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The role of mother-offspring contact in wild Bornean orangutans (*Pongo pygmaeus morio*)

by

Morgane Allanic

Danau Girang Field Centre
Lot 6, Lower Kinabatangan Wildlife Sanctuary, Sabah, Malaysia

Dr Benoit Goossens and Danica Stark

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1. Introduction

Primates differ from other mammals in their slow life history (van Schaik & Deaner 2003), including relatively long inter-birth intervals and long periods of juvenility (Pereira & Fairbanks 1993). This long period spent with the mother is due to the skills that must be learned prior to independence and adulthood (Janson & van Schaik 1993). Amongst the great apes, gorillas (*Gorilla sp.*) have an inter-birth interval of 3-5 years (Galdikas & Woods 1990; Tutin 1994; Watts 1991), chimpanzees (*Pan troglodytes*) around 5-7 years (Galdikas & Woods 1990; Tutin 1994) and approximately 8 years for orangutans (*Pongo sp.*) (Galdikas & Woods 1990). Great ape inter-birth intervals are longer than those of others mammals of the same body size, and are similar to the longest intervals found amongst mammals (i.e elephants and whales; van Noordwijk & van Schaik 2005). A long inter-birth interval indicates late weaning, and thus slow infant development (van Noordwijk & van Schaik 2005). Weaning is an important indicator of independence during infant development and corresponds with the end of lactation. This marker allows the distinction from infant to juvenile (van Noordwijk & van Schaik 2005). Juvenility begins when the immature individual is able to survive the death of its mother, and ends when sexual maturity is reached (Janson & van Schaik 1993). Gorilla offspring are weaned at the age of 3-4 years old (Watts & Pusey 1993), chimpanzee offspring around 5 years old (Watts & Pusey 1993) and orangutan offspring around 7 years old (van Noordwijk & van Schaik 2005; van Noordwijk et al 2013). Gorillas tend to grow and mature faster than the other great apes (Leigh 1996; Watts & Pusey 1993). Both gorillas and chimpanzees are weaned sooner and have shorter inter-birth intervals than orangutans, but the reason orangutans have this particular status among great apes is not fully understood.

Orangutans have a longer inter-birth interval, are weaned later, and the offspring stays longer with the mother after weaning than other great apes. There are three hypotheses for why orangutans differ from other great apes in this respect. The first is the “slow life history” hypothesis. Orangutan development may be slower than other great apes due to their more energetically costly arboreal habits (Knott 1998, 2001; van Schaik & Deaner 2003; Wich et al 2004b). Moreover, it has been suggested that frugivorous animals have slower life histories than folivorous ones (Ross & Jones 1999; Stoinski et al 2013), which may also explain why orangutans have a slower development than the more terrestrial and folivorous gorillas (Wich et al 2004b). The second hypothesis is the "development-of-skills" hypothesis, which suggests that the offspring learns different skills at different stages. The mother serves multiple functions, by providing nutrition, transportation, shelter against elements, protection against conspecifics and predators, and demonstrates numerous skills that her offspring can learn, including knowledge of food species, foraging techniques, and efficient use of the range (van Noordwijk & van Schaik 2005). The offspring has to reach independence in all of these skills, but masters each at different stages before reaching complete independence (van Noordwijk & van Schaik 2005). The final hypothesis is the "solitary-lifestyle" hypothesis. It has been suggested that the general fruit availability in Southeast Asia is lower than in Africa (Terborgh & van Schaik 1987). As a result, orangutan mothers may not be able to associate permanently with both a new infant and an older offspring (Galdikas & Teleki 1981). The solitary-lifestyle hypothesis has been suggested to explain why orangutan mother associates with the latest offspring until it is ecologically independent, but because she cannot permanently associate with an older offspring while caring for an infant, the mother has an extended inter-birth interval (van Noordwijk & van Schaik 2005). Orangutan mothers have to wean later and extend their inter-birth interval compared to chimpanzees, which can wean offspring earlier and have another infant sooner since the higher food availability in African forests allows weaned offspring to remain in association with the mother and her new infant (Wich et al 2004b). Although gorillas and chimpanzees are both weaned sooner and have shorter inter-birth intervals than orangutans, these shorter periods of lactation do not necessarily correspond to a faster pace of development. Although chimpanzees are weaned sooner and have shorter inter-birth intervals compare to orangutans, both chimpanzees and orangutans seem to develop competences (locomotor, nutritional, ranging competences) at the same speed (van Noordwijk & van Schaik 2005; van Adrichem et al 2006). The fact that chimpanzees and orangutans become ecologically independent at the same age seems to refute the two first hypotheses: slow life history and development-of-skills. These results tend to support the third hypothesis: solitary life-style. The lower fruit availability of Southeast Asian forests compared to African forests seems to force orangutan mothers to delay the weaning of their infants and extend their inter-birth intervals since this low availably does not allow a permanent association between the older offspring and the new infant with the mother (Wich et al 2004b).

The low fruit availability in Southeast Asian forests supports why orangutans have a later weaning age and a longer inter-birth interval than others great apes (Sumatran orangutans, van Adrichem 2006; van Noordwijk & van Schaik 2005). However, to understand why orangutan offspring remain with their mother for so long, it is important to look at the role of the mother at each stage of the offspring's development. In effect, orangutan mothers may serve a different function at different stages of their infant's development, explaining this long period of juvenility. The cost of reproduction to females includes dramatically increasing net energy intake from conception until the end of lactation (van Noordwijk et al 2013). Even after the offspring is weaned, there is still a substantial investment by the mother, thus the mother has to ensure that her offspring can live and survive on its own until it reaches sexual maturity. The offspring becomes ecologically independent when it has achieved the following skills: (i) feeding competence: the offspring is able to ingest solid food by itself; (ii) nutritional competence: the offspring is able to independently select appropriate food sources and to localize food patches at different periods of time (throughout the year and over the years); (iii) locomotor competence: the offspring is able to move throughout the canopy from tree to tree independently; (iv) ranging competence: the offspring is able to range into the canopy, deciding where to go with an efficient travel, without the presence of its mother. Ecological independence corresponds with proficiency in all of these skills. The long process prior to ecological independence, particularly nutritional competence, has been attributed to the relatively unpredictability of food availability in the forests where orangutans occur (Galdikas 1995; Knott 1998). Orangutans live in the forests of Southeast Asia where there is low fruit availability and the phenomenon of masting appears. During this a masting event, many trees produce abundant food, however a number of tree species, including important food species for orangutans, produce fruit only in during these events (Knott 1998; Wich & van Schaik 2000). Since masting events occur at irregular and long intervals, types of food available vary throughout the year and over the years, therefore young orangutans must learn what is available at different times, which may require an extended period to learn about these important food sources (van Adrichem et al 2006; Wich et al 2004b). The change in food availability makes learning how to forage on their own a long process. Since an immature individual has not mastered all the necessary skills for independent survival, it is fully dependent on its mother for the skills it is still learning. This dependence can be direct, using physical contact with the mother, or indirect, with the importance on proximity to the mother rather than physical contact. Amongst wild Sumatran orangutans, immature individuals are almost locomotor competent at 3 years old but still depend on their mothers to cross gaps in the canopy until 5 years of age. Sumatran orangutans become nutritionally independent at the weaning age (around 7 years old), but require additional time to learn specific and more complex foraging skills (until 10 years old); ranging competence is achieved around 10-11 years old (van Adrichem et al 2006; van Noordwijk & van Schaik 2005). The mother serves different functions in the learning process of her offspring, but how these functions evolve during the development of the immature is unclear. The mother provides nutrition, transportation, and protection against conspecifics or predators (van Noordwijk & van Schaik 2005). The mother also teaches different skills such as foraging for a specific food type, complex food manipulation learning, social skills (Joffe 1997) or ranging skills for efficient travel (van Noordwijk & van Schaik 2005). The functions of the mother are numerous and the role of the mother is crucial in the successful development of her offspring.

This study aims to explore the role of the mother during the process of development of skills, examining the role the mother plays at each step of the offspring's development. By focusing on the contact between the mother and offspring, this study will examine the function of mother-offspring contact and how this function and the relationship between the offspring and the mother evolve as the offspring develops their skills towards independence. In this study, contact is viewed as help from the mother and is an indication of what activities the offspring still requires aid in, as well as demonstrating which skills the offspring is already proficient in. The mother-offspring contact can only be studied outside the night and day nests, thus, the nutritional function of the contact (e.g. lactation) and behaviors rarely seen outside of the nests (e.g. suckling) cannot be studied since orangutans are arboreal and therefore behaviors occurring within the nest are not visible to the observers. Furthermore, most of the known information on the development of Bornean orangutans comes from the sub-specie *P. p. wurmbii* and little is known on *P. p. morio*, and this study focusing on the latter will allow to complete this lack of knowledge.

We hypothesize that:

(i) From the birth until around three years old, the function of contact is for feeding and transportation purposes. The percentage of time that the infant is in contact with the mother is predicted to be high and the feeding and moving behaviors are mainly done when in contact with the mother. It is also predicted that the infant takes solid food directly from the mother (being in contact with her) and not directly from the tree.

(ii) At around three years of age, contact has a transportation function. It is predicted that the infant can feed by itself but still needs assistance from the mother to move. Contact is predicted to still serve an important function for transportation, with the majority of the moving behaviors made in contact with the mother and the majority of feeding behaviors are when the infant is alone.

(iii) After three years of age, contact has no critical function except maintaining protection. The dependence of the offspring is now mainly indirect with the importance of a close proximity to the mother for learning skills. We predict that there is a very low amount of contact, and that this contact is mainly associated to resting behaviors. We predict, also, that the offspring spend the majority of its time in close proximity to its mother (less than 10 meters).

2. Materials and methods

2.1. Study site and subjects

The study was conducted in the secondary rain forest in the vicinity of Danau Girang Field Centre (5°41’ N; 118°04’ E) located in Lot 6 along the Kinabatangan River, Sabah, Malaysian Borneo.

Habituation of the wild Bornean orangutan population (*Pongo pygmaeus morio*) around Danau Girang Field Centre began in September 2013 as part of another study. For this study, the focal individuals were four offspring orangutans, which were followed from January 17th to May 16th 2014. The four offspring were from different mothers. Ages of the offspring were estimated, using pictures, by experienced researchers and were based on the size of offspring of known ages born of the same species living downriver from this study site (Lot 2, Kinabatangan River). In ascending age, Carlos was estimated between 1 and 2 years old, Butir 3 years old, Baloo between 4 and 5 years old and Keo 6 years old. Carlos, Butir, and Baloo were considered as infants, and Keo was considered as a juvenile, since he made and slept in his own nest during the night, which is considered the best marker of completed weaning (van

Noordwijk et al 2013). Carlos was a female and the three others individuals were males. All individuals travelled with their mothers. When data collection started, the mother-offspring pair did not display against the observer.

2.2.Data collection

To ensure consistency, observations were always made by the same researcher. Nest to nest follows of an offspring were conducted when possible, following the focal once it left the morning nest until immediately moving into the night nest. If a full day follow was not possible, then follows less than three hours were excluded from the analyses. Due to the difficulties of locating individuals, no predetermined sampling schedule could be followed. Therefore once an individual was found, it was followed as a focal animal for as long as possible, up to fifteen days. Carlos was followed for 85.06 hours over 14 days, Butir was followed for 120.33 hours over 15 days, Baloo for 38.00 hours over 5 days and Keo for 134.83 hours over 15 days.

2.2.1. Behavioral sampling

Data were collected using continuous focal sampling, with a focus on the offspring. Each time the offspring was visible during the follow, the time of visibility was noted. During this time of visibility, it was recorded whether the offspring was in contact with the mother or alone. Contact was defined as directly touching the mother, which included clinging/full body contact or just one part of the body (hand, foot, etc). Alone was defined as no part of the offspring is touching the mother. Whether the offspring was in contact with the mother or alone, the following behaviors were recorded: feeding, moving, resting, playing and grooming. The time (00h00m00s) that the behavior started and ended was recorded.

When the offspring was in contact with the mother, all the following behaviors were recorded: (i) feeding in contact: the offspring is in contact with the mother and is collecting items by hand, ingesting food items, and/or chewing on a food item; (ii) moving in contact (e.g. transportation): the offspring is carried by the mother (by hanging onto a part of the mother's body) or when the mother makes a bridge between two trees and the offspring changes location with the assistance of the mother; (iii) resting in contact: the offspring is in contact with the mother but does not move or feed, even if the mother is feeding; (iv) playing in contact: the offspring is playing with its mother, which means touching the mother and/or being touched by the mother without a clear goal; and (v) grooming in contact: the offspring is being groomed by the mother or is grooming the mother, using only one hand or both hands at the same time.

When the offspring was alone, all the following behaviors were recorded: (i) feeding alone: the offspring is alone and collecting items by hand, ingesting food items, and/or chewing on a food item; (ii) moving alone: the offspring is moving from branch to branch without the assistance of the mother; (iii) resting alone: the offspring is not in contact with the mother and stays in the same place without moving or feeding (iv) playing alone: the offspring is alone and moving and/or manipulating an object without a clear goal, or the offspring is moving in contact with another offspring without a clear goal and/or is chasing or being chased by another offspring; and (v) grooming alone: the offspring is cleaning itself with one or both hands at the same time.

Additional data recorded included (i) estimated distance between the mother and the offspring: 0-2 meters, 3-5 meters, 6-10 meters, 10-20 meters, 20-30 meters and greater than 30 meters; (ii) whether the mother and offspring were in the same tree; and (iii) which individual (mother or offspring) initiated the contact: contact initiator was defined as the individual who first touched the other individual.

2.3.Statistical analyses

As in most other studies of great ape development, the sample size was limited in the number of individuals. Due to the small number (4 individuals), the number of days was taken as the statistical unit to do statistical analyses for each age-category. When the statistical unit was less than n = 5 (i.e, when a rare event appeared such as grooming), no statistical analyses were possible and only descriptive results were calculated.

For each age-category and for all the behaviors of interest (feeding, moving, resting, playing and grooming), the proportion of behaviors done in contact with the mother (which corresponds to the time spent doing a behavior in contact with the mother divided by the total time of this behavior) and proportion of behaviors done alone (which corresponds to the time spent doing a behavior alone divided by the total time of this behavior) were calculated.

For each age-category, the following variables were calculated: proportion of time spent in contact with the mother (which corresponds to the time spent in contact with the mother divided by the total time of visibility), proportion of time spent in the same tree as the mother (which corresponds to the time spent in the same tree as the mother divided by the total time of visibility), proportion of time spent in a different tree as the mother (which corresponds to the time spent in a different tree as the mother divided by the total time of visibility), proportion of contact initiated by the offspring (which corresponds to the number of contacts initiated by the offspring divided by the total number of contacts), and the proportion of contact initiated by the mother (which corresponds to the number of contacts initiated by the mother divided by the total number of contacts).

For each age-category and for all the distances between the mother and the offspring (0-10 meters, 10-20 meters, 20-30 meters, > 30 meters) the proportion of time spent at each distance (which corresponds to the time spent at one distance divided by the total time of visibility) was calculated.

A Kruskal-Wallis test was used to compare the proportions of time spent in contact with the mother at 1-2 years old, at 3 years old, at 4-5 years old and at 6 years old. In case of significant results, two-by-two comparisons with a permutation test ("exact" method) for independent data were done and corrected by the Holm-Bonferroni method (corrected significant levels are noted as p').

For the different age-category (1-2, 3, 4-5 and 6), a permutation test ("exact" method) for dependant data was used to compare the proportion of behaviors done in contact with the mother and the proportion of behaviors done alone for the following behaviors: feeding, moving, resting, playing and grooming. The permutation test was also used to compare the proportions of time spent in the same and different trees than the mother, and to compare the proportion of contacts initiated by the infant and by the mother.

A Friedman test was used to compare the proportions of feeding, moving, resting, playing and grooming behaviors during the contact with the mother. Friedman's test was also used to compare the proportions of time spent in 0-10 meters, 10-20 meters, 20-30 meters and more than 30 meters from the mother at 1-2 years old, 3 years old, 4-5 years old and 6 years old. In case of significant results, two-by-two comparisons with a permutation test ("exact" method) for dependent data were done and corrected by the Holm-Bonferroni method (corrected significant levels are noted as p').

All Friedman and Kruskal-Wallis tests were done with R.2.14.1 software and all permutation tests were done with StatXact 3.1 software. The significant level used for the tests was $\alpha = 0.05$.

3. Results

3.1. Time spent in contact with the mother

There is a significant difference between the age-categories (1-2 years old (0.711), 3 years old (0.342), 4-5 years old (0.026) and 6 years old (0.007)) for the proportion of time the offspring spent in contact with the mother (Kruskal-Wallis test: $\chi^2 = 42.69$, df = 3, $p < 0.0001$, S) (Fig. 1). The proportion of time spent in contact with the mother at 1-2 years of age (0.711) is significantly greater than the proportion of time spent in contact with the mother at 3 years of age (Permutation test: 3 years old = 0.342, $p' < 0.0001$, S), 4-5 years of age (Permutation test: 4-5 years old = 0.026, $p' < 0.0001$, S) and 6 years of age (Permutation test: 6 years old = 0.007, $p' < 0.0001$, S). The proportion of time spent in contact with the mother at 3 years of age (0.342) is significantly greater than the proportion of time spent in contact with the mother at 4-5 years of age (Permutation test: 4-5 years old = 0.026, $p' < 0.0001$, S) and 6 years of age (Permutation test: 6 years old = 0.007, $p' < 0.0001$, S). The proportion of time spent in contact with the mother at 4-5 years of age (0.026) is significantly greater than the proportion of time spent in contact with the mother at 6 years of age (Permutation test: 6 years old = 0.007, $p' = 0.016$, S).

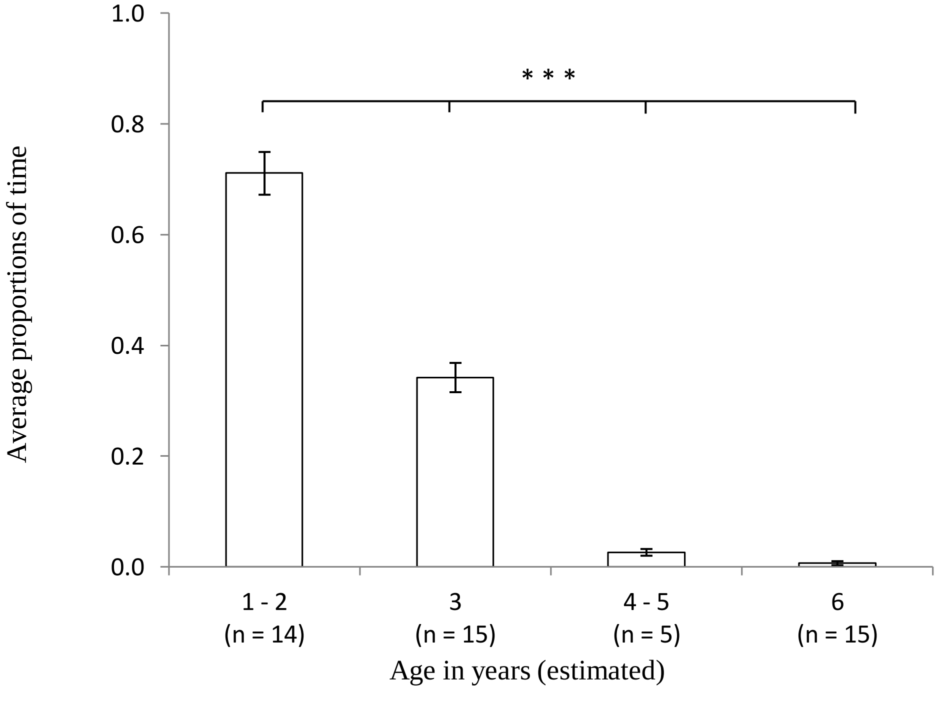


Figure 1: Average proportions (±Standard Error of the Mean) of time spent in contact with the mother for each age-category (1-2, 3, 4-5 and 6 years old). Kruskal-Wallis test, ***: $p < 0.0001$.

3.2. Behaviors during the contact with the mother

At 1-2 years of age, there is a significant difference between the proportion of feeding (0.072), moving (0.319), resting (0.569) and playing (0.040) behaviors (Friedman test: $\chi^2 = 36.51$, df = 3, $p < 0.0001$, S). No contact grooming behavior was observed at this age. The proportion of resting behaviors is significantly greater than the proportion of moving (Permutation test: p’ = 0.004, S), feeding (Permutation test: p’ = 0.0001, S) and playing (Permutation test: p’ = 0.0001, S) behaviors. The proportion of moving behaviors is significantly greater than the proportion of feeding (Permutation test: p’ = 0.0001, S) and playing (Permutation test: p’ = 0.0001, S) behaviors. There is no significant difference between the proportion of feeding behaviors and the proportion of playing behaviors (Permutation test: p’ = 0.094, NS) (Fig. 2).

At 3 years of age, there is a significant difference between the proportions of feeding (0.053), moving (0.562) and resting (0.384) behaviors (Friedman test: $\chi^2 = 21.73$, df = 2, $p < 0.0001$, S). No contact playing and grooming behaviors were observed. The proportion of moving behaviors is significantly greater than the proportion of resting (Permutation test: p’ = 0.032, S) and feeding behaviors (Permutation test: p’ = 0.0001, S). The proportion of resting behaviors is significantly greater than the proportion of feeding behaviors (Permutation test: p’ = 0.0005, S) (Fig. 2).

At 4-5 years of age, there is no significant difference between the proportions of moving (0.229), resting (0.740) and playing (0.033) behaviors (Friedman test: $\chi^2 = 5.06$, df = 2, p = 0.08, NS). Feeding and grooming behaviors were not observed whilst in contact with the mother (Fig. 2).

At 6 years of age, there is a significant difference between the proportion of feeding (0.125), resting (0.748) and grooming (0.127) behaviors (Friedman test: $\chi^2 = 7.15$, df = 2, p = 0.028, S). There is no significant difference between the proportion of resting and feeding behaviors (Permutation test: p’ = 0.08, NS), between resting and grooming behaviors (Permutation test: p’ = 0.047, NS), and between feeding and grooming behaviors (Permutation test: p’ = 1.00, NS) (Fig. 2).

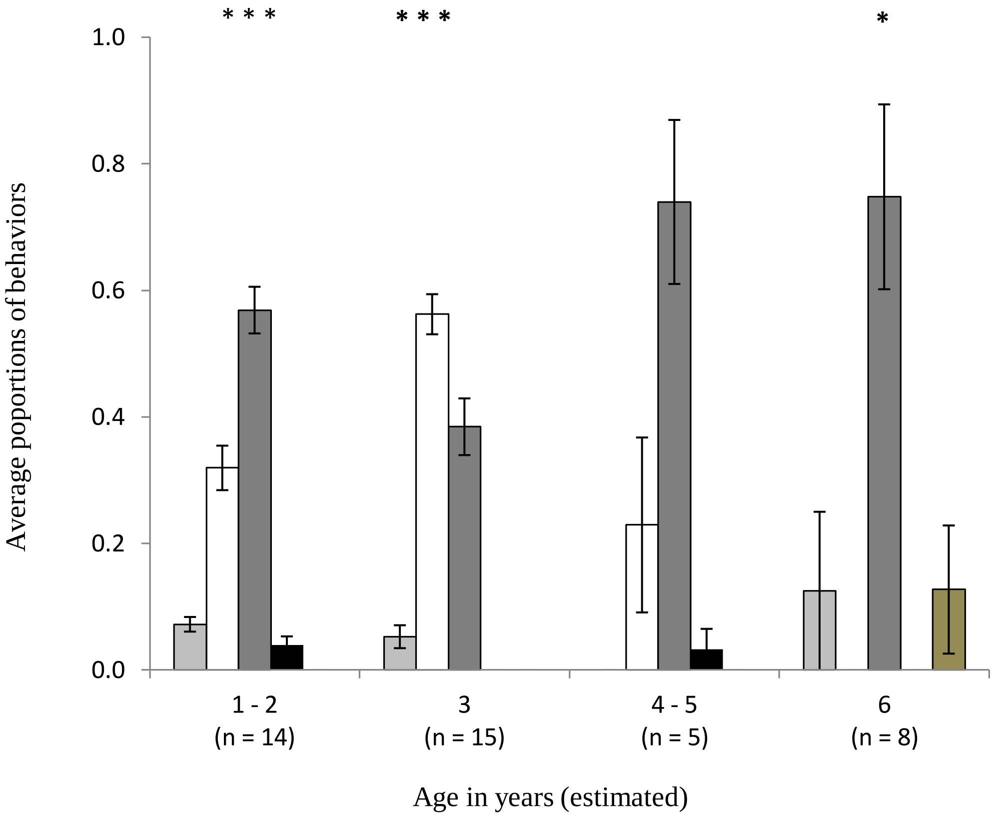


Figure 2: Average proportions (±Standard Error of the Mean) of behaviors during the contact with the mother for each age-category (1-2, 3, 4-5, and 6 years old). Light grey: feeding behaviors, White: moving behaviors, Dark grey: resting behaviors, Black: playing behaviors, Brown: grooming behaviors. Friedman test, *: p < 0.05, ***: p < 0.0001.

3.3. Proportions of behaviors done alone and in contact with the mother

3.3.1. 1-2 years old

There is no significant difference between the proportion of feeding behaviors done in contact with the mother (0.382) and the proportion of feeding behaviors done alone at 1-2 years of age (Permutation test: feeding alone = 0.618, p = 0.06, NS). The proportions of moving (0.869) and resting (0.816) behaviors done in contact with the mother are significantly greater than the proportion of moving (Permutation test: moving alone = 0.131, p = 0.0001, S) and resting (Permutation test: resting alone = 0.184, p = 0.0001, S) done alone. There is no significant difference between the proportion of play behaviors done in contact with the mother (0.455) and the proportion of play behaviors done alone (Permutation test: playing alone = 0.543, p = 0.69, NS) (Fig. 3).

3.3.2. 3 years old

The proportion of feeding behaviors in contact with the mother (0.039) is significantly less than the proportion of feeding behaviors done alone (Permutation test:

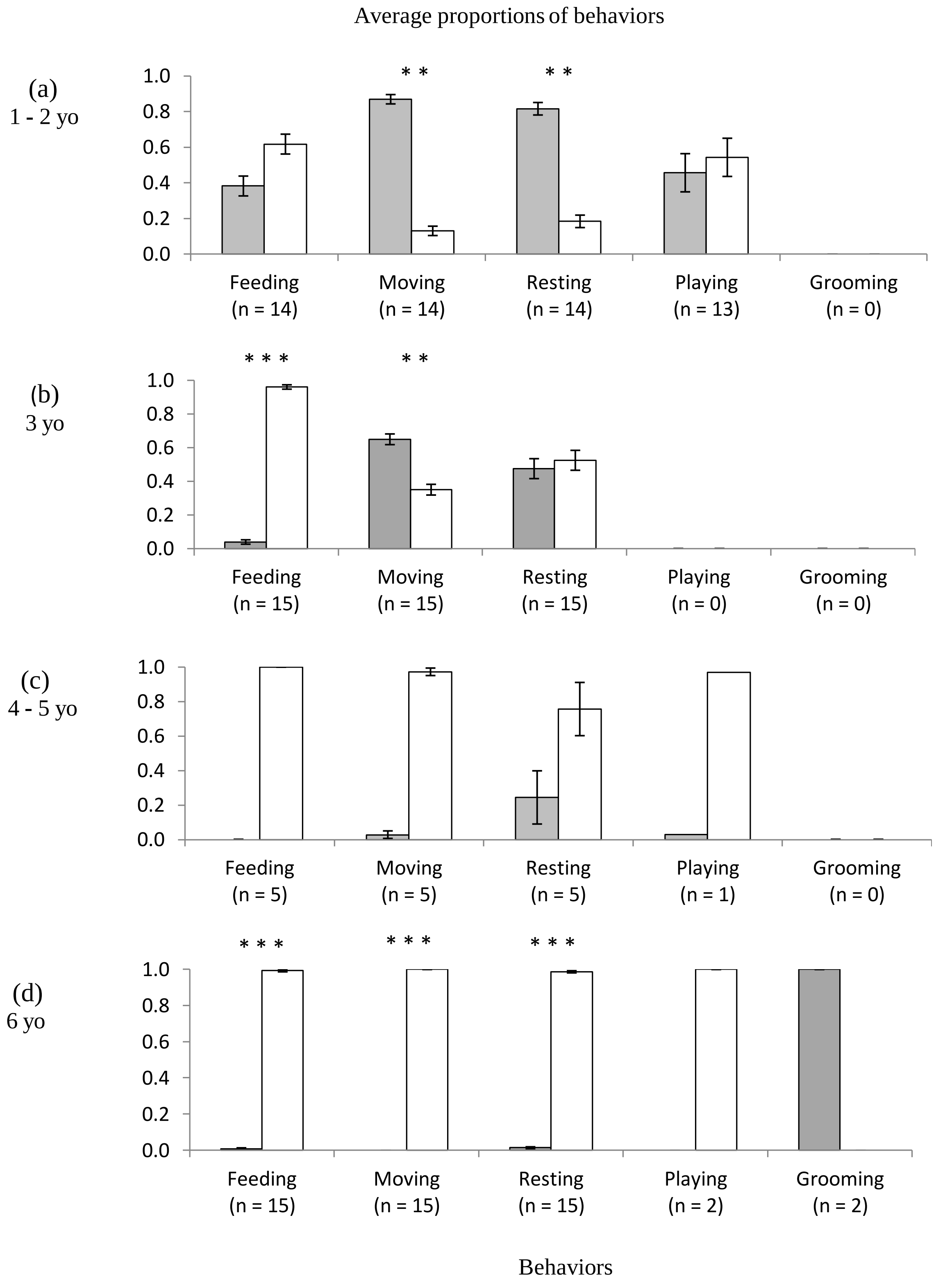
feeding alone = 0.961, p = 0.0001, S). The proportions of moving behaviors in contact with the mother (0.650) is significantly greater than the proportion of moving behaviors done alone (Permutation test: moving alone = 0.350, p = 0.0004, S). There is no significant difference between the proportion of resting behaviors in contact with the mother (0.475) and the proportion of resting behaviors done alone (Permutation test: resting alone = 0.525, p = 0.68, NS) (Fig. 3).

3.3.3. 4-5 years old

There is no significant difference between the proportions of feeding (0.000), moving (0.028) and resting (0.244) behaviors done in contact with the mother and the proportions of feeding (Permutation test: feeding alone = 1.000, p = 0.63, NS), moving (Permutation test: moving alone = 0.972, p = 0.06, NS) and resting (Permutation test: resting alone = 0.756, p = 0.19, NS) behaviors done alone. . Play behavior was only observed on one follow day, and was done mainly with another infant (1hr13min16sec), as compared to 0h02min06sec play behavior with the mother. No statistical test was possible due to small sample size (Fig. 3).

3.3.4. 6 years old

The proportions of feeding (0.007), moving (0.000) and resting (0.014) behaviors done in contact with the mother are significantly less than the proportion of feeding (Permutation test: feeding alone = 0.993, p = 0.0001, S), moving (Permutation test: moving alone = 1.000, p = 0.0001, S) and resting (Permutation test: resting alone = 0.986, p = 0.0001, S) behaviors done alone. Playing and grooming behaviors were only observed on two of the fifteen days of data collection, therefore no statistical tests were possible. These play behaviors were done once alone and once with another infant but never in contact with the mother. The grooming behaviors occurred twice in contact with the mother, and the mother groomed the infant (Fig. 3).



<u>Figure 3:</u> Average proportions (±Standard Error of the Mean) of behaviors done in contact with the mother and average proportions of behaviors done alone at (a) 1-2 years old, at (b) 3 years old, at (c) 4-5 years old and at (d) 6 years old. Grey: behaviors done in contact, White: behaviors done alone. Permutation test, *: $p < 0.05$, **: $p < 0.01$ and ***: $p < 0.0001$. “yo” = years old.

3.4. Initiation of contact

The proportion of contact initiated by the offspring is significantly greater than the proportion of contact initiated by the mother at 1-2 years of age (Permutation test: by offspring = 0.950, by mother = 0.050, $p = 0.0001$, S) and 3 years of age (Permutation test: by offspring = 0.778, by mother = 0.222, $p = 0.002$, S). However, there is no significant difference between the proportion of contacts initiated by the offspring and the proportion of contacts initiated by the mother at 4-5 years of age (Permutation test: by offspring = 0.878, by mother = 0.122, $p = 0.13$, NS) and at 6 years of age (Permutation test: by offspring = 0.400, by mother = 0.600, $p = 1.00$, NS).

3.5. Infant location: same versus different tree

The proportion of time spent in the same tree as the mother is significantly greater than the proportion of time spent in a different tree as the mother at 1-2 years of age (Permutation test: same = 1.000, different = 0.000, $p = 0.0001$, S) and 3 years of age (Permutation test: same = 0.856, different = 0.142, $p = 0.002$, S). There is no significant difference between the proportion of time spent in the same tree as the mother and the proportion of time spent in a different tree than the mother at 4-5 years of age (Permutation test: same = 0.655, different = 0.345, $p = 0.38$, NS) and 6 years of age (Permutation test: same = 0.531, different = 0.469, $p = 0.53$, NS).

3.6. Infant location: distance from the mother

At 1-2 years of age, there is a significant difference between the proportion of time spent 0-10 meters (1.000), 10-20 meters (0.000), 20-30 meters (0.000) and more than 30 meters (0.000) from the mother (Friedman test: $\chi^2 = 42.00$, df = 3, $p < 0.0001$, S). The proportion of time spent 0-10 meters from the mother is significantly greater than the proportion of time spent 10-20 meters (Permutation test: $p' = 0.0001$, S), 20-30 meters (Permutation test: $p' = 0.0001$, S), or greater than 30 meters from the mother (Permutation test: $p' = 0.0001$, S).

At 3 years of age, there is a significant difference between the proportion of time spent 0-10 meters (0.987), 10-20 meters (0.013), 20-30 meters (0.000) and more than 30 meters (0.000) from the mother (Friedman test: $\chi^2 = 27.00$, df = 3, $p < 0.0001$, S). The proportion of time spent at 0-10 meters from the mother is significantly greater than the proportions of time spent at 10-20 meters (Permutation test: $p' = 0.002$, S), 20-30 meters (Permutation test: p’ = 0.002, S), or greater than 30 meters from the mother (Permutation test: p’ = 0.002, S). There is no significant difference between the proportion of time spent at 10-20 meters and the proportion of time spent at 20-30 meters (Permutation test: p = 0.13, NS), and between the proportion of time spent at 10-20 meters and the proportion of time spent more than 30 meters from the mother (Permutation test: p = 0.13, NS).

At 4-5 years of age, there is a significant difference between the proportions of time spent at 0-10 meters (0.780), 10-20 meters (0.174), 20-30 meters (0.044) and more than 30 meters (0.000) from the mother (Friedman test: $\chi^2 = 10.02$, df = 3, p = 0.018, S). There is no significant difference between the proportions of time spent at 0-10 meters and 10-20 meters (Permutation test: p = 0.13, NS), between 0-10 and 20-30 meters (Permutation test: p = 0.06, NS), between 0-10 meters and >30 meters (Permutation test: p = 0.06, NS), between 10-20 and 20-30 meters (Permutation test: p = 1.00, NS), between 10-20 meters and >30 meters (Permutation test: p = 0.25, NS) and between 20-30 meters and >30 meters (Permutation test: p = 0.50, NS).

At 6 years of age, there is a significant difference between the proportions of time spent at 0-10 meters (0.800), 10-20 meters (0.155), 20-30 meters (0.006) and more than 30 meters (0.003) from the mother (Friedman test: $\chi^2 = 37.49$, df = 3, p < 0.0001, S). The proportion of time spent 0-10 meters from the mother is significantly greater than the proportion of time spent 10-20 meters (Permutation test: p’ = 0.0001, S), 20-30 meters (Permutation test: p’ = 0.0001, S), and more than 30 meters from the mother (Permutation test: p’ = 0.0001, S). The proportion of time spent 10-20 meters is significantly greater than the proportion of time spent 20-30 meters (Permutation test: p’ = 0.0001, S), and more than 30 meters from the mother (Permutation test: p’ = 0.0005, S). There is no significant difference between the proportion of time spent 20-30 meters and the proportion of time spent more than 30 meters away from the mother (Permutation test: p = 1.00, NS).

4. Discussion

This study shows that orangutan offspring are directly dependent on contact with the mother until three years of age. After three years, dependence becomes more indirect, with an emphasis on the proximity with the mother and no longer on body contact. The infant of 1-2 years old spent the majority of its time (71%) in contact with the mother. In Sumatra (Ketambe and Suaq Balimbing), orangutans are almost always in constant body contact with the mother during the first year of life when then declines to less than 50% at the start of their second year (van Adrichem et al 2006; van Noordwijk & van Schaik 2005). In this study, the 3-year-old spent 34% of its time in contact, whereas contact time decreased to 3% for the 4-5 year old infant and reduced even further just to an occasional touch for the 6 year old juvenile. In Suaq Balimbing, Sumatran orangutans spend around 10% of their time in contact with the mother until 8 years of age, the contact becoming occasional once a new infant is born to the mother (van Noordwijk & van Schaik 2005). Sumatran orangutans stay longer with their mothers than Bornean orangutans, suggesting a longer process to achieve independence in Sumatran orangutans. An infant over one year old is often in contact with its mother in order to beg for food. Begging is achieved by holding its hand to its mother's mouth or by directly taking food from her hands (van Noordwijk et al 2009). During the first few years of an offspring's life, transfers of food are frequent (van Noordwijk et al 2009). Younger inexperienced Bornean orangutans (Tuanan) solicited food more often than older ones (Jaeggi et al 2008). In this study, the 1-2-year-old infant was feeding on solid food as much in contact with its mother as it did alone. Feeding in contact includes food transfers between the mother and the infant or the infant taking the food directly from the same food source (e.g. same branch). This result suggests that mother-infant contact for the youngest offspring still serves for obtaining food. However, the 3, 4-5, and 6 years old offspring were, during the majority of their time, feeding alone which suggest that they can largely or completely obtain their own food. Until three years of age, the main function of contact seems to be transportation. When there is contact behavior occurring between the 3-year-old infant and its mother, it is mainly for moving through the canopy. At 1-2 years of age, the infant was almost always in contact when it was moving, which is consistent with orangutans in Sumatra (Ketambe and Suaq Balimbing) and Borneo (Tuanan) (van Adrichem et al 2006; van Noordwijk & van Schaik 2005; van Noordwijk et al 2009). At 3 years of age, the infant was still carried for 65% of its moving behaviors. From 2 to 4 years old, Bornean orangutans may be carried a little more than Sumatran orangutans. In Sumatra, 2 to 4-year-old infants were carried less than 50% of the time when the mother was moving. However in Borneo, infants were still carried 80% of the time at the Tuanan field site and around 50% at the Kinabatangan field site (van Noordwijk et al 2009). At 4-5 years, the infant in this study was occasionally carried whereas the 6-year-old juvenile was never seen carried by its mother. These data are consistent with the results found in Tuanan, Borneo were the 6-year-old orangutans were never carried, in contrast to Sumatran ones which may occasionally be carried after this age (van Adrichem et al 2006; van Noordwijk & van Schaik 2005; van Noordwijk et al 2009). This suggests that Sumatran infants are independent slightly later than Bornean orangutans for locomotion and therefore the function of contact seems to be mainly for transportation for a longer time.

The 1-2, 3 and 6 year-old offspring in this study spent almost all their time within 10 meters from their mothers. There was no significant difference in distance from the mother for the 4-5-year-old infant, which may be due to the small sample size, however 78% of the time it was within 10 meters of the mother. Even once weaned, the 6 year-old juvenile spent 80% of its time less than 10 meters from the mother. This corresponds with the behavior of Sumatran (Ketambe and Suaq Balimbing) and Bornean (Tuanan) orangutans that spend more than 60% of their time within 10 meters of their mother until at least 6 years old (van Adrichem et al 2006; van Noordwijk & van Schaik 2005; van Noordwijk et al 2009). In this study, contact decreased by 4-5 years of age and became occasional by 6 years of age, suggesting that contact does not have a critical function at this age. Furthermore, the occasional contact at those ages were initiated as much by the mother as by the offspring, suggesting that the offspring are less dependent on body contact with their mothers. The main contact behavior with their mothers at the age of 4-5 and 6 years old was predominately resting. Due to small sampling size, statistical tests showed no difference between the proportions of different behaviors, however there appeared to be a trend in resting behaviors as the main behavior during the contact (74% of resting behaviors for the 4-5-year-old infant and 75% for the 6 year old juvenile). This contact function could serve for protection against predators or competitors for food such as long-tailed macaques (*Macaca fascicularis*). In Borneo, both clouded leopards and big pythons can prey on younger orangutans (Rijksen 1978). A mother orangutan has been shown to have a major positive effect on offspring survival by early detection of predators (Nieuwenhuis 2006). Offspring detected the predator model later than their mother, and after detection they initiated body contact with their mother. Predation could be avoided by extra vigilance of the mother, and close proximity with the mother could be beneficial (van Noordwijk et al 2009). An additional explanation for prolonged close proximity is that the offspring still requires assistance in crossing gaps in the canopy even if they are no longer being carried across. The mother can hold on to branches of the tree on either side of the gap until her offspring has clambered across, but she can also assist her offspring by swaying a tree to another and not releasing this position until her child has crossed (van Noordwijk et al 2009). Alternatively, the close proximity of the offspring on their mother could be to learn skills by observation, especially food-processing. Weaned orangutans have the experience and the knowledge to eat the same diet as their mothers, however even if the offspring are able to eat all foods their mothers eat, they are not necessarily able to find or recognize feeding opportunities on their own (van Noordwijk et al 2009). The more difficult food is to process, the more attention offspring tend to give when their mothers feed on it (Jaeggi et al 2010). Recognizing rare food items or learning specific or complex food processing skills could explain the few years orangutans spend in close proximity to their mothers before dispersing on their own.

The mother orangutan provides nutrition, transportation, and protection for their offspring, but also for achieving skills including food-processing or social skills (van Noordwijk & van Schaik 2005). Even if social grooming may happen on the nest, outside the view of terrestrial observers, this behavior is rare among orangutans, providing the function for cleaning fur and wounds (van Noordwjk et al 2009). In this study, only the 6-year-old juvenile was observed being groomed by its mother. Mothers rarely groom their offspring so it is not possible to give an estimate any trends with offspring age (van Noordwijk et al 2009). However, grooming behavior may have a social function in addition to the cleaning function, and it is possible that these social skills are learned not during the first years of life but later on. As orangutans are semi-solitary, the offspring only have their mother as a permanently available play partner until dispersal (van Noordwijk et al 2009). However, social play with mother does not seem to be common and it does not occur once the offspring is weaned (van Noordwijk et al 2009). Social play with the mother was only regularly observed for the youngest infant in this study, suggesting that at this age the mother could try to stimulate the infant in movements to build strength and coordination. If the mother and offspring are in association with another mother-offspring pair, social play between offspring can occur, but these opportunities are rare (van Noordwijk et al 2009). Social play with other offspring was observed only once with the 4-5 and the 6-year-old offspring in this study. These events, even rare, may have an important role in learning social skills.

Orangutans are represented by two species: Sumatran orangutans (*Pongo abelii*) and Bornean orangutans (*Pongo pygmaeus*) and, in Borneo, it is split into three subspecies: *P.p. pygmaeus*, *P.p.wurmbii* and *P.p.morio* (Goossens et al 2009). Inter-birth intervals significantly decrease from Sumatra to West and Central Borneo, and then to East Borneo (Wich et al 2009). In Sumatra, *P. abelii* orangutans showed an inter-birth interval of 9.3 years in Ketambe (Wich et al 2004b) and of 8.2 years in Suaq Balimbing (van Noordwijk & van Schaik 2005). In Borneo, *P. p. wurmbii* showed an inter-birth interval of 7.7 years in Tanjung Putting (Galdikas & Wood 1990) and of 7.0 years in Gunung Palung (Knott 2001), whereas *P. p. morio* showed one of 6.5 years (unpublished data, Ancrenaz). It is suggested the difference in the inter-birth interval of Sumatran (8-9 years) and Bornean (6-7.5) orangutans is that Bornean orangutans either develop faster to independence or stay in association with their mother after the birth of a sibling for longer than Sumatran ones (van Noordwijk et al 2009). In accordance to the earlier inter-birth interval for Bornean orangutans compared to Sumatran orangutans, the weaning age is also earlier. In Borneo, orangutans are weaned around 5-6 years of age in the Kinabatangan and Tuanan (unpublished data, Ancrenaz; van Noordwijk et al 2009), which was also supported in this study, in that the 6-year-old offspring was already weaned. In Sumatra, orangutans are still nursing at 6-7.5 years old (van Adrichem et al 2006; van Noordwijk & van Schaik 2005). Bornean orangutans seem to be fully weaned at least 1-2 years earlier, and they appear to have a slightly earlier development than Sumatran orangutans (van Noordwijk et al 2009). Although the mortality rate on orangutans is quite low (Wich et al 2004b), the presence of tigers in Sumatra increases the potential risk of death and could explain the difference between Sumatran and Bornean orangutans in their inter-birth interval and age of independence, with a prolonged association of the offspring with their mothers in Sumatra (van Noordwijk et al 2009).

Amongst great apes, orangutans are weaned the latest, with a weaning age of around 5-8 years old (van Noordwijk et al 2009), whereas chimpanzees are weaned at around 4-6 years old, and gorillas around 3-4 years old (Watts & Pusey 1993). However, these shorter periods of lactation for both gorillas and chimpanzees do not necessarily correspond to a faster pace of development, and chimpanzees and orangutans seem to develop skills at a similar speed (van Noordwijk & van Schaik 2005). Both, chimpanzees and orangutans are almost locomotor-competent around 3 years old (Tutin 1994; van Noordwijk & van Schaik 2005). Food-processing skills and familiarity with at least the maternal diet is acquired before weaning in all great apes (van Noordwijk et al 2009), but feeding efficiency and specific and complex techniques are being learned and refined until 8-10 years old for gorillas, chimpanzees, and orangutans (Byrne & Byrne 1993; Matsuzawa 1994; van Noordwijk & van Schaik 2005). Sumatran orangutans start to range independently at a similar age as chimpanzees (Pusey 1990; van Noordwijk & van Schaik 2005). Thus, the late weaning age of orangutans does not seem primarily due to a later acquisition of skills. However, as gorillas and chimpanzees are more gregarious, they are developing with exposure to additional potential models to learn from, whereas orangutan offspring have mainly only their mother as a model (van Noordwijk et al 2009). Both gorillas and chimpanzees therefore have more opportunities for social learning (van Noordwijk et al 2009).

This study presented several limitations, the main limitation being the number of individuals. With only four individuals, it was not possible to cover inter-individual variations. Additionally, as it was a short term study, it was only possible to collected data for only one specific age-category per individual instead of observing them developing through the age-categories. This study should be continued by following more offspring throughout more years to be able to generalize on the development of infants for this population of orangutans. The ages of infants were estimated, and although the estimations were given by experienced researchers, it was possible that the ages were under or over-estimated. Orangutans are weaned around the age of 5-8 years old and stay with their mothers for a few more years after. Therefore, since our oldest infant was 6 years old but weaned, we could not cover all the ages where offspring remain in proximity to their mother. However, as our study found there is minimal contact past the age of 6, we can assume there will be minimum contact after this age as well. In addition, we could not determine if the individuals were fully habituated as habituation efforts only began in September 2013. However, all focal individuals had approximately the same amount of following time before this study began and did not display towards the observers during the study. In this study, only one of the four focal animals was female, and therefore differences in the development of sexes cannot be discounted in variation in development. Therefore it would be interesting for the future studies to increase the number of individuals and to balance the female-male ratio to see if there is a difference in the growth and maturation between males and females. Although this study presents several limits, the found results are in accordance with the others studies of Bornean and Sumatran orangutan populations.

To conclude, this study suggests that until three years of age, Bornean orangutans depend mainly on their mothers for transportation. After this age, the dependence becomes more indirect, with an importance on the proximity with the mother and no longer on body contact. This proximity could serve for protection, assistance in crossing gaps and/or learning skills such as complex food-processing. Bornean orangutans appear to have reach independence slightly earlier than Sumatran orangutans. However, for Bornean orangutans, data on offspring development mainly comes from studies on *P. p. wurmbii,* with little data coming from *P. p. morio,* and none on *P. p. pygmaeus*. This preliminary study on *P. p. morio* is a first step towards filling the gap, and the data are consistent with other studies. By continuing this study over time, it will be possible to investigate any differences in infant development between the sub-species of Bornean orangutans.

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Abstract

Orangutans (*Pongo sp.*) are weaned later and stay with their mother for longer after weaning than other great apes. Amongst orangutans, Bornean orangutans (*Pongo pygmeaus*) appear to reach independence slightly earlier than Sumatran orangutans (*Pongo abelii.*). This study aimed to examine the function of mother-offspring contact and how the function and relationship between the offspring and mother changed as the offspring developed their skills towards independence. For Bornean orangutans, data on offspring development mainly comes from studies on *P. p. wurmbii*, with little data coming from *P. p. morio*. This preliminary study on *P. p. morio* is a first step towards filling the gap by conducting nest to nest focal sampling on four Bornean orangutan offspring (*P. p. morio*). Data were collected on time spent in contact with the mother, behaviors performed during contact time, and proximity to mother. In this study, orangutan offspring were directly dependent on body contact with their mother until three years of age, with the main function of transportation. After the age of three, the dependence becomes more indirect, with a greater importance on proximity to the mother rather than direct body contact. This proximity could serve as protection, assistance in crossing gaps and/or learning skills such as complex food-processing.

Key words: *orangutan, great apes, development, mother-offspring contact*