased whereas distress intensity increased. Interestingly, both of these components are offspring oriented, compared to rejection intensity which is mother oriented and was not influenced by food availability. Therefore, it might be that orangutan offspring generally resist less strongly, but also cry more intensely if they are hungry.

Party members

Irrespective of opportunities, overall conflict frequency per hour was increased if three or more party members were present per day, yet the duration of each conflict was shorter compared to days with no party members present. This suggests that, according to our hypothesis, orangutan mother-offspring pairs might be stressed by the presence of others, or are not as attentive to each other, resulting in more conflicts, which are then resolved quickly to not draw too much attention to themselves.

Site

During a conflict, more rejection by the mothers and more resistance to offspring collects was found at Suaq Balimbing, whereas more distress vocalizations were heard at Tuanan.

The question arises, whether this is caused by a real differences between the sites or rather a difference in the possibility of hearing the vocalizations. The fact that the hourly rate of high intensity distress vocalizations are more similar at two sites than those of low intensity (Amount Suaq/Tuanan: Whine=0.39, Cry=0.46, Scream=0.49, pers. obs.) points to a site bias in the ability to hear offspring distress vocalizations. However, mipping was more common at Suaq Balimbing (Mip=1.44, pers. obs.). Mips are not very loud, therefore this speaks against the sampling bias. It could just be that distress vocalizations are used differently at the two sites. Especially the mipping seems to differ between the sites, as it was more commonly used in 'food solicit' contexts at Tuanan, whereas it was very often used in 'too far' context at Suaq Balimbing, likely as a contact call.

4.3 Nutrition

4.3.1 Milk

4.3.1.1 Suckle

Only 7.5% of the attempted or observed 'suckle' events resulted in a conflict. Whether a 'suckle' event led to a conflict depended mainly on offspring age and number of party members present per day.

Offspring Age

The frequency of observed 'suckle' events slightly increased to a peak at the offspring's age of four years and then decreased again until the offspring was weaned at around eight years of age. Since it is easier to detect a mostly non-clinging offspring suckling compared to a young offspring that is clinging to the mother's body most of the time, the increase in suckling frequency could be partly due to an observation bias. However, the subsequent decrease is very likely to reflect an actual decline in frequency. The steady decrease in suckling frequency from age four to eight indicates an extended weaning period, with gradual weaning.

Final weaning

The number of suckle events which resulted in a conflict increased slightly with offspring age. However, the conflicts started two to three years earlier than the actual final weaning, which occurs in offspring between 5.5 to 6.5 years of age at Tuanan (van Noordwijk et al. 2009, 2013a) and 6-7.5 years of age at Suaq Balimbing (van Noordwijk and van Schaik 2005). At Tuanan, two offspring, Kino (7.5y) and Mawas (6y), had a younger sibling born during or shortly after the study period and were still seen suckling a few times before the birth of their sibling. On average, one quarter of their suckle attempts resulted in conflict in contrast to four-year old Sony and Danum, whose suckling attempts resulted in conflict only in 2% of the cases, indicating classic final weaning conflict during the new pregnancy of the mother. Ipsy (7.5y), who is about the same age as Kino and already had a one year old brother, and Kino after the birth of his little brother, were never seen at the nipple anymore. However, conflicts around weaning were prominently indicated by intense offspring distress without preceding refusal of nipple access by the mother. Thus, weaning conflict in orangutans deviates from the classic rejection-driven weaning conflict. It could be that milk production in orangutans is reduced when the mother is pregnant or receptive again, but no mothers of the latter conditions were present during the study period. An example of offspring distress as a response to potentially drastically reduced milk production outside the typical age of final weaning comes from the mother-offspring pair Sidony-Sony. After Sidony had been lethally injured during a fight, Sony was still allowed to suckle, but a few days before Sidony died, Sony started to suckle, then let go of the nipple and cried. Then he tried to suckle again but only for five seconds, suggesting that there might have been no milk left, as there was no rejection by Sidony. Due to similar observations of the reaction of Mawas after attempting to suckle while her mother was pregnant, the same might be true during final weaning under 'normal' circumstances.

However, at Suaq, conflict rate was already increased in offspring at the age of four years. Unfortunately, no offspring around final weaning age was present during the study period. The eight and nine year old offspring present at Suaq Balimbing already had a younger sibling and were never seen suckling anymore. The characteristics of the conflicts between the four-year old Suaq offspring Lois and his mother Lisa differed from the weaning conflicts in Tuanan. Even though some of the conflicts between Lisa and Lois were accompanied by distress (42%), most of them were characterized by rejections (92%). All rejections, except for the nursing snaps, happened while the mother was feeding or about to travel indicating that a coordination conflict could exist, but not enough detailed data was available to test this. Nursing snaps happened in all contexts but mainly resting. It could be that the mothers snapped at their offspring because the suckling of the offspring hurt them. However, this would have to be examined more closely, for example by looking at whether the offspring is

allowed to suckle again if it switches nipples. The two nursing snap events we caught on video, support this idea.

If more detailed data was available, it would be interesting to test whether the different ages of final weaning between the two sites is due to a later start of weaning at Suaq Balimbing, leading to a weaning periods of similar durations at both sites, or if weaning starts at the age of four at both sites but with a prolonged complete weaning period at Suaq Balimbing. It would possibly also shed light on the difference in suckling conflicts between the sites.

Milk insufficiency

Contrary to our hypothesis, no peak in conflict was observed around the offspring age of one year with the onset of solid food eating. Thus, in contrast to the prediction of van Noordwijk et al. (2013), there is no evidence for conflict at the milk insufficiency point. It seems as if the offspring try to feed on solid food by their own initiative, maybe even before the milk insufficiency point is actually reached, according to the view of Bateson (1994). However, in seven to 14-month old offspring there were still on average 0.4 distress vocalizations per hour for which we don't know the context. There was a large site difference with almost no unknown distress at Suaq Balimbing and 0.9 distress vocalizations per hour at Tuanan. However, it is not clear if this difference is real or if vocalization, especially those of young offspring, are drowned out by the surrounding noise. Nevertheless, particularly at Tuanan, a large number of distress vocalization with unknown context were heard. Since those offspring are still 45% of the time in cling (comparable to van Noordwijk and van Schaik 2005 for Suaq Balimbing) it is difficult to detect if a young offspring is suckling or not. So it could be that some of the distress vocalizations were in the context of suckling. Still, even if the distress vocalizations indicated 'suckle' conflicts, it would be more a physiological conflict because milk supply is short, rather than behavioral conflict, like for final weaning conflicts. However, more precise data would be needed to draw this conclusion. Studies in captive orangutans might be more revealing, due to better visibility of the offspring. In addition, one could try to install video cameras at the nest to record suckling in the nest. If there is a conflict at the milk insufficiency point, this should also be evident in captivity.

Overall, we see that 'suckle' conflict rate increases with offspring age, due to increased offspring distress rather than increased rejections by the mother. These results indicate that weaning conflict exists in orangutans, but is more physiologically mediated rather than behaviorally, and thus controlled by the mother. In addition, no evidence of conflicts at the milk insufficiency point was found, suggesting that young orangutans are naturally curious to try solid food, maybe even well before milk supply is at its limit.

Daily number of association partners

'Suckle' event frequency as well as 'suckle' conflict frequency increased during days with three or more party members present. The increase in conflict rate was mostly due to more frequent rejections by the mother, whereas for conflict intensity, mainly offspring distress decreased with increasing number of party members. Since offspring suckle often after intense travel or proximity conflicts, it suggest that suckling can also be for comfort, not only for energy. The frequency of observed comfort suckles after travel and distance conflicts was significantly increased during days with parties. The increased suckle frequency during days with parties could therefore indicate that offspring are stressed by the presence of others and suckle rather for comfort than for milk. Since the increase rate of conflicts is mainly based on rejections by the mother, it suggests that she might also be stressed and therefore does not want the offspring to suckle at that moment. This indicates a coordination conflict not due to the mother's activity per se but due to the social environment. These results also match with the decrease of distress vocalizations and distress intensity per conflict when more party members are present, suggesting that it is in both the mother's and the offspring's interest not to draw too much attention to themselves.

4.3.2 Solid food

4.3.2.1 Food solicit

Offspring age

The amount of 'food solicit' events decreased very gradually as the offspring aged. However, 'food solicit' events were still observed even in one of the oldest offspring (as in Jaeggi et al. 2008). This is in accordance with Jaeggi et al.'s (2008) 'begging for information hypothesis'. Even the youngest offspring, Ivan, begged when he was only seven-months old though he still seemed to get all of his caloric input through the milk of his mother. Yet, he already solicited the food items that his mother was feeding on at a high frequency, suggesting he was begging for information rather than nutritional value.

No difference in the proportion of 'food solicit' events resulting in conflict was found across offspring age. However, differences concerning the characteristics of conflict varied with offspring age. Conflicts in mother-offspring pairs with older offspring tended to be characterized by more rejections, whereas the opposite was tendency was found for distress vocalizations. As the offspring ages, it gains more skill competence and therefore it needs to solicit less (Jaeggi 2006). However if the offspring solicits food when it is older, the 'food solicit' event is also more likely to result in a rejection. Sometimes the offspring was seen feeding by itself on the same food item before the 'food solicit' event happened. This goes against the 'begging for information hypothesis' of Jaeggi et al. (2008), which states young orangutan solicit food items from their mother to gain information about the affordances and nutritional values of the specific item, unless the immature was is still not able to properly process the food item. However, the 'begging for information hypothesis' and the possibility of mother-offspring conflict are not exclusive. For some items, especially rare or difficult-to-process items, the offspring could be begging for information, whereas it might try to get additional maternal investment by begging for more common and easier-to-process items from its mother.

Moreover, this study suggests that a tendency for offspring around the age of four to be most successful in obtaining food from their mother. Jaeggi et al. (2008) did not find any correlation of successful food solicitations and offspring age. However, in contrast to this study, they did not consider co-feeding -mostly on large pieces of termite wood- as a food solicitation because the offspring did not take the item away from the mother. This might partly account for the differences between the two studies, as most food solicitations for insects occurred between in offspring between two and four years of age.

Site and total food availability

Conflict rates at Tuanan seemed to be higher than at Suaq Balimbing due to a general difference in food availability. This supports our hypothesis, that when food availability is low, the demand of energy costly behavior of the mother will result in conflict more often. In addition, the number of distress vocalizations heard was higher at Tuanan than at Suaq Balimbing. In Tuanan, it was observed more often that the offspring was mipping and whimmering in the begging context, the so called "begging calls", which were not heard at Suaq Balimbing. The lack of the beginning calls could be due to difference in cultural repertoires or just because offspring distress calls in Suaq Balimbing drown in the noise of the rest of the forest. In contrast to distress vocalizations, rejections were more commonly found at Suaq Balimbing. It could be, since there is general a higher food availability at Suaq Balimbing than Tuanan, this provides a better environment to learn how to eat food on your own. Thus the mothers might reject their offspring more often to provide them with learning opportunities.

Processing steps

The most important explanatory factor of conflict frequency were the number of steps it took to process a certain food item. Easy to process items were rejected more frequently than difficult to process food items, which was reflected also in the age of the offspring. This shows awareness by the mother to the skill competence of their offspring and that they react according to it. As proposed by

Jeaggi et al. (2008), the rarity of a food item might have an influence on 'food solicit' conflict rate. However, it was not possible to examine this during the time course of this project.

4.3.2.2 Theft

A mother taking food items away from her offspring was observed only twelve time during the course of this study. Only once did this result in conflict. These results are consistent with the findings of Jaeggi et al. (2008).

4.4 Locomotion

4.4.1 Carry

4.4.1.1 No carry

Offspring age

'No carry' conflicts per travelling hour of the mother decreased with offspring age and were not observed anymore after an offspring reached four years of age. This makes sense since carrying frequency decreases with offspring age, steeply between an offspring's second and fourth birthday (concurring with: van Noordwijk et al. 2009, Phillips 2011). Nevertheless we observed conflicts already in offspring that were less than one year old, who are usually still carried almost all of the time. As an approximation of the opportunities for carrying conflicts to occur, we measured 'carrying' conflicts in relation to the time an offspring was clinging when the mother was travelling and we did not find any factor explaining the variation in conflict frequency. However, this might not be the best measurement for opportunities. Once an offspring was clinging for travelling, the mother was never observed to actively push the infant off of her. Rarely the mother was observed pushing her offspring away once she has stopped travelling. However, this is then a conflict about clinging in proximity and not locomotion context. Therefore the amount of changes form when the offspring is not in cling to when the offspring goes into cling for travel, would probably be a better measurement for 'no carry' conflict opportunities. In this study we did not record all these changes. However an approximation was made using the 2-min scan data. Even though a correlation between the two variables existed, there still was some amount of daily variation, which then might have a large influence since data is limited. Yet, in both cases, the approximation to the amount of time in cling during movement and the changes into cling, it could be that no factor was found to influence 'no carry' conflicts since they were very rare. Furthermore, by controlling for time in cling during movement, sample size was reduced from 133 to 63 and conflicts from eleven to seven compared to the analysis per total travel time of the mother. Plots hinted however, that the frequency of conflicts increase until the offspring is around three or four years old, showing that the number of conflicts increases during the time of the steepest decrease in carrying time and after an offspring reached four years of age it rarely tries to cling anymore. The one exception was seven year old offspring Mawas, who was shortly carried because she seemed very scared of an unflanged male.

Most interesting is the difference between the conflicts of the young offspring up to three years and the older offspring. Rejection intensity increased with offspring age, so young offspring seemed to be rather "forgotten" than actually passively rejected like three to four year olds. Therefore those 'carry' conflicts are in between the 'actual carry' conflicts for which cling access to travel is denied and 'left behind' conflicts. Thus according to our prediction, the 'actual carry' conflicts happen toward the end of the phase, during which the offspring have to learn how to travel independently. Both the increase in conflict frequency with offspring age visible in plots and the increase in rejections with offspring age suggest a termination conflict about maternal carrying investment.

4.4.1.2 Carry collect

Offspring age

Offspring collects to travel gradually decreased and were not observed anymore after the offspring was four years old (concurring with Phillips 2011). This matches exactly the period in which offspring carrying rate also goes towards zero. This shows that the mothers are aware of the skill level of their offspring and often collect them before they move on, if the offspring is not in cling already and still in need of assistance for locomotion. Especially when offspring are young, most of their energy needs are covered through lactation by the mother. Thus when offspring move independently if they are not yet efficient, the mothers might spend more energy through lactation than they would by carrying the

offspring (baboons: Altmann & Samuels 1992, humans: Kramer 1998, orangutans: van Noordwijk et al. 2013). As we found no evidence of conflict at the start of solid food eating, milk supply might not be at its limit yet. Therefore the mother might still pay for the increased travelling costs of her offspring even for some time beyond its first birthday. Younger offspring had more conflicts when being collected than older ones. Offspring activities prior to conflict were mixed: sometimes the offspring was playing, moving or even resting. The increase in conflict intensity could indicate that the immatures are also aware of their skill levels, or just be a result of increased strength as the offspring ages and therefore it is also able to resist more. Ivan the youngest immature cried mostly and showed no signs of resistance, whereas four year old Lois held on to branches so that Lisa had to use both hands to collect him. Another, more speculative interpretation would be that orangutan offspring, like human children(Colson et al. 1997), are naturally motivated to try things on their own and strive for autonomy, as it was already suggested in the section of this thesis about milk for the start of solid food eating.

Site

'Carry collect' events tended to be more common at Suaq Balimbing than Tuanan. As locomotion might be more costly for the immatures at Suaq Balimbing, mothers might more readily collect their offspring for travel.

4.4.2 Gap

4.4.2.1 Independent crossing

Since not all gap crossings could be recorded, 'independent crossing' conflicts were measured in relation to different variables: Total active time, total time a mother spent moving and time an offspring was not in cling while the mother was moving. The first analysis provides us with general information on conflict frequency. In the second analysis conflict frequency is normalized as a function of the time a mother spent moving. This varies with total food availability and therefore also site. It should give us the best estimate of number of gaps crossed by the mother per day. The third analysis corresponds to the total travelling time of the offspring, which is the best estimate for independently crossed gaps by the offspring and therefore also for the opportunities of 'independent crossing' conflicts to occur. However, all variables are not an exact measure of the number of (independently) crossed gaps per day. This might also be the reason why all models were not significantly different from the null model, even though we found significant explanatory factors. To get a complete record of all gap crossing data, very focused and detailed data has to be collected, like it was done in the study by Phillips (2011). Nevertheless, we still found evidence of 'independent crossing' conflicts to vary across offspring age and site.

Offspring age

The only offspring ages at which 'independent crossing' conflicts were observed, were between two and four years, with the highest daily conflict frequency found in four-year old offspring. The period between the offspring age of two to four years, is when carrying rate drops most steeply from almost 100% to 50% (van Noordwijk et al. 2009). Thus independent gap grossing conflicts occur most often during the period in which the offspring has to learn how to travel independently. Evidence for the acquisition of locomotor skills during this period have also been found by Kunz (2015), who showed that solitary locomotor play peaked during this period. As one would expect 'independent crossing' conflicts to occur until gap crossing skills are fully mastered, our results do not match the findings of Chappell (submitted), who reported that gap crossing skills are not fully developed until an immature is around six years of age. Yet, our data is limited for offspring between four and six years of age, thus the lack of conflicts might be due to lack of data, as conflicts are expected to become rarer with increasing skill and size. However, 'independent crossing' conflict frequency in relation to independent travel was not affected by offspring age, suggesting that mothers are aware of their offspring skills and assist younger offspring more frequently to cross gaps, as indicated by Chappell (submitted) in Bornean orangutan. This assumption was supported by the lack of evidence for reduced willingness of the

mother to provide assistance on hearing her offspring's distress. However, conflict duration increased with offspring age, which might be due to increased maternal encouragement to cross gaps independently. The three longest conflicts – two at Suaq Balimbing and one at Tuanan- occurred in four year old offspring and seemed to be a result of maternal encouragement. During the longest conflict, which lasted almost fifteen minutes, Lois was searching for a way to cross a gap Lisa had just crossed before. Lisa kept ignoring Lois' temper tantrum for ten minutes, before she moved lower in the tree and then waited and looked at him. As a reaction Lois also moved lower in the tree and found a way to cross. Evidence of maternal encouragement for independent travel had already been found in Bornean orangutans (Bard 1995, Phillips 2011). Here we provide further evidence for maternal encouragement in the context of independent gap crossing.

Site

Across one full day, there was a tendency to more 'independent crossing' conflicts at Suaq Balimbing than at Tuanan, but when taking into account total travelling time of the mother or independent traveling time of the offspring, this difference disappeared. However, both variables are not an exact measure of the number of (independently) crossed gaps per day. Due to differences in canopy structures, the amount and kinds of gaps having to be crossed may differ greatly between the two sites. Given the past logging disturbance, the lower canopy of Tuanan has a high density of small and more flexible trees compared to the tall and rigid trees found in the primary forest at Suaq Balimbing. Thus the number of gaps crossed per day might be higher at Tuanan, whereas on average the size of gaps is most probably larger at Suaq Balimbing. At Sabangau, a highly degraded peat-swamp forest near Tuanan, orangutans exploit the high density of small and flexible trees in the lower canopy by travelling mostly in the lower canopy and bending the flexible trees to cross gaps (Manduell et al. 2011), which might be already possible for smaller offspring compared to Suaq Balimbing. Therefore also the number of independently crossed gaps might be higher at Tuanan, because more assistance is needed to cross between larger gaps formed by more rigid trees at Suaq Balimbing (Phillips 2011). A further study examining gap crossing conflicts in a primary forests, such as Suaq Balimbing, should be conducted. To get comparable results with secondary forests, such as Tuanan, the total number of crossed gaps and independently crossed gaps as well as the size of the gap and the support type should be taken into account as it was done in Phillips' study on development of independent travel in orangutans at Tuanan (Phillips 2011) to be able to compare gap crossing conflicts in relation to different types of forest structure.

Nevertheless, we also found that the duration of an 'independent crossing' conflict tended to be higher at Suaq Balimbing than at Tuanan. As explained above, this could be a result of the mother encouraging their offspring to cross the gaps on their own and since gaps seem to be more difficult to cross at Suaq Balimbing, conflicts might last longer.

4.4.2.2 Gap collect

Offspring age

Mothers were observed to collect their offspring when in a body bridge between two trees more often when their offspring was younger, with collects starting shortly before the offspring is one year old and ending around two years of age. The percentage of time an offspring spends in body contact with its mother decreases to less than 50% by the time it is two years old (van Noordwijk and van Schaik 2005). Thus mothers have to collect their offspring less often to cross gaps if the offspring is younger. However, compared to the time an offspring travels independently, 'gap collects' decrease with age, indicating that the mothers are aware of the needs of their offspring. However, no effect of offspring age on the rate of 'gap collect' conflicts was found.

Food availability

During low food availability, 'gap collect' conflict rate tended to be higher, but each conflict was shorter. During periods of low food availability, energy is limited. Spending time waiting for the offspring is thus more costly as this time could be used to find new food resources. The shorter

duration of the conflicts supports this as the mother might be more insistent to keep on travelling, to find new feeding trees.

Daily number of association partners

In contrast to suckle and left behind conflicts, 'gap collect' events were less likely to result in a conflict if more than two party members were present per day. In addition, the conflicts were shorter compared to when no party members were present. This difference between the contexts in reaction to association partners, could be related to whether the mother or the infant tries to invoke a reaction of the other individual of the pair. During 'suckle' conflicts, the offspring is trying to get either nipple access or proximity to the mother, but in 'gap collect' conflicts it is the mother trying to get the offspring to move on, suggesting that the difference of the effect of party members depends on the conflict is offspring or mother oriented. Thus, this result suggests that it is mainly the offspring that is intimidated by other individuals and therefore it resists less when it is collected.

Site

Mothers were observed to collect their offspring to cross a gap only at Suaq Balimbing. This could be due to the forest structure at this site. Compared to Tuanan, Suaq Balimbing has more large and thicker trees with a more stratified canopy due to trees of different heights, making gaps between the trees larger, and probably the trees more difficult to bend. As in our data set only mothers at Suaq Balimbing were observed to collect their offspring to cross a gap, but independent gap crossing conflict frequency did not differ between the sites, it suggests that mothers are aware of the difficulty for the offspring to cross gaps. This was also indicated by the study of Phillips (2011), which showed that mothers provide more assistance to their offspring if gaps were larger or between unbendable supports like tree trunks. In the course of this project, it was not possible to systematically measure the rigidity of the support or the size of gaps. However, if further studies find that mothers collect their offspring more often to cross large gaps with unbendable support, this would be further evidence to show that mothers are aware of their offspring's needs. If possible, this study should be carried out at both sites to test whether the gaps at Suaq Balimbing are truly more difficult to cross and if it is only those gaps that are more difficult to cross, where mothers collect their offspring.

4.5 Proximity

4.5.1 Cling

4.5.1.1 No cling

Offspring age and daily number of association partners

The time an offspring spends clinging to its mother's body decreases with offspring age (comparable to time in body contact: van Noordwijk and van Schaik 2005). Like 'no carry' conflicts, 'no cling' conflicts occurred very rarely and active rejection was only observed in older offspring. Like we predicted, the frequency of 'no cling' conflicts increased with offspring age until it is rarely in cling anymore, indicating a termination conflict. Since more time was spent clinging to the mother when party members were present but no 'no cling' conflicts happened during that time, it suggests that the mothers allow their offspring to cling to offer them social protection. This was especially evident in the case of Mawas, a six year old female, who was clinging to her mother the whole time when an unflanged male was present, even though the only other time she clings, is normally for suckling (Kunz, pers. comm.). The costs to the mother of letting a very young offspring cling are probably not that large, but they quickly increase with the growing weight and size of the offspring (van Noordwijk et al 2013). Unlike during carrying the main costs might not be the increased weight of the offspring, but rather its size, which interferes with to mother's ability of movement, especially when foraging (Altmann 1980). Mothers of older offspring -starting around the offspring's third birthday- very often stopped feeding when the offspring came to suckle and thus lost time to forage (pers. obs.). In addition, ecological factors can influence clinging rate. Orangutan offspring of all ages were found to cling more often during rainy weather (van Noordwijk, unpubl. data), similar to findings in Japanese macaques (Schino & Troisi 1998). This shows that mothers invest in their offspring by protecting them from potential social and ecological dangers.

4.5.1.2 Stay Cling

Offspring age, daily number of association partners and site

Only young infants were restrained, suggesting mothers still provide protection for them, especially in situations which might be potentially dangerous, for example an unflanged male being within 2 meters of the mother-offspring pair. It is interesting that this behavior was recorded only in Tuanan especially in the context of an unflanged male being present. Hinting again that unflanged males are potentially more intimidating to orangutans at Tuanan than at Suaq Balimbing as also observed by Kunz (2015) in the context of social play. This might be mainly due to familiarity reasons, as there are very peaceful mother-offspring pair associations and sometimes even play with unflanged males also in Tuanan (van Noordwijk, pers.com), which then is expressed in site differences due to the fact that mother-offspring pairs at Suaq Balimbing associate more with other individuals, especially non-related ones (van Schaik 1999, Kunz 2015). Increased protectiveness in social context has also been shown in other primates, but mainly group living species, for example macaques (Wolfheim 1970, Maestripieri 1993). In macaques, during non-social high risk situations such as being high in the canopy, mothers also increased body contact to their offspring.

Thus the mother maintaining body contact with her offspring apart from the costs of carrying, seems to be an often overlooked but still important aspect of maternal investment in the sense of protection from social, but also environmental factors.

4.5.2 Distance

4.5.2.1 Too far

Offspring age, sex and daily number of association partners

A general decrease in 'too far' conflicts with increasing offspring age was evident for both males and females, which is easily explained by the increasing time and offspring spends further away from its mother (van Noordwijk and van Schaik 2005, van Noordwijk et al. 2009). Thus, as we observed, the distance at which the offspring seems to be distressed is also increased. Almost all distance conflicts happened after the mother left the offspring. For the youngest offspring this can be just a few centimeters, whereas the distance at which conflicts happened generally increased with offspring age (pers. obs.). Distance is important to tell if a conflict is due to the general age related conflict-threshold distance between mother and offspring or if it is an extraordinary conflict.

A special case with very many 'too far' conflicts in relation to the time he spent not clinging to the mother was the youngest offspring Ivan, with an average of six conflicts per non-cling hour in two follows. As a comparison, the next highest average conflict rate was 1.5 conflicts per hour. Ivan's conflict rate was probably so high because he was in cling more than 85% of the time and started to cry sometimes even if he just lost body contact to his mother. This suggests that there might be a peak of conflict when the offspring first starts leaving body contact to the mother, which has to be looked at separately. It also indicates that some periods of intense conflict can be rather short and that the distance between mother and offspring at which conflicts happen play an important role. Thus further studies on mother-offspring conflict in proximity or travelling context should try to include distance measurements as they seem to be essential to relate conflict frequency to offspring age.

Young female offspring had more 'too far' conflicts than young male offspring did, but the rates for both females and males decreased with increasing offspring age, with the female rate approaching the male rate somewhere in between three and six years of age. However, female data is missing from offspring between two and seven years of age. Thus it is difficult to tell if this is a real effect or just due to data gaps, especially, since conflict rate in the oldest female offspring in the sample seems to be higher again than in her male counterparts.

From what we experienced in the field, young female orangutans seem to develop a little quicker than males. Therefore they might wander away from their mothers earlier to explore, but are nevertheless still in distress when the mother gives signs of leaving a certain proximity range. It would be very interesting to test this hypothesis in further studies as the data on distress vocalizations and distances between mother and offspring is available. If possible one should try to compare daughters and sons of the same mothers to account for possible differences in maternal style. If that is not possible, the age of the mother should be taken into account, as the experience of the mother seems to have an influence on maternal style with younger mothers tending to aim more at maintaining proximity to her offspring (Phillips 2011, also Japanese macaques: Schino et al 1995, vervets: Fairbanks 1996). As we found an interaction effect between mother age and food availability we cannot interpret too much into the effect of mother age class alone, but supporting the evidence found by Phillips 2011, young mothers seemed to have less 'too far' conflicts with their offspring than ancient mothers.

Juvenile and prejuvenile (dependent offspring, but mother already pregnant) females seemed to have more conflicts about maintaining proximity compared to juvenile and prejuvenile males, who were very rarely observed having conflicts about proximity maintenance. The only conflicts observed in males were in Kino, a 7.5 year old immature at Tuanan. The many 'too far' conflicts of juvenile and prejuvenile females is explained by an effect of party members, as conflict rate in juvenile and prejuvenile males and females is similar during days with no associations, but greater in females during days with associations. The differences should not be an artefact of differences in the kind of party, because all parties were with unflanged males, except for one. This other part, in a male offspring, Fredy, was with a flanged male. Especially older female offspring seem to be afraid of unflanged males. For example, Ipsy, a seven-year old female at Tuanan, stayed in very close proximity to her mother

when an unflanged male was present and already cried when she was more than 10m away, even though she normally spends much of her time further than 10m away from her mother (pers. obs.). One of the main differences in offspring social play with associates is, that immatures -or at least male immatures- at Suaq Balimbing play with unflanged males if the opportunity is arises, but play with unflanged males was rarely observed at Tuanan (Kunz 2015) for both sexes. It would be interesting to analyze data of female individuals between two and four years of age to fill the gaps and have some older female immatures in Suaq Balimbing, to examine if at Suaq Balimbing older female offspring show a similar trend as the ones in Tuanan or if unflanged males are potentially considered as less intimidating also for females.

Young mothers vs. ancient mothers in relation to food availability

Moreover, we found an interaction effect of maternal age and food availability per site. Ancient mothers tended to have fewer conflicts when food availability decreased, whereas younger mothers tended to have more conflicts under poor food conditions. The increase in conflicts with decreasing food availability would correspond to our hypothesis that if less energy in the form of food is available, more conflicts about energy costly activities should take place. Thus the energy costly activity from the perspective of the offspring, in this case would be the following or moving toward the mother, whereas the mother would incur costs by waiting for the offspring because she loses feeding time. Young mothers might be influenced by low food availability more strongly, because their chance of reproducing again is still high. Thus they gain more from their own survival enabling future reproduction than very old females, whose probabilities of having additional offspring is strongly reduced (Williams 1966, Trivers 1974). However, conflict frequency stays the same or even slightly decreases with decreasing food availability in ancient mothers. Even though this is contradictory to our hypothesis about food availability, it can still be explained by the fact that ancient mothers should shift their priorities from future offspring towards the current offspring. It might be that the food availability hypothesis does not apply to ancient mother, because ancient mothers invest more resources into their current offspring if food availability is low, since the prospect of further offspring is very low. This result is especially interesting if it holds in a larger data set, since the food availability index did not have an influence on conflict frequency, indicating that the mothers react to the food availability changes within site and not due to overall food availability. The elevated distress intensity during food shortages strengthens the assumptions that food availability not only affects the mother, but also the offspring as it tries to solicit maternal investment more rigorously.

This interaction between maternal age and food availability indicates, that even though maternal experience might play a role in explaining differences in conflict frequencies concerning the distance between mother and offspring, as mentioned above, it can still be affected by ecological factors like food availably (also in vervets: Hauser and Fairbanks 1988).

4.5.2.2 Too close

Offspring age

'Too close' conflicts only arose when the offspring already had a younger sibling. Orangutan mothers are very tolerant towards their weaned offspring. Offspring up to six years at Tuanan and up to eight years at Suaq Balimbing are still at least 50% of their time within 10m and thus mostly in the same tree as their mother. Even up to ten years of age, offspring spend half of their time within 50m of their mothers, which means being in association and able to coordinate travel (van Noordwijk & van Schaik 2005, van Noordwijk et al. 2009).

Site

Even though orangutans at Suaq Balimbing are more sociable and live at higher densities than at Tuanan (van Schaik 1999), no difference in 'too close' conflict frequency was found, suggesting that the tolerance of weaned offspring is similar at both sites. 'Too close' conflicts only occurred when the

mother and offspring were in proximity of less than five meters (pers. obs.). Henceforth, conflict frequency should be corrected for the time spent in less than five meters distance to the mother. Apart from revealing more about the relationship between a mother and her weaned offspring, analysis of proximity data can be used for more precise approximations for opportunities for conflicts.

Although no difference in conflict frequency was found between the two sites, more distress vocalizations after having been rejected by the mother were heard at Tuanan than at Suaq Balimbing. The question arises, whether this is a cause by real differences between the sites or -as already proposed for the lack of unknown distress vocalizations in young immatures at Suaq Balimbing- rather a difference in the possibility of hearing the vocalizations. As the two distress vocalizations recorded at Suaq Balimbing were both screams whereas Tuanan had both screams and cries, it suggests that lower intensity distress vocalizations might be missed more often at Suaq Balimbing.

4.5.2.3 Stay close

Number of association partners

Events during which the mother tried to maintain proximity to her offspring, but did not put it to cling, did not happen often. Still there is potential for conflict, since one out of the seven 'stay close' events resulted in conflict. 'Stay close' events are probably rare because it is usually very much in the offspring's interest to stay close to its mother, seeing 226 'too far' conflicts compared to six 'stay close' events respectively one 'stay close' conflict. The fact that more 'stay close' events happened at Tuanan, might be an observation bias. Van Schaik et al. (2006) state that the throat scrape is an innovation of the orangutans at Tuanan, not heard at any other known site. However, we think to have heard a throat scrape at Suaq Balimbing as well, seemingly in the same context as it is used at Tuanan. This could mean that the lack of throat scrapes is an observation bias, either because observer did not pay much attention to it because it was unknown to occur at this site or, as already suggested for the offspring's distress vocalizations, that vocalizations at Suaq Balimbing are not as easily heard as at Tuanan. Another explanation could be the different use of vocalizations between the two sites. Orangutan mothers at Tuanan seemed to throat scrape more commonly when party members were present, yet they also did so when no other individuals were in association. The only throat scrapes at Suaq Balimbing heard so far, occurred when the mother was very stressed because of the presence and agonistic interactions with another female. Thus mothers at Suaq Balimbing might only throat scrape in very urgent context. Moreover, since orangutans of Suaq Balimbing are more gregarious than the ones at Tuanan (van Schaik 1999), they should be more used to the presence of other individuals and thus less stressed. Therefore offspring collects due to the presence of other individuals might be less common, even though more associations are formed at Suaq Balimbing than at Tuanan (see also van Schaik 1999). The only 'stay close' conflict to happen was at Suaq Balimbing, probably not due to a site difference but to a difference in the association partners during the offspring collect call, as the two offspring of the other mother-offspring pair were potential play partners to the focal offspring at Suaq Balimbing, but the unflanged and flanged male at Tuanan were not (Kunz 2015).

5 Conclusion

5.1 In what contexts does mother-offspring conflict occur?

In this study found three main contexts of mother-offspring conflict to occur in orangutans: nutrition, locomotion and proximity. Each of those conflicts can be divided further into different 'subjects' , which can be split up into more fine-grained, contrasting 'problems', depending on whether it is the mother or the offspring who initiates the conflict (mother vs offspring oriented conflicts). In total, fourteen different conflict problems were teased apart. In our hypothesis, we did not consider mother oriented conflicts in nutrition ('theft') and locomotion conflicts ('carry collect' and 'gap collect') or offspring oriented proximity conflicts ('too far' and 'too close'), that were now found to occur in orangutans.

5.2 What are the trajectories of mother-offspring conflict during offspring development?

Generally, the first mother-offspring conflicts to occur clinging, carrying and food solicit conflicts, which are followed by gap crossing conflicts, then suckling conflicts and finally conflicts due to decreased tolerance by the mother towards her offspring. Conflicts that result in offspring distress, because either the mother or the offspring itself had increased the distance between them, are found in offspring of all ages. However, they tend to decrease with increasing offspring age and peak when to offspring is two years old. These 'too far' conflicts were also the most commonly observed conflicts, with hourly conflict frequencies at their peak being almost twice as high in comparison to the conflicts with the second highest peaks, namely 'independent crossing' and 'food solicit' conflicts. Probably also as cause of the great amount of 'too far' conflicts, overall conflict frequency is highest in offspring around two to three years of age. This is the offspring's age at which the mother's investment is most increased for several reasons: The offspring still needs to be carried and assisted in locomotion and when it is not carried its energy expenditure is still relatively high, because it has only started to learn to move through the canopy (van Noordwijk et al. 2009, Phillips 2011, van Noordwijk et al. 2013a). Furthermore, it engages in energy consuming play for a large part of the day (van Noordwijk and van Schaik 2005, Kunz 2015). Moreover, the offspring still suckles and solicits food, as it is not yet competent to process all food items. In addition, maintaining proximity to its mother also still seems important for protection and shelter from environmental factors. In conclusion, conflict 'problems' peak according to the competence and needs of an offspring.

5.3 Which factors influence mother-offspring conflict and how?

All six factors that were examined in this project seemed to have an effect on mother-offspring conflict in relation to the opportunities for it to occur. If an effect of offspring age was evident, conflict rates increased with offspring age. In this study, conflict over the termination of investment was found for suckling and proximity. 'Too close' conflicts in proximity context were caused through active rejection by the mother, whereas 'suckle' conflicts seem to be physiologically mediated rather than through active behavioral rejection. However, the opposite kind of conflict was observed as well: Not only did rejections by the mother increase with offspring age, but offspring resistance to its mother's collects increased up to the point at which the offspring was not collected anymore. Thus, it seems as if it is also in the offspring's interest be independent. These conflicts of active resistance to a mother's attempts to retrieve her offspring occurred mainly in three- to four-year old offspring.

As expected, conflict frequencies increase with decreasing food availability. This effect was evident in gap crossing conflicts in relation to changes of food availability within a site as well as in conflicts about

solid food in relation to food availability differences across sites. This result shows that more mother-offspring conflicts occur if energy levels are low.

Moreover, we found evidence that supports the 'Terminal Investment Hypothesis'. Very old mothers tend to have less conflicts about proximity to their older offspring. In addition, mother-offspring pairs with younger mothers showed a significant increase in 'too far' conflicts during low food availability, whereas the effect was the slightly into the other direction for old mothers.

Furthermore, distinct effects of association partners on mother-offspring conflict were visible. Conflict rates of offspring oriented 'problems' such as 'suckle' and 'too far' conflicts increased if more party members were present, whereas mother oriented conflicts like 'gap collect' conflicts decreased with increasing party size. Thus, it seems as if mainly the offspring was intimidated by other individuals. This is also the case for 'too far' conflicts in which specifically very young females and those around weaning show significantly elevated conflict frequencies if party members are present, possibly because most of the parties were with unflanged males.

Overall, we found effects of all six factors on conflict frequencies, except offspring sex only seemed to have an influence in combination with the presence of other individuals. We also find contrasting effects of the influencing factors on mother-offspring conflict, but these effect can mostly be explained by the direction of conflict (mother or offspring oriented).

5.4 Are there differences in mother-offspring conflict between the Sumatran and Bornean study sites?

Indeed, we found differences in mother-offspring conflict between the two study sites, Suaq Balimbing and Tuanan. 'Suckle' conflict rate tends to be higher at Suaq Balimbing than at Tuanan starting already in the youngest offspring. Moreover, conflicts at Suaq Balimbing are indicated more often through rejection by the mother compared to Tuanan. This could be an effect of the generally higher food availability at Suaq Balimbing, similar to what was found for baboons (Barrett et al. 2006): Offspring, which grow up in conditions of low food availability tend to meet their energy needs more with milk than solid food compared to those offspring developing in high quality environments.

In accordance with the predicted site differences, 'food solicit' conflict rate as well as distress rate was increased at Tuanan, probably due to the lower food availability at this site (Marshall et al. 2009). In addition, 'carry collect' conflict rate was elevated in Tuanan as well, possibly due to the mother's increased need of having to find new food sources.

In contrast, both, 'independent crossing' and 'gap collect' conflict frequencies, were higher at Suaq Balimbing. This is partly due to the fact that mothers at Suaq Balimbing tend to travel more than those at Tuanan, but probably also due to the differences in canopy structure between the sites (Vogel et al. 2009). Not only conflict frequency of gap crossing conflict was increased at Suaq Balimbing, but also conflict duration. This suggests that the gaps at Suaq Balimbing are more difficult to cross. However, mothers did not just ignore their offspring, but seemed to actively encourage them to find a way to cross by themselves. Thus, we do find differences between the two study sites, Suaq Balimbing and Tuanan, which seem to be caused by differences in forest structure and productivity.

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7 Statement of Authorship

I declare that I have used no other sources and aids other than those indicated. All passages quoted from publications or paraphrased from these sources are indicated as such, i.e. cited and/or attributed. This thesis was not submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Zürich, 01 May 2015

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11 Appendix

11.1 Additional output tables from linear mixed models

11.1.1 Milk

Suckle events per hour
Best fit model: $\chi^2(5)=24.65$, $p<0.0002$
Full model: $\chi^2(7)=27.73$, $p=0.0005$
Nr. Observations: 140
Groups: Mother 13/Name 17/Period 30
Table 21 '**Suckle' event frequency.**
Model output from linear mixed model testing suckle events per active hour

	Value	DF	t	p
(Intercept)	0.178	108	2.10	0.04
AgeO	0.006	10	1.99	0.08
FAIN	-0.030	10	-1.81	0.10
Sex (m)	0.071	3	1.24	0.30
AgeM (y)	0.037	10	0.70	0.50
NPM (1-2)	-0.010	108	-0.28	0.78
NPM (3+)	0.132	108	1.90	0.06
Site (T)	-0.040	10	-0.77	0.46
AgeO^2	0.000	10	-3.20	0.01

11.1.2 Food

Food solicit events per feeding hour of the mother
Best fit model: $\chi^2(2)=18.17$, $p<0.0001$
Full model: $\chi^2(8)=19.32$, $p=0.007$
Nr. Observations: 132
Groups: Mother 13/Name 17/Period 30
Table 22 **'Food solicit' event frequency.**
Model output from linear mixed model testing suckle events per feeding hour of the mother

	Value	DF	t	p
(Intercept)	0.039	100	4.48	0.00
AgeO	0.000	11	-4.75	0.00
FAIN	0.003	11	1.44	0.18
Sex (m)	-0.003	3	-0.47	0.67
AgeM (y)	0.003	10	0.54	0.60
NPM (1-2)	0.001	100	0.21	0.83
NPM (3+)	0.000	100	0.02	0.98
Site (T)	-0.005	10	-0.86	0.41

Success rate per food solicit try
Best fit model: $\chi^2(4)=11.53$, $p=0.021$
Full model: $\chi^2(8)=12.86$, $p=0.117$
Nr. Observations: 77
Groups: Mother 13/Name 15/Period 23
Table 23 **'Food solicit' success rate.**
Model output from linear mixed model testing success per begging try.

	Value	DF	t	p
(Intercept)	0.079	52	0.63	0.53
AgeO	0.009	5	1.89	0.12
FAIN	-0.013	5	-0.58	0.59
Sex (m)	0.025	1	0.30	0.81
AgeM (y)	0.033	10	0.43	0.68
NPM (1-2)	0.145	52	1.98	0.05
NPM (3+)	0.224	52	1.90	0.06
Site (T)	0.056	10	0.80	0.44
AgeO^2	0.000	5	-1.89	0.12

11.1.3 Carry

Carrying rate per hour move of the mother

Best fit model: $\chi^2(2)=46.03$, $p<0.0001$
Full model: $\chi^2(8)=49.98$, $p<0.0001$
Nr. Observations: 127
Groups: Mother 13/Name 17/Period 30

Table 24 **Carrying rate.**

Model output from linear mixed model testing time in cling during travel in relation to total travel time of the mother.

	Value	DF	t	p
(Intercept)	0.892	95	15.35	0.00
AgeO	-0.023	10	-10.43	0.00
FAIN	0.003	10	0.35	0.73
Sex (m)	-0.063	3	-1.63	0.20
AgeM (y)	0.026	10	0.71	0.49
NPM (1-2)	0.019	95	0.98	0.33
NPM (3+)	0.012	95	0.34	0.73
Site (T)	-0.005	10	-0.12	0.91
AgeO^2	0.000	10	7.73	0.00

Carry collects per hour move of the mother

Best fit model: $\chi^2(3)=26.83$, $p<0.0001$
Full model: $\chi^2(8)=32.95$, $p=0.0001$
Nr. Observations: 133
Groups: Mother 13/Name 17/Period 30

Table 26 **'Carry collect' frequency.**

Model output from linear mixed model testing offspring collect frequency in relation to total travel time of the mother.

	Value	DF	t	p
(Intercept)	1.043	101	7.70	0.00
AgeO	-0.022	10	-4.65	0.00
FAIN	0.033	10	1.31	0.22
Sex (m)	-0.087	3	-0.96	0.41
AgeM (y)	0.065	10	0.77	0.46
NPM (1-2)	-0.108	101	-1.28	0.20
NPM (3+)	0.105	101	0.66	0.51
Site (T)	-0.165	10	-1.95	0.08
AgeO^2	0.000	10	3.19	0.01

'No carry' conflict frequency per hour move of the mother

Best fit model: $\chi^2(2)=6.76$, $p=.034$
Full model: $\chi^2(7)=9.55$, $p=0.216$
Nr. Observations: 133
Groups: Mother 13/Name 17/Period 30

Table 25 **'No carry' conflict frequency.**

Model output from linear mixed model testing time in 'carry' conflict frequency in relation to total travel time of the mother.

	Value	DF	t	p
(Intercept)	0.822	101	1.15	0.25
AgeO	-0.001	11	-2.27	0.04
FAIN	0.004	11	0.29	0.78
Sex (m)	0.016	3	0.29	0.79
AgeM (y)	-0.066	10	-1.38	0.20
NPM (1-2)	0.023	101	0.51	0.61
NPM (3+)	0.057	101	0.69	0.49
Site (T)	0.103	10	2.10	0.06

11.1.4 Gap

Independent crossing conflicts per hour

Best fit model: $\chi^2(3)=6.33$, p=0.100
Full model: $\chi^2(8)=9.50$, p=0.301
Nr. Observations: 141
Groups: Mother 13/Name 17/Period 30

Table 27 '**Independent' crossing conflict frequency (1)**
Model output from linear mixed model testing infant collect events in gap cross context per active hour.

	Value	DF	t	p
(Intercept)	-0.032	109	-0.811	0.419
AgeO	0.004	10	2.827	0.018
FAIN	-0.012	10	-1.564	0.149
Sex (m)	0.023	3	0.848	0.459
AgeM (y)	0.017	10	0.680	0.512
NPM (1-2)	0.010	109	0.654	0.515
NPM (3+)	0.012	109	0.395	0.694
Site (T)	-0.043	10	-1.723	0.116
AgeO^2	0.000	10	-3.103	0.011

Independent crossing conflicts per h move of mother

Best fit model: $\chi^2(4)=8.36$, p=0.079
Full model: $\chi^2(8)=8.80$, p=0.359
Nr. Observations: 133
Groups: Mother 13/Name 17/Period 30

Table 28 '**Independent crossing' conflict frequency (2)**
Model output from linear mixed model testing conflicts per hour movement of the mother.

	Value	DF	t	p
(Intercept)	0.000	101	-0.09	0.93
AgeO	0.013	10	2.38	0.04
FAIN	-0.051	10	-2.13	0.06
Sex (m)	0.014	3	0.14	0.89
AgeM (y)	0.032	10	0.35	0.73
NPM (1-2)	0.005	101	0.04	0.93
NPM (3+)	0.115	101	1.04	0.30
Site (T)	-0.124	10	-1.28	0.22
AgeO^2	0.000	10	-2.70	0.02

Gap collect events per hour move of the mother

Best fit model: $\chi^2(3)=18.17$, p=0.0001
Full model: $\chi^2(7)=19.92$, p=0.006
Nr. Observations: 109
Groups: Mother 13/Name 16/Period 28

Table 29 **'Gap collect' event frequency.**
Model output from linear mixed model testing infant collect events in gap cross context per hour move of the mother.

	Value	DF	t	p
(Intercept)	0.988	79	4.66	0.00
AgeO	-0.006	10	-2.88	0.02
FAIN	-0.015	10	-0.32	0.75
Sex (m)	-0.013	2	-0.08	0.95
AgeM (y)	-0.059	10	-0.37	0.72
NPM (1-2)	-0.069	79	-0.48	0.63
NPM (3+)	-0.245	79	-0.94	0.35
Site (T)	-0.532	10	-3.19	0.01

11.1.5 Cling

Proportion of time in cling

Best fit model: $\chi^2(4)=59.33$, $p<0.0001$
Full model: $\chi^2(8)=63.37$, $p<0.0001$
Nr. Observations: 119
Groups: Mother 13/Name 17/Period 30
Table 30 '**Too far' conflict frequency.**
Model output from linear mixed model testing conflicts per no move hour of the mother.

	Value	DF	t	p
(Intercept)	0.551	87	11.478	0.000
AgeO	-0.017	10	-11.432	0.000
FAIN	0.000	10	-0.006	0.996
Sex (m)	0.040	3	1.689	0.190
AgeM (y)	0.041	10	1.067	0.311
PM (yes)	0.064	87	3.294	0.001
Site (T)	0.036	10	0.946	0.367
AgeO^2	0.000	10	8.168	0.000
AgeO:PM	-0.001	87	-2.551	0.013

11.1.6 Distance

Too close conflicts per non-move and no rest-in-nest h of the mother

Best fit model: $\chi^2(1)=4.74$, $p=0.030$
Full model: $\chi^2(7)=8.02$, $p=0.331$
Nr. Observations: 131
Groups: Mother 13/Name 17/Period 30
Table 31 '**Too close' conflict frequency.**
Model output from linear mixed model testing conflicts per of the mother not moving and not being in a nest.

	Value	DF	t	p
(Intercept)	0.020	99	0.67	0.50
AgeO	0.001	11	2.65	0.02
FAI	0.003	11	0.67	0.52
Sex (m)	-0.021	3	-0.98	0.40
AgeM (y)	-0.003	10	-0.17	0.87
NPM (1-2)	-0.011	99	-0.94	0.35
NPM (3+)	-0.012	99	-0.57	0.57
Site (T)	-0.029	10	-1.35	0.21