

Factors influencing the cognitive development of infant Sumatran orangutans (*Pongo abelii*) in Suaq Balimbing, Aceh Selatan, Indonesia.



Figure 1: Lois try-feeding on a stick, credits for Caroline Schuppli (8 June 2016).

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Index

Index	2
Abstract	5
Lekensamenvatting	6
Introduction	7
Cognition: from humans to Sumatran orangutans	7
Research question I: Which factors influence the sociability of an infant's mother?	9
Sociability of the mother	9
Factors influencing sociability of the mother	10
Environmental factor: food availability	10
Family size and composition	
Age of the infant	12
Sex of the infant	13
Maternal dominance rank of the infant's mother	13
Maternal age of the infant's mother	
Presence of an older sibling	14
Conclusion: factors influencing sociability of the mother	15
Research question II: Which factors influence an infant's exploratory tendency?	15
Influence of the mother	15
Restrictiveness of the mother	15
Activity of the mother	
Influence of the infant	
Age of the infant	
Sex of the infant	
Influence by external factors	
Environmental factor: food availability	
Presence of an older sibling	
Percentage association partners related with the infant	
Extension of research question II: Which factors influence a juvenile's exploratory tende	ncy? 20
Aim of the study	
Research hypotheses recapitulation	22
Material & methods	25
Study area and study period	25
Data collection	26

Study subjects and conected data	26
Data collected between November 2016 and April 2017	26
Long-term data	27
For the immatures (infants and juveniles): exploratory tendency protocol	29
For the infants' mothers: general protocol	29
Data analyses	30
Characteristics of the mother	30
Sociability of the mother	30
Restrictiveness of the mother	
Activity of the mother	
External and internal factors	32
Statistics	
Results	
Factors influencing the sociability of an infant's mother	
Factors influencing an immature's exploratory tendency	40
Infants	40
Juveniles	46
Discussion	48
Research question I: Which factors influence the sociability of an infant's mother?	48
Sociability of the mother	48
Environmental factor: food availability	48
Family size and composition	
Family size and composition	
Age of the infant	49
Age of the infant Sex of the infant	49 50
Age of the infant Sex of the infant Maternal dominance rank of the infant's mother	49 50 51
Age of the infant Sex of the infant Maternal dominance rank of the infant's mother Maternal age of the infant's mother	
Age of the infant Sex of the infant Maternal dominance rank of the infant's mother Maternal age of the infant's mother Presence of an older sibling	
Age of the infant Sex of the infant Maternal dominance rank of the infant's mother Maternal age of the infant's mother Presence of an older sibling Research question II: Which factors influence an infant's exploratory tendency?	
Age of the infant Sex of the infant Maternal dominance rank of the infant's mother Maternal age of the infant's mother Presence of an older sibling Research question II: Which factors influence an infant's exploratory tendency? Influence of the mother	
Age of the infant Sex of the infant Maternal dominance rank of the infant's mother Maternal age of the infant's mother Presence of an older sibling Research question II: Which factors influence an infant's exploratory tendency? Influence of the mother Sociability of the mother	
Age of the infant Sex of the infant Maternal dominance rank of the infant's mother Maternal age of the infant's mother Presence of an older sibling Research question II: Which factors influence an infant's exploratory tendency? Influence of the mother Sociability of the mother Restrictiveness of the mother	
Failing size and composition Age of the infant Sex of the infant Maternal dominance rank of the infant's mother Maternal age of the infant's mother Maternal age of the infant's mother Presence of an older sibling Research question II: Which factors influence an infant's exploratory tendency? Influence of the mother Sociability of the mother Activity of the mother	
Age of the infant	

Sex of the infant	. 58
Influence by external factors	. 58
Environmental factor: food availability	. 58
Presence of an older sibling	. 59
Percentage association partners related with the infant	. 59
Extension of research question II: Which factors influence a juvenile's exploratory tendency?	. 59
Conclusion: from Sumatran orangutans to humans	. 60
-uture research questions	. 61
Acknowledgements	. 67
Appendix	. 68

Abstract

Cognition is defined as the ability to learn. Humans show a level of cognition that is significantly higher than that of any other species. However, growing evidence suggest that general intelligence is not a uniquely human phenomenon but can be found in a variety of species. Therefore, a certain degree of evolutionary continuity is expected in the development of cognition. To understand the evolution of human cognition, cognition of closely related taxa should be investigated. Since Sumatran orangutans are one of humans' closest relatives, they are an ideal species to understand the basics of the more complex cognitive development in humans. For humans, mainly the quality and quantity of social inputs an individual receives during childhood determines an individual's later cognitive development. Therefore, in my thesis, I investigated which factors have an effect on the development of cognition in infant Sumatran orangutans. Most of the factors can be linked to the number of social inputs an infant receives. The behavioral observations were performed on a population of wild infant Sumatran orangutans in Suag Balimbing, located in Sumatra, Indonesia. Behavioral data of 11 infants, between and 0.5 of 9 years of age, were collected. The main interest of this study was to determine the cognitive performance of these infants, which was achieved by measuring the exploratory tendency of the infants. The factors, which were expected to influence an infant's exploratory tendency, were divided into three categories, namely (1) characteristics of an infant's mother, (2) characteristics of an infant itself and (3) external factors. When investigating which characteristics of an infant's mother influenced an infant's exploratory tendency, it was found that (1) the more sociable an infant's mother was, the higher the exploratory tendency of an infant and (2) the more time a mother spent on feeding, nesting and exploring, or the less time a mother spent on traveling, the lower the exploratory tendency of an infant was. No evidence for an effect of an infant's mother restrictiveness on the exploratory tendency of an infant was found. When investigating which characteristics of an infant itself influenced an infant's exploratory tendency, it was found that (1) the infant's exploratory tendencies were highest between the ages of 2 to 4 years of an infant, and ceased abruptly around the age of 5 years. However, no evidence for a difference in exploratory tendency between infants of different sexes was found. Last, the effect of some external factors on an infant's exploratory tendency was investigated, i.e. food availability, the presence of an older sibling and the percentage of association partners related with an infant. Only the presence of an older sibling had a significant positive effect on an infant's exploratory tendency. To conclude, I found evidence for effects of the sociability of a mother, the activity of a mother, the age of an infant and the presence of an older sibling on an infant's exploratory tendency. Thus, different factors influence an infant's exploratory tendency. In a second part of this study, since this study and previous studies showed a strong effect of the sociability of an infant's mother on an infant's exploratory tendency, factors, which were expected to influence an infant's mother's sociability, were also investigated. The two main findings were that age and sex of an infant had a significant effect on the sociability of an infant's mother. Infants' mothers having a female offspring and/or older infants were found to have a higher sociability than infants' mother's having a male offspring and/or younger infants. To conclude, the factors which were found to influence an infant's exploratory tendency can be linked to the number of social inputs an infant receives. Therefore, as for humans, it is proposed that the quantity and quality of social inputs an infant Sumatran orangutan receives, will mostly determine an infant's later cognitive performance. This result suggests that the human sensitivity to opportunities for social learning was inherited from our great ape ancestors.

Lekensamenvatting

Cognitie is gedefinieerd als het vermogen om te leren. Het vermogen om te leren bij mensen is aanzienlijk hoger dan bij andere diersoorten. Echter, tal van onderzoeken hebben aangetoond dat gelijkaardige processen voor de ontwikkeling van het leervermogen aanwezig zijn bij verschillende diersoorten, waaronder ook bij de Sumatraanse orang-oetans. Wetende dat orang-oetans een van de meest verwante soorten zijn van de mens, is het een goede soort om de basis van de ontwikkeling van het meer complexe leervermogen bij mensen te leren te begrijpen. Daarvoor heb ik een studie uitgevoerd waarin ik specifiek het exploratief gedrag van jonge orang-oetans heb bestudeerd. Het exploratief gedrag is een maat om de leerprestaties van een jonge orang-oetan te meten. De gedragsstudies werden uitgevoerd op een populatie van wilde Sumatraanse orangutans, in het onderzoeksgebied Suag Balimbing, gelegen in Indonesië. In totaal werden 11 verschillende jonge orang-oetans geobserveerd, tussen de leeftijden van 0.5 tot 9 jaar. Op basis van verschillen in de leerprestaties van jonge orang-oetans konden ik onderzoeken welke factoren een effect hebben op de leerprestaties van jonge orang-oetans. Bij mensen is aangetoond dat het aantal en de kwaliteit van sociale prikkels die een persoon ontvangt grotendeels het leervermogen van deze persoon zal bepalen. Daarom werden verschillende factoren, die meestal gelinkt kunnen worden aan sociale prikkels, onderzocht die de leerprestatie van orangutans mogelijks beïnvloeden. De leerprestaties van jonge orang-oetans kunnen vanuit drie verschillende richtingen beïnvloed worden: (1) door het gedrag van de moeder, (2) door bepaalde eigenschappen van de jonge orang-oetan zelf en (3) door externe factoren. Ten eerste, bewijs voor de invloed van het gedrag van een moeder op het leervermogen van een jonge orang-oetan werd gevonden. Hoe socialer een moeder van een jonge orang-oetan was, hoe hoger de leerprestaties van de jonge orang-oetan. Verder, hoe meer tijd een moeder spendeerde aan eten, bouwen van nesten en het exploreren van haar omgeving, hoe lager de leerprestaties van jonge orang-oetans waren. Er is geen bewijs voor het effect van de terughoudendheid van een moeder op de leerprestaties van een jonge orang-oetan gevonden. Ten tweede, bewijs voor het effect van bepaalde eigenschappen van een jonge orang-oetan zelf op zijn/haar leerprestaties werd gevonden. Voor jonge orang-oetans, tussen de leeftijd van 1 tot 4 jaar, zijn de leerprestaties het hoogst. Er werd echter geen verschil in de leerprestaties tussen mannelijke en vrouwelijke jonge orang-oetans gevonden. Ten derde, externe factoren, zoals de hoeveelheid voedsel die aanwezig is, de aanwezigheid van een oudere broer of zus of de verwantschap met dieren waarmee een associatie wordt gevormd, werden onderzocht. Enkel de aanwezigheid van een oudere broer of zus leek een positief effect te hebben op de leerprestatie van jonge orang-oetans. Uit deze studie kan worden besloten dat zowel de socialiteit van een moeder, de activiteit van een moeder, de leeftijd van een jonge orang-oetan en de aanwezigheid van een oudere broer of zus een effect hebben op het exploratief gedrag van jonge orang-oetans. Aangezien de socialiteit van een moeder een aanzienlijke invloed heeft op het exploratief gedrag van een jonge orang-oetan, werden de verschillende factoren die de socialiteit van een moeder kunnen beïnvloeden ook onderzocht. Er werd gevonden dat moeders met oudere of/en met vrouwelijke jonge orang-oetans meer sociaal zijn dan moeders met jongere en mannelijke jonge orang-oetans. Gebaseerd op de resultaten van mijn studie kan ik besluiten dat de verschillende factoren, die een invloed hebben op de leerprestaties van jonge orang-oetans, gelijkaardig zijn aan de factoren die de leerprestaties van mensen beïnvloeden. Dit doet vermoeden dat het belang van sociale prikkels op de ontwikkeling van het leervermogen in mensen al afstamt van de mensapen.

Introduction

Cognition: from humans to Sumatran orangutans

Cognition is the ability to learn or more specifically, the ability to memorize, understand and apply (Anderson *et al.*, 2001; Dictionary, 2008). The better an individual's ability to learn, the higher its cognitive performance. The cognitive performance is different for every human being (Von Eckardt, 1999). Differences in cognitive performance between individuals and the developmental determinants of these differences in cognitive performance have been the focus of a variety of studies (e.g. Hetherington, Parke & Locke, 1999; Nelson *et al.*, 2007). To be able to understand how these individual differences in cognitive performance emerge, it is important to understand which mechanisms contribute to the development of an individual's cognition.

Plomin & Spinath (2004) found evidence that developmental inputs, more than genetic inputs, determine an individual's cognitive development. The two main learning mechanisms, which contribute to the development of an individual's cognition, are social learning and asocial learning (Nisbett, 2009; Heyes, 2012). Social learning is defined as learning which is influenced by observing, associating or interacting with other individuals. Asocial learning is defined as learning from an observed event in the absence of another individual (Schuppli, Forss, Meulman, Atmoko et al., 2016). Thus, the experiences and abilities an individual gains through social learning are transferred to new situations and will automatically increase an individual's asocial learning abilities (Custance, Whiten & Fredman, 2002; Caldwell & Whiten, 2007; Rapaport & Brown, 2008; Nisbett, 2009; Jaeggi et al., 2010; van Schaik & Burkart, 2011; Schuppli, Meulman et al., 2016). Therefore, social and asocial learning are considered to be closely connected with each other and contribute both to the development of an individual's cognition (Custance, Whiten & Fredman, 2002; Caldwell & Whiten, 2007; Rapaport & Brown, 2008; Reader et al., 2011). However, in the absence of social learning, asocial learning would be very limited or non-existent too. Therefore, social learning is argued to be from major importance in the development of an individual's cognition (Vygotsky, 1978; Nelson et al., 2007). Nelson et al. (2017) found evidence that individuals who receive a higher quantity and quality of social inputs during childhood have a higher cognitive performance. Therefore, social inputs are considered to be the main factor influencing an individual's cognitive development in humans (Maggi et al., 2010).

Although humans show a level of cognition that is significantly higher than that of any other species, growing evidence suggest that cognition is not a uniquely human phenomenon but that it can be found in a variety of species (e.g. pigeons: Blough, 1989; cattle: Fernandes *et al.*, 2015; horses: Schuetz, Framet & Kreuger, 2016). Therefore, a certain degree of evolutionary continuity is expected in the development of an individual's cognition (Schuppli, manuscript). Since Sumatran orangutans are one of humans' closest relatives, they are an ideal species to investigate the evolutionary continuity of the development of cognition in humans. By investigating which factors influence the cognitive development in Sumatran orangutans and whether the role of social inputs on the development of cognition in similar, the evolutionary roots of cognitive development in humans will be better understood.

Why study differences in cognitive performance in (infant) Sumatran orangutans?

The aim of this study is to investigate how the variation in cognitive performance between infant wild Sumatran orangutans (*Pongo abelii*) emerges. Orangutans can be divided into two species, namely Bornean and Sumatran orangutans. In addition, both species can be splitted in multiple subspecies, whereof our study species, Sumatran orangutans (*Pongo abelii*), is one of the two subspecies of Sumatran orangutans (Knott, 1999; Steiper *et al.*, 2005) (Figure 2).



Figure 2: The classification of different orangutan (sub)species.

There are multiple reasons why orangutans are considered an ideal species to investigate their cognitive performance.

First, as for humans, it was found that the number of social interactions an individual receives has a significant effect on an individual's cognitive development (Schuppli, Forss, Meulman, Atmoko *et al.*, 2016). In orangutans, the degree of sociability differs significantly between individuals and populations (van Noordwijk *et al.*, 2009). They spend on average between 5 and 50% of their time in association with at least one conspecific (van Noordwijk *et al.*, 2009). The high variability in the level of sociability make orangutans the ideal model species to look at the effect social interactions have on an individual's cognitive development.

Second, aside from humans, orangutans have the longest childhood dependency of all mammals (Galdikas & Wood, 1990; Tilson, 1993; Knott, 2001; van Schaik & Knott, 2001; Cawthon Lang, 2005; van Noordwijk & van Schaik, 2005; Wich *et al.*, 2004; 2009; Humphrey, 2010; van Noordwijk *et al.*, 2009, 2013). In the first six to nine years of an immature's life, orangutans are in permanent association with their mother (Wich *et al.*, 2004; Cawthon Lang, 2005; van Noordwijk & van Schaik, 2005; van Noordwijk *et al.*, 2009). In detail, for the first two years of an immature's life, immatures are almost permanent in body contact with their mother followed by a period of constant a close distance between mother and infant (Rijksen, 1978; van Noordwijk *et al.*, 2009). One of the reasons for this strong and long association between mother and infant is the broad range of skills infants need to learn before they are able to survive on their own (Jaeggi *et al.*, 2008). It takes infants more than ten years to learn the full range of necessary cognitive skills (van Noordwijk *et al.*, 2005, 2009; Schuppli, Forss, Meulman, Zweifel *et al.*, 2016). This long childhood dependency is crucial and unique in both humans and orangutans (Galdikas & Wood, 1990).

Third, Sumatran orangutans are one of the great ape species with the highest cognitive performance (Reader *et al.*, 2011; Deaner *et al.*, 2006). Orangutans rely on a set of complex feeding techniques to survive in the forest, including the use of tools to feed on e.g. termites (van Schaik & van Hooff, 1996; Russon, 2002; Russon & Begun, 2004; Jaeggi *et al.*, 2008). However, tool use has only been reported in a few populations of Sumatran orangutans. In addition, the number of complex feeding techniques orangutans use strongly differs between populations (van Schaik & van Hooff, 1996; Fox, Sitompul & van Schaik, 1999; Fox, 2002). The ability to make and use tools or to come up with complex feeding

techniques shows that orangutans have a high cognitive performance. In addition, the variation in these abilities reflect a high number of individual variation in the cognitive performance of orangutans (Russon, 2002; Russon & Begun, 2004; Marshall, Ancrenaz *et al.*, 2009). Both, orangutan's overall high cognitive performance and the individual variation in the cognitive performance make orangutans an ideal species to investigate the variation in cognitive performance.

Fourth, orangutans are one of the closest living human relatives (Glazko & Nei, 2003). Orangutans and humans are overall very similar, genetically as well as in terms of physiology and growth (Russon, 1998; Grehan & Schwartz, 2009; Locke *et al.*, 2011). Moreover, orangutans also share several behavioral and developmental characteristics, such as the long period of nutritional and social dependency of an immature (Wich *et al.*, 2004; van Noordwijk & van Schaik, 2005; van Noordwijk *et al.*, 2009). Due to the great similarities between humans and orangutans, orangutans seem to be an important model species to understand the more complex development of cognition in humans.

Last, since the inputs an individual receives during childhood determines an individual's later cognitive development (Nelson *et al.*, 2007), this study is performed with infant Sumatran orangutans.

Research question I: Which factors influence the sociability of an infant's mother?

Cognitive performance of infant Sumatran orangutans is assessed by looking at an infant's exploratory tendency (Overington *et al.*, 2009; Reader *et al.*, 2011; *see material and methods*). Previous research in humans showed that the quality and quantity of social inputs an individual receives during its childhood has an effect on the individual's later cognitive performance (Nelson *et al.*, 2007). Even small differences in the number of social interactions an individual receives, have shown to affect an individual's cognitive development. Similar results have been found across species (Vygotski, 1978; van Schaik, 2003, 2006) and in a previous research on Sumatran orangutans (Schuppli, Forss, Meulman, Atmoko *et al.*, 2016). Therefore, I am interested to investigate whether a similar effect of social interactions on the exploratory tendency of infants' Sumatran orangutans is found and if so, how do these differences in the number of social interactions arise.

Sociability of the mother

For a long time, orangutans were thought to be a solitary species, in which there is only a strong association existing between a mother and her dependent infant (Setia et al., 2009). Orangutans were considered to avoid, as much as possible, contact with conspecifics and only during consort ship, when females are ready to conceive, female orangutans form associations with males (Setia et al., 2009). Therefore, beside the close mother-infant bond, no other social relationships were expected to exist (Setia et al., 2009). However, numerous studies confirmed that orangutans, especially mother-infant pairs, do form associations with other orangutans and have various social bonds with conspecifics (van Schaik, 1999; van Noordwijk et al., 2009, 2012). Therefore, orangutans are nowadays defined as having a semi-solitary lifestyle with a tendency for low-level fission-fusion grouping (van Schaik, 1999; van Noordwijk et al., 2009, 2012). The semi-solitary lifestyle with a tendency for low level fission-fusion grouping of orangutans can be linked with the costs and benefits the formation of associations impose. On the one hand, the main cost linked to the formation of association is food availability (Knott, 1999; van Schaik, 1999). By tolerating other individuals in the same food patch, an individual must share the available food resources and spend more time finding enough food (Knott, 1999; van Schaik, 1999). This is expected to negatively affect an orangutan's energy level (Knott, 1999; van Schaik, 1999). On the other hand, the benefits linked to the formation of associations strongly depends on the age-sex class of orangutans (Table 12). The main benefit to the formation of associations for infants is the increased number of social inputs an infant receives by being in association (van Schaik, 1999; van Schaik *et al.*, 1999). When a mother-infant pair is in association with another (adult) orangutan, an infant is often very eager to interact with the association partner (Rijksen, 1978; Setia *et al.*, 2009). While the association partner is performing certain interesting activities, infants (usually) approach the association partner and pay close attention to what and how the association partner is performing a certain activity. This attentive close-range watching is called peering (Schuppli, Forss, Meulman, Atmoko *et al.*, 2016; Schuppli, Forss, Meulman, Zweifel *et al.*, 2016; Schuppli, Meulman *et al.*, 2016). Peering enables infants to learn new cognitive skills and ultimately increase their cognitive performance (Schuppli, Forss, Meulman, Atmoko *et al.*, 2016; Schuppli, Forss, Meulman, Zweifel *et al.*, 2016; Schuppli, Forss, Meulman, Zweifel *et al.*, 2016; Schuppli, Forss, Meulman, 2016). Hereby, infants with more sociable mothers will receive more opportunities for social learning. Since social and asocial learning are closely connected to each other (Custance, Whiten & Fredman, 2002; Caldwell & Whiten, 2007; Rapaport & Brown, 2008; Jaeggi *et al.*, 2010), an infant's exploratory tendency will increase which ultimately is expected to lead to an increase of an infant's cognitive performance. Therefore, the sociability of an infant's mother is suggested to be the main factor influencing the differences in exploratory tendency between infant Sumatran orangutans.

Factors influencing sociability of the mother

Individual differences in the level of sociability between adult female orangutans has been recorded in different studies (e.g. van Schaik, 1999; van Noordwijk *et al.*, 2009). In general, variation in sociability between infants' mothers reflect the fluctuations between the benefits and costs associations imposes (van Schaik, 1999). van Schaik (1999) investigated a number of factors which were expected to cause these differences in sociability between female orangutans. Based on the research of van Schaik (1999), the two main factors, that are expected to cause variation in a mother's sociability, are (1) food availability and (2) the size and composition of an infant's mother's family.

Environmental factor: food availability

First, food availability is expected to be one of the main factors influencing the sociability of an infant's mother (Chapman, 1990). Orangutans favourite and main food source is fruit, especially of orangutans living in Suaq Balimbing (Rijksen, 1978; Sugardjito, te Boekhorst & van Hooff., 1987; Galdikas, 1988; Leighton, 1993; Knott, 1999; Marshall, Boyko et al., 2009; Morrogh-Bernard et al., 2009). As mentioned before, orangutans are a semi-solitary species whereby occasionally female orangutans form associations and even can have various social bonds with other individuals (Knott et al., 2008; Te Boekhorst, Schürmann & Sugardjito, 1990; Singleton & van Schaik, 2002). Depending on the population, mother-infant pairs spend between 10 and 55% of their time in association with other individuals (van Noordwijk et al., 2009). As mentioned above, the formation of associations can be very costly for the mother (Knott, 1999; van Schaik, 1999; Singleton et al., 2009). By tolerating other individuals in the same food patch, the mother must share the available food resources and spend more time finding enough food for her and her infant (Knott, 1999; van Schaik, 1999). Therefore, to reduce food competition, each adult female orangutan has her own stable home range (Singleton et al., 2009). An individual's home range is defined as the area that an individual uses in its normal movements (Jolly, 1985; Setia et al., 2009). By staying loyal to their own home range, orangutans are able to avoid most competition over resources (Knott et al., 2008). However, home ranges often overlap in heterogeneous and productive habitats (Singleton et al., 2009). The productivity and heterogeneity of a home range mainly depends on the fruit availability and the number of different fruit species present (van Schaik, 1999; Singleton & van Schaik, 2001). If home ranges overlap with each other, more associations will take place (Singleton et al., 2009). Therefore, females having their home ranges in heterogeneous and productive habitats are hypothesized to be more sociable, due to overlapping home ranges with neighboring orangutans, than females whose home ranges are located in rather low heterogeneous and productive habitats (van Schaik, 1999; Singleton & van Schaik, 2001). Further, orangutans often face fluctuations of fruit availability throughout the year, which can affect their biology and behavior (Rijksen, 1978; Chapman, Chapman & Wrangham, 1995; Anderson et al., 2002; Lwanga, 2002; Wich et al., 2006). Similar to other primate species, orangutans are able to adapt to fruit fluctuations in different ways, dependent on the characteristics of their environment (Knott, 1998). Orangutans have been reported to cope with changes in food availability by changing their diet composition (Rijksen, 1978; Galdikas, 1988; van Schaik & Rao, 1997; Stanford & Nkurunungi, 2003, Wich et al., 2006), increasing their search effort (Rijksen, 1978; Chapman, 1988, Wich et al., 2006), minimizing their energy expenditure (Chapman, 1988; Wich et al., 2006; van Noordwijk et al., 2013), changing their ranging pattern (Oluput et al., 1997; Buij et al., 2002; Wich et al., 2006; van Noordwijk et al., 2013), changing the timing of conceptions or copulation rates (van Schaik & van Noordwijk, 1985; Koenig et al., 1997; Knott, 1998; Di Bitetti & Janson, 2000; Wich et al., 2006; Knott, 2011) and/or changing their average party size (Chapman, Chapman & Wrangham, 1995; Utami et al., 1997; Knott, 1998; Mitani, Watts & Lwanga, 2002; Wich et al., 2006). By changing their average party size, food competition will be reduced (Te Boekhorst, Schürmann & Sugardjito, 1990; Chapman, Chapman & Wrangham, 1995; Knott, 1998; Anderson et al., 2002; Lwanga, 2002; Wich et al., 2006). Therefore, it is hypothesized that in periods with low food availability, an infant's mother will be less sociable despite the negative effect it is expected to have on an infant's exploratory tendency (Singleton et al., 2009).

Family size and composition

Second, it is expected that an infant's mother's family size and composition has an effect on the sociability of an infant's mother. Previously, it was shown that orangutans prefer to associate with related individuals. Hereby, most association patterns are kin-biased (Singleton & van Schaik, 2002; Russon et al., 2009; Singleton et al., 2009; van Noordwijk et al., 2009; 2012; Arora et al., 2012; Marzec et al., 2016). There are still some uncertainties why orangutans have a preference to form associations with related instead of unrelated individuals (van Noordwijk et al., 2012). The costs linked to the formation of associations is the most probable factor explaining the kin-biased preference. Therefore, an individual will try to avoid as much as possible other costs when associating. In case of a motherinfant pair, when a mother associates with a conspecific for the infant's benefit, a mother is expected to have a preference to associate with related conspecifics since they have a higher predictability and common interest. Therefore, related individuals are most likely to impose the lowest physiological stress for a mother (van Noordwijk et al., 2012). This explains the bias to form associations preferential with related individuals. In addition, besides a bias towards associating with related conspecifics, more specifically, a bias towards forming associations with female related individuals has been found (King, 2015). The different dispersion patterns of male and female orangutans explain why such kin-biased associations are formed between female but not between male related individuals. When female orangutans become independent, they tend to stay in their natal area and set up their own home range in or close to their mother's home range. However, male orangutans tend to disperse form their natal area (Rodman, 1973; MacKinnon, 1974; Rijksen, 1978; Galdikas, 1985, 1988; Mitani, 1989; van Schaik & van Hoof, 1996; Utami et al., 1997; Knott, 1998, 1999; van Noordwijk et al., 2002, 2012; Singleton & van Schaik, 2002; Setia et al., 2009; Morrogh-Bernard et al., 2011; Arora et al., 2012). Therefore, female related individuals often have adjacent, overlapping home ranges and associations are more likely to be formed (Singleton & van Schaik, 2002; Singleton et al., 2009; van Noordwijk et al., 2009; 2012; Arora *et al.*, 2012; Marzec *et al.*, 2016). Therefore, it is hypothesized that the higher the number of female related individuals an infant's mother has, the higher an infant's mother's sociability will be.

Sociodemographic factors

Besides the food availability and an infant's mother family size and composition, which are expected to influence the sociability of an infant's mother, also the effect of some sociodemographic factors on the sociability of an infant's mother are investigated. The sociodemographic factors are (1) the age of an infant, (2) the sex of an infant, (3) the maternal age of an infant's mother, (4) the maternal dominance rank of an infant's mother and (5) the presence of an older sibling.

Age of the infant

First, the age of an infant is expected to have an effect on the sociability of an infant's mother (Hansen, 1966; Rijksen, 1978; van Schaik, 1999; Nowell & Fletcher, 2007). Results have shown that the older an infant becomes, the more they will be learning from other individuals than their mother (Schuppli, Meulman *et al.*, 2016). This suggests that inputs from other role models may be more important than from the mother (Schuppli, Meulman *et al.*, 2016). Therefore, it is expected that an infant's mother will be more sociable with increasing age of her offspring. In addition, based on a sociability study performed in Sumatran orangutans, it is expected that there will be a clear difference in sociability between mothers with infants of different age-classes (van Schaik, 1999). van Schaik (1999) reported a significant higher sociability in females with very young (0-2 years of age) or older infants (>4 years of age) and a significant lower sociability in females with mid-aged infants (2-4 years of age). Mid-aged infants are defined as infants who are in the transition period from being carried to moving independently of their mother (Phillips, 2012). There are two possible explanations for the difference in sociability between mothers with infants of different age-classes.

Firstly, the sociability of an infant's mother is influenced by the level of dependency of an infant on its mother and the connected costs an infant imposes on its mother. On the one hand, when infants are still very young, their needs are rather limited and carrying them around, due to their small body size, is not very costly for the mother. On the other hand, older infants, who are around the age of weaning¹, are usually able to move independently of the mother and provide their own food (van Adrichem et al., 2006; van Noordwijk et al., 2009). Therefore, the costs very young or older infants impose on an infant's mother are relatively low. In contrast, the costs for an infant's mother of having a mid-aged infant are relatively high. During most traveling, the mother still carries the infant and frequently needs to wait and provide travel assistance. Further, since the infant only does very little effective feeding by itself, most of the nutrition is still provided through the breast milk of the mother (van Schaik, 1999; van Noordwijk et al., 2009). Therefore, mid-aged infants bring the highest costs for the mother (Prentice & Whitehead, 1987; Gittlean & Thompson, 1988; Dufour & Sauther, 2002; van Noordwijk et al., 2013). Since the formation of associations bring even extra costs, because of food competition (Singleton et al., 2009), it is expected that mothers with mid-aged infants will be less sociable compared to mothers with very young or older infants. Similar results have been recorded in other primate species (rhesus macaques: Hansen, 1966; gorillas: Nowell & Fletcher, 2007).

Secondly, a mother with a mid-aged infant is expected to have a lower sociability due to the potential risks associations imposes. When a mother-infant pair is in association, infants tend to pay less attention to their movements and surroundings. Hereby, if the infant is distracted by other

¹Weaning is defined as the process of getting independent from mother's milk and switching to other (solid) food (Cawthon Lang, 2005; van Noordwijk *et al.*, 2009). Weaned infants are completely responsible for their own food intake.

conspecifics, a potentially dangerous environment is created and accidents are more likely to happen (Goodall, 1986; van Schaik, 1999; Phillips, 2012). This is especially valid for mid-aged infants who are in the transition period from being carried to moving independently and are not yet completely in control of their own movements (Phillips, 2012).

To conclude, two hypotheses about the effect of an infant's age on the sociability of the mother can be made. First, mothers will become more sociable with increasing age of the infant. Second, mothers with mid-aged infants are expected have a lower sociability than mothers with very young or older infants.

Sex of the infant

Second, also the sex of an infant is expected to influence the sociability of an infant's mother. In a variety of non-human animal species, a difference in parental investment has been found depending on the sex of the infant (Lee & Moss, 1986; Trillmich, 1986; Komdeur et al., 1995; Komdeur et al., 1997). Overall, a higher parental investment is expected in the sex which provides (one of) the parents the highest fitness return (Salmon & Shackelford, 2007). In orangutans, fathers rarely play a role in raising their infant and therefore only maternal investment in the infant will be present (Galdikas & Wood, 1990). Since male-male competition in the mating system of orangutans is very high, male reproductive success is more variable than female reproductive success (Trivers, 1972; Utami et al., 2009). Therefore, investing in a male infant and having a smart, high cognitive male infant will be more beneficial for the maternal fitness than having a high cognitive female infant (Trivers, 1972). In line with the idea that social interactions increase an infant's exploratory tendency and ultimately an infant's cognitive performance (van Schaik, 1999; van Schaik et al., 1999), it is expected that mothers with a male infant will be more sociable than mothers with a female infant. Another reason why mothers are expected to be more social when having a male infant is due to the difference in dependency time between male and female infants. Male infants are in close association with their mother for a shorter time period than female infants (Miller, 2013). Miller (2013) reported that in Bornean orangutans, males tend to stay close to their mother until the age of ten while females are dependent on their mother for a couple of extra years. This means that males have to learn the same number of essential cognitive skills, to be able to survive independently, in a shorter time period than females. As mentioned before, in line with the idea that social interactions increase an infant's exploratory tendency (van Schaik, 1999; van Schaik et al., 1999), it is hypothesized that an infant's mother will be more sociable when raising a male infant than when raising a female infant.

Maternal dominance rank of the infant's mother

Although the presence of a clear dominance hierarchy in female orangutans has been doubted (Roman, 1977; Rijksen, 1978; Tuttle, 1986; Tuttle & Cortright, 1988; Kaplan & Rogers, 1994; Galdikas, 1995) (Galdikas, 1995; van Schaik & van Hooff, 1996), anecdotal data of females displacing other females has been collected (Sugardjito, te Boekhorst & van Hooff., 1987; Utami *et al.*, 1997). Therefore, based on the idea that a reliable dominance rank can be assigned to each adult female, a mother's dominance rank is expected to influence her own sociability. In a variety of species it has been found that adult females, with a higher dominance rank, establish their home ranges in higher quality habitats than adult females with a lower dominance rank (e.g. chimpanzees: Williams *et al.*, 2002; Murray, Eberley & Pusey, 2006; Thompson *et al.*, 2007; Kahlenberg *et al.*, 2008; red-winged blackbirds: Eckert & Weatherhead, 1987; northern spotted owl: Franklin *et al.*, 2000). In addition, higher dominant females were found to be better in defending their home range than less dominant females. At the same time, females with a lower dominance rank were found to avoid as much as possible areas where

females with a higher dominance rank are living (Wrangham, 1980; Knott *et al.*, 2008). Hereby, higher dominant females will have access to more and better quality food resources than lower dominant females. Further, having high quality home ranges lead to improved physical condition and less food competition (Thompson, 2005; van Schaik, Marshall & Wich, 2009). Therefore, more dominant females are able to afford more associations with conspecifics and is it hypothesized that infant's mothers with a higher dominance rank will be more social than infant's mothers with a lower dominance rank.

Maternal age of the infant's mother

Fourth, the maternal age as well is expected to have an effect on the sociability of an infant's mother (Clutton-Brock, 1991). On the one hand, according to the 'Terminal Investment Theory', there is a trade-off between reproduction and future survival (Williams, 1966). Energy or resources invested in reproduction cannot be used to invest in characteristics of future survival, such as growth and maintenance. With increasing maternal age, the mother's chances for survival will be declining. Therefore, more resources will be invested in reproduction (Williams, 1966; Figure 3). In other words, the mother will invest more in her infant than in herself. In line with the idea that social interactions increase an infant's exploratory tendency and ultimately an infant's cognitive performance (van Schaik, 1999; van Schaik *et al.*, 1999), it is hypothesized that there will be an increase in sociability of an infant's mother with increasing maternal age.



Figure 3: 'The Terminal Investment Theory'. The balance between investment of energy and resources for future survival or reproduction.

Presence of an older sibling

Fifth, the presence of an older sibling is expected to have an effect on the sociability of an infant's mother. Often, the older offspring is still in close association with its mother when the mother gives birth to a newly born infant (van Noordwijk *et al.*, 2009). On that moment, the older sibling reached the age of a juvenile (van Noordwijk *et al.*, 2009). In general, the exploratory tendency in juveniles is rather low while the engagement in social play is rather high, in comparison with infants (Groos, 1898; Kunz, 2015). Social play is an important source of social learning and will enlarge an individual's cognitive performance (Kunz, 2015). Therefore, it is very important for juveniles to engage in social play with conspecifics. On the one hand, if an older sibling is still in close association with the mother-infant pair, the older sibling could engage in social play with the mother and/or the infant. However, older siblings are expected to have a preference to engage in social play with same-aged, same-sexed and/or same-ranked play partners instead of engaging in social play with the mother and/or the infant (e.g. gorillas: Maestripieri & Ross, 2004; great apes: Lewis & Barton, 2006; Kunz, 2015). Therefore, because an older sibling's need for social play, an older sibling is expected to initiate a number of associations. Thus, the associations, which are formed between the mother-infant pair and the older

sibling with conspecifics, will mainly be initiated by the older sibling. Although a mother-infant pair is not expected to directly benefit by forming associations (van Schaik, 1999), a mother-infant pair will (obligatory) have to follow the older sibling, whether or not from distance, since the mother is not confident about the abilities of the older sibling to be on its own yet. In addition, a mother's indirect fitness will increase by having an older sibling who engages more in social play, and hereby has a higher cognitive performance (Williams *et al.*, 2002). Therefore, it is hypothesized that if an older sibling is still in close association with a mother-infant pair, the sociability of a mother will be higher than when no older sibling is in association with a mother-infant pair.

Conclusion: factors influencing sociability of the mother

To conclude, the sociability of an infant's mother is expected to influence an infant's exploratory tendency and is expected to be influenced by different factors itself. Higher sociability of an infant's mother will have a positive influence on an infant's exploratory tendency and ultimately an infant's cognitive performance.

Research question II: Which factors influence an infant's exploratory tendency?

However, it is expected that only part of the variation in exploratory tendency between infants can be explained by the sociability of the mother. Therefore, the effect of other factors on the exploratory tendency of infants is investigated. Basically, it is expected that an infant's exploratory tendency will be influenced by (1) characteristics of an infant's mother, (2) own characteristics of an infant and (3) external factors.

Influence of the mother

First, the influence of a mother on an infant's exploratory tendency is investigated. Three main characteristics of an infant's mother are expected to affect the development of an infant's cognition. Firstly, the sociability of a mother is expected to influence an infant's exploratory tendency. This is already explicit discussed in the first part of the introduction. Secondly, the restrictiveness of a mother and thirdly, the activity of a mother, are investigated as potential factors influencing an infant's exploratory tendency.

Restrictiveness of the mother

Besides the sociability of an infant's mother, it is also expected that the restrictiveness of an infant's mother will influence the exploratory tendency of an infant. Restrictiveness of an infant's mother is defined as the interfering of an infant's mother with an infant's activity by collecting the infant. In a number of different non-human primate species, an infant's mother's restrictiveness was recorded to be the highest when in association with conspecifics (pig-tailed macaques: Wolfheim, Jensen & Bobbit, 1970; squirrel monkeys: Kaplan, 1972; vervet monkeys: Fairbanks & McGuire, 1993). A similar pattern is expected to be found in orangutans, due to the arboreal nature of orangutans (van Schaik, 2000). As mentioned before, the highest risk of an orangutan's arboreal nature is the possibility of falling out of a tree, which can lead to severe injuries or even dead (chimpanzees: Goodall, 1986). Since infants pay less attention to their movements and surroundings when encountering conspecifics, being in association creates a potentially dangerous environment for an infant (Phillips, 2012; Falkner, 2015). Therefore, a higher restrictiveness of an infant's mother is expected when the mother-infant pair is in association with conspecifics (Hansen, 1966; Nowell & Fletcher, 2007; Falkner, 2015). However, by restricting an infant when being in association, an infant will receive less social inputs. Therefore, high restrictiveness, during associations, is expected to negatively affect an infant's exploratory tendency. In addition, infants' mothers are also expected to be restrictive when they are not in association with conspecifics (humans: Broberg *et al.*, 1997). Also in these situations, the restrictiveness of an infant's mother is expected to negatively affect an infant's exploratory tendency. For instance, when having a highly restrictive mother, an infant will have fewer opportunities to e.g. explore its environment (humans: Broberg *et al.*, 1997). Therefore, it is hypothesized that the higher the restrictiveness of an infant's mother, undetermined whether or not the mother-infant pair is in association with conspecifics, the less opportunities an infant will have to perform any kind of object manipulation behavior and the lower an infant's exploratory tendency will be.

Activity of the mother

Next to the sociability and the restrictiveness of an infant's mother, the activity of an infant's mother is also expected to influence the exploratory tendency of an infant (Altman, 1980; Maestripieri, 1995; van Schaik, van Noordwijk & Vogel, 2009; Jaeggi *et al.*, 2010). A mother's main daily activities consist



Figure 4: Average daily activity budget of an orangutan (Knott, 1999).

of traveling, feeding and resting (Williamson & Dunbar, 2001; Morrogh-Bernard et al., 2009). The percentage of time used for each activity, forms the overall activity budget (Morrogh-Bernard et al., 2009). Based on the results of three different studies, investigating activity patterns in orangutans, an average daily activity budget for orangutans was calculated (MacKinnon, 1974; Rodman, 1979; Mitani, 1989). According to Knott (1999), orangutans spend approximately 13% of their time traveling, 41% of their time feeding, 44% of their time resting and 3% of their time on nest building and engaging in other activities such as fighting, mating and socializing (Figure 4).

Due to the strong mother-infant dependency in the first few years of an infant's life (Wich et al., 2004; Cawthon Lang, 2005; van Noordwijk & van Schaik, 2005; van Noordwijk et al., 2009), a mother's activity is expected to have an important influence on an infant's exploratory tendency and ultimately its cognitive performance (Jaeggi et al., 2010; Kunz, 2015). First, when a mother is traveling, especially when an infant is still dependent on its mother for traveling, an infant must spend its time either closely following or clinging to its mother (van Noordwijk & van Schaik, 2005; Kunz, 2015). Therefore, the time available for an infant to perform any kind of object manipulation behavior will be limited. Second, while a mother is feeding, nest building or exploring, an infant will be positively influenced and stimulated, due to the social inputs an infant receives, by a mother's activity to perform any kind of object manipulation behavior themselves (Jaeggi et al., 2010; Kunz, 2015). In addition, in a study performed on chimpanzees (Pan troglodytes), researchers showed a positive relationship between the exploratory tendency performed by a mother and by an infant (Lonsdorf, 2006). Therefore, feeding, nesting and exploring by the mother are expected to have a positive effect on the exploratory tendency of an infant (Jaeggi et al., 2010; Kunz, 2015). Last, when a mother is resting, an infant is neither restricted nor stimulated by the activity of its mother to perform any kind of object manipulation behavior (Kunz, 2015). Therefore, an infant's exploratory tendency is expected to be rather neutral, compared to situations where the mother is performing any other activity, while the mother is resting.

To conclude, different hypotheses about the effect of the activity of an infant's mother on an infant's exploratory tendency are formed. First, it is hypothesized that an infant will have the highest exploratory tendency while an infant's mother is feeding, nest building or exploring, less while an infant's mother is resting and the least while an infant's mother is traveling (Jaeggi *et al.*, 2010; Kunz, 2015). Second, based on the first hypothesis, an infant's exploratory tendency is hypothesized to be influenced by the daily activity budget of an infant's mother (Jaeggi *et al.*, 2010; Kunz, 2015). On the one hand, the more time an infant's mother is performing activities that positively influence an infant's activity, such as feeding, nest building and exploring, the higher the exploratory tendency of an infant is expected to be. On the other hand, the more time an infant's activity, the lower the exploratory tendency tendency of an infant will be. Third, it is hypothesized that there will be a positive effect of the exploratory tendency of an infant's mother on the exploratory tendency of an infant itself (Lonsdorf, 2006). To conclude, the higher the number of social inputs an infant receives, due to the activity of the mother, the higher an infant's exploratory tendency is expected to be.

Influence of the infant

Thus, the three main characteristics of a mother, which are expected to influence an infant's exploratory tendency, are (1) a mother's sociability, (2) a mother's restrictiveness and (3) a mother's activity. Besides the mother who is expected to influence an infant's exploratory tendency, part of the variation in the exploratory tendency between infants might also be caused by some specific characteristics of the infants themselves, such as (1) the age and (2) the sex of an infant.

Age of the infant

First, the age of an infant is expected to be one of the most important characteristics of an infant influencing its own exploratory tendency. In several primate species, different ontogenetic trajectories for try-feeding and exploration were found (chimpanzees: Cordoni & Palagi, 2011; gorillas: Maestripieri & Ross, 2004; vervet monkeys: Fairbanks, 2000). Also for orangutans, the ontogenetic trajectories of the two different object manipulation behaviors have been studied (van Adrichem *et al.*, 2006; Kunz, 2015). First, rates of try-feeding were found to be generally high until the age of three to four years, with a peak around the age of two years, and were followed with a quite abrupt ceasing around the age of four to five years (van Adrichem *et al.*, 2006; Kunz, 2015). Second, rates of exploration were found to be high until the first two to three years of an infant's life and then sharply decreases (Kunz, 2015). Therefore, it is expected that the rates of try-feeding and exploration will have a similar age-pattern. It is hypothesized that the exploratory tendency of the infants will be the highest between the age of one to four years followed by a quite abrupt ceasing of their exploratory tendency around the age of four to five years.

Sex of the infant

Second, the effect of an infant's sex on its exploratory tendency was investigated. Studies performed in closely related primate species, found different outcomes (Power, 1999). In rhesus (*Macaca mulatta*) and colobus monkeys (*Colobus*), it was found that females engaged more in any kind of object manipulation behavior than males, while the opposite result was found in capuchin monkeys (*Cebinae*) (rhesus monkeys: Wilcoxon *et al.*, 1969; O'Neill & Price, 1991; Novak *et al.*, 1993, colobus monkeys: Starin, 1990; capuchin monkeys: Visalberghi, 1988). In addition, no sex difference in exploratory tendency was found in a study conducted in gorillas (*Gorilla gorilla*) (Gold, 1992). Due to the variation in the outcomes, between closely related primate species, it is difficult to draw any expectation about

the effect of an infant's sex on its exploratory tendency. However, a more recent study, investigating termite fishing in chimpanzees, did find evidence for sex differences in infants' cognitive performances (Lonsdorf, Eberly & Pusey, 2004; Lonsdorf, Markham et al., 2014). According to Lonsdorf, Eberly and Pusey (2004), female chimpanzees start using tools at a younger age and are more frequently peering, when a mother is performing tool use, than male chimpanzees. The more an individual engages in tool use, the higher its cognitive performance (Koops et al., 2015). This explains why young female chimpanzees were found to have a higher cognitive performance than young male chimpanzees (Lonsdorf, Eberly & Pusey, 2004; Lonsdorf, Markham et al., 2014). For orangutans, a similar expectation about the effect of an infant's sex on its exploratory tendency is made. Based the difference in future interest between male and female orangutans, female infant orangutans are expected to have a higher exploratory tendency than male infant orangutans. Adult males are primarily focused on finding mating partners (Galdikas, 1985), while the main focus of adult females is their offspring (Gittlean & Thompson, 1988). Pregnancy, lactating and raising offspring are highly energetically demanding activities for an adult female (Gittlean & Thompson, 1988). Therefore, it is suggested that adult females are in a higher need of a broad energetically rich diet, consisting of a variety of fruits, insects and plants. In contrast, it is suggested that the need for adult males to acquire all this knowledge of different food resources, is notably lower. Thus, based on the difference in the future energetic requirements of male and female orangutans, it is expected that female infants will engage more in the performing of any kind of object manipulation than male infants. Therefore, similar as what was found in the most recent study performed in chimpanzees (Lonsdorf, Eberly & Pusey, 2004), it is hypothesized that female infants will have a higher exploratory tendency than male infants.

Influence by external factors

Last, besides the influence of certain characteristics of a mother and an infant, external factors are also expected to influence an infant's exploratory tendency. The external factors which are expected to influence an infant's exploratory tendency are (1) food availability, (2) the presence of an older sibling and (3) an infant's relatedness with association partners.

Environmental factor: food availability

As mentioned before, the level of food availability is expected to have an effect on the sociability of an infant's mother, and hereby indirectly affect an infant's exploratory tendency (van Schaik, 1999; Maggi et al., 2010). Besides an indirect effect, also a direct effect of food availability on an infant's exploratory tendency is expected (Wich et al., 2006; van Noordwijk et al., 2009). If the level of food availability and/or quality is rather low, this will negatively affect an infant's energy balance and availability of "free" time due to a need for longer processing of lower quality food and/or due to an increase in time needed for searching enough food (Wich et al., 2006; Harrison et al., 2011). Consequently, there will be less time available for performing any type of object manipulation behavior (van Noordwijk et al., 2009). In addition, during a high level of food availability, infants are expected to be healthier and in better condition whereby it is more likely to explore their environment (Schuppli, Forss, Meulman, Atmoko et al., 2016). Originally, this hypothesis was only expected to be valid for fully weaned and not for unweaned infants. Based on the idea that mother milk supplies unweaned infants with enough energy, their exploratory tendency was expected to be not or less influenced by a change in the level of food availability and/or quality (van Noordwijk et al., 2009, 2013; Kunz, 2015). However, some researchers argue that, although a low level of food availability and/or quality can be buffered by the provision of mother milk, it cannot be excluded that the composition and/or the amount of mother milk will change in periods with a low level of food availability and/or quality (Kunz, 2015). Hereby, a decrease in the level of food availability and/or quality will also negatively affect the unweaned infants' energy balance and time, resulting in a decreasing infant's exploratory tendency. Furthermore, some researchers also argue that from the age of one year, indefinite the provision of mother milk, infants tend to be influenced by a change in the level of food availability and/or quality since from that age infants already feed on solitary food themselves (van Noordwijk & van Schaik, 2005; van Noordwijk *et al.*, 2013). Therefore, it is hypothesized that during periods of a low level of food availability and/or quality, for both unweaned and fully weaned infants, the infants' exploratory tendency will decrease.

Presence of an older sibling

Whether or not there is an older sibling in close association with a mother-infant pair is expected to influence an infant's exploratory tendency (Sutton-Smith & Rosenberg, 1970; Jolly, 1985; Teti *et al.*, 1986; Zukow, 1989; Broberg *et al.*, 1997; Barr & Hayne, 2003). Most cognitive skills an infant possesses are learned from their mother (Jaeggi *et al.*, 2008, 2010; Schuppli, Meulman *et al.*, 2016). However, part of an infant's cognitive skill set are also learned from other conspecifics, such as from an older sibling (van Schaik, 1999; van Schaik *et al.*, 1999). In humans, different studies have been conducted to determine the effect of the presence of a sibling on a child's cognitive performance (Barr & Hayne, 2003). It was found that children with siblings imitated more behavior without explicit instruction than children without siblings. In addition, children with an older sibling imitated other children more often than children with both its mother as well as an older sibling, the number of social inputs are expected to be larger than when an infant only lives in close association with its mother (Sutton-Smith & Rosenberg, 1970; Lamb, 1978; Teti *et al.*, 1986; Zukow, 1989). Therefore, it is hypothesized if an older sibling is in close association with a mother-infant pair, the infant's exploratory tendency will be higher.

Percentage association partners related with the infant

Last, it is expected that the percentage of association partners who are related with an infant will influence the exploratory tendency of an infant. Although a high tolerance level towards both related as unrelated conspecifics by mother-infant pairs have been previously recorded in Suaq Balimbing (van Schaik, 1999; Fragaszy & Perry, 2008; Kunz, 2015), the tolerance level does not reveal the difference in the type of interactions, which take place during an association with related or unrelated conspecifics. Whenever mother-infant pairs associate with related conspecifics, it is expected that more beneficial interactions will take place, such as social learning (i.e. peering), social play, food sharing etc. (van Noordwijk *et al.*, 2012). In contrast, during associations between a mother-infant pair and unrelated conspecifics, besides the tolerance of the unrelated individuals, little beneficial interactions with related conspecifics impose a higher number of social inputs than interactions with unrelated conspecifics. Thus, it is hypothesized that the higher the percentage of association partners who are related with an infant, the higher the exploratory tendency of an infant will be.

Extension of research question II: Which factors influence a juvenile's exploratory tendency?

In this study, the focus lays on infant Sumatran orangutans. However, limited data was collected on a number of juvenile Sumatran orangutans too. Therefore, the effect of some factors on a juvenile's exploratory tendency was determined. The first two factors, which are investigated and expected to influence a juvenile's exploratory tendency, are (1) the immediate sociability of a juvenile and (2) the food availability. The same hypotheses as for the effect of these factors on an infant's exploratory tendency are made, stated by the same arguments. First, it is hypothesized that the higher the immediate sociability of a juvenile, the higher the exploratory tendency of the juvenile (Schuppli, Meulman *et al.*, 2016). Second, it is hypothesized that the higher the level of food availability, the higher the exploratory tendency of a juvenile (van Schaik, 1999; Maggi *et al.*, 2010). Besides the effect of these two factors on the exploratory tendency of juveniles. Whether the sociability of a juvenile's mother, during the time a juvenile was still dependent on its mother, has an effect on the current exploratory tendency of a juvenile. It is hypothesized, based on the same arguments as for the immediate sociability of a juvenile. It is hypothesized, based on the same arguments as for the immediate sociability of a juvenile. It is hypothesized, based on the same arguments as for the immediate sociability of a juvenile, the higher the sociability of a juvenile's mother during the infancy period of a juvenile, the higher a juvenile's exploratory tendency will be now.

Aim of the study

The aim of this project is to investigate which factors influence the exploratory tendency of infant Sumatran orangutans. Based on the results of previous research, the sociability of an infant's mother is expected to be one of the most important characteristics influencing an infant's exploratory tendency (Schuppli, Forss, Meulman, Atmoko *et al.*, 2016). The orangutans at Suaq Balimbing show individual differences in their levels of sociability. Since factors influencing the sociability of an infant's mother indirectly influence an infant's exploratory tendency, it was relevant for the aim of this project to investigate the factors influencing an infant's mother's sociability. The factors which are expected to influence an infant's mother sociability are (1) food availability, (2) family size and composition, (3) age of the infant, (4) sex of the infant, (5) maternal dominance rank of the infant's mother, (6) maternal age of the infant's mother and (7) presence of an older sibling (Figure 5).

However, besides the sociability of an infant's mother, other factors are expected to have an effect on an infant's exploratory tendency. These factors can be divided into three different categories, namely (1) characteristics of the infant's mother, such as the sociability, restrictiveness and the activity of the infant's mother (2) characteristics of the infant itself, such as age and sex of the infant, and (3) external factors, such as food availability, whether or not the infant lives together with an older sibling and the percentage of association partners related with the infant (Figure 6).



Figure 5: Scheme of possible factors influencing the sociability of an infant's mother.



Figure 6: Scheme of possible factors influencing an infant's exploratory tendency.

Research hypotheses recapitulation

Research question: Which factors influence the exploratory tendency of infant Sumatran orangutans?

Research question I: Which factors influence the sociability of an infant's mother?

Research question II: Which factors, besides the sociability of an infant's mother, influence an infant's exploratory tendency?

Extension of research question II: Which factors influence <u>a juvenile's</u> exploratory tendency?

Research question I: Which factors influence the sociability of an infant's mother?

Sociability of the mother is expected to be the main factor influencing the exploratory tendency of infant Sumatran orangutans. The higher the sociability of an infant's mother, the higher the exploratory tendency of the infant.

- 1. **Food availability:** The sociability of an infant's mother increases with increasing food availability.
- 2. **Family size and composition:** The higher the number of female related individuals an infant's mother has, the higher the sociability of the infant's mother.
- 3. Age of the infant: An infant's mother will be less sociable when the infant is around the age of two to four years. In the years preceded and followed, there will be an increase in sociability of the mother.
- 4. **Sex of the infant:** The mother will be more social when having male infant than when having female infant.
- 5. **Maternal dominance rank of the infant's mother:** The higher the dominance rank of the infant's mother, the higher the sociability of the mother.
- 6. **Maternal age of the infant's mother:** More associations will be formed with increasing maternal age as proposed by the 'Terminal Investment Theory'.
- 7. **Presence of an older sibling:** An infant's mother will be more sociable when an older sibling is still in permanent association with the mother-infant pair.

Research question II: Which factors, besides the sociability of an infant's mother, influence an infant's exploratory tendency?

- 1. <u>Influence of the mother on an infant's exploratory tendency</u>
 - a. **Sociability of the mother:** The higher the sociability of an infant's mother, the higher the exploratory tendency of an infant.
 - b. **Restrictiveness of the mother:** The higher the restrictiveness of an infant's mother, the lower the exploratory tendency of an infant.

c. Activity of the mother:

- i. Activity of an infant's mother while an infant is performing any kind of object manipulation behavior: The exploratory tendency of an infant is the highest when an infant's mother is feeding, nesting or exploring, lower when an infant's mother is resting and the lowest when an infant's mother is traveling.
- ii. *Daily activity budget of an infant's mother:* An infant's exploratory tendency is influenced by the daily activity budget of an infant's mother. On the one hand, the more time an infant's mother is performing activities which positively affect an infant's activities, such as feeding, nesting and exploring, the higher the exploratory tendency of an infant will be. On the other hand, the more time an infant's mother is traveling or resting, and hereby negatively or not affecting an infant's activities, the lower the exploratory tendency of an infant will be.
- iii. *Exploratory tendency of an infant's mother:* There is a positive effect of the exploration level of an infant's mother and the exploratory tendency of an infant.

2. Influence of the infant on its exploratory tendency

- a. **Age of the infant:** The exploratory tendency of an infant will be the highest between the ages of one to four years, followed by a quite abrupt ceasing of its exploratory tendency around four to five years of age.
- b. **Sex of the infant:** Female infants have a higher exploratory tendency than male infants.

3. Influence of external factors on an infant's exploratory tendency

- a. **Food availability:** In periods with low food availability, infants have less time and energy to perform any kind of object manipulation behavior and thus have a lower exploratory tendency compared to periods with high food availability.
- b. **Presence of an older sibling**: Infants, who live in close association with both their mother as well as an older sibling, have a higher exploratory tendency than infants who are not living in close association with an older sibling.
- c. **Percentage of association partners related with an infant:** The higher the percentage of association partners which are related with the infant, the higher the exploratory tendency of the infant.

Extension of research question II: Which factors influence <u>a juvenile's</u> exploratory tendency?

- 1. Sociability of a juvenile's mother during the time the juvenile was still dependent on its **mother:** The higher the sociability of a juvenile's mother, during the time a juvenile was still in close association with its mother, the higher the exploratory tendency of a juvenile now.
- 2. **Immediate sociability of the juvenile:** The higher the sociability of a juvenile, the higher its exploratory tendency.
- 3. **Food availability:** Similar as for infants, in periods with low food availability, juveniles have less time and energy to perform any kind of object manipulation behavior and thus have a lower exploratory tendency compared to periods with high food availability.

Material & methods

Study area and study period

The field study was conducted at the Suaq Balimbing research area in the Kluet region of Gunung Leuser National Park (3º 42'N; 97º 26'E, Aceh Selatan, Sumatra, Indonesia) on a population of wild Sumatran orangutans (*Pongo abelii*) (Figure 7). Suaq Balimbing is a functioning orangutan study area run by the Department of Anthropology of the University of Zürich in collaboration with Fakultas Biologi of Universitas Nasional (UNAS), Sumatran Orangutan Conservation Program (SOCP) and PanEco. The study area is located near Sumatra's west coast, consists of a variety of floodplain and hill forest habitats (van Schaik, 1999; Wich & van Schaik, 2000) and has an extensive trail system with many habituated orangutans who are individually known. With 7.4 individuals per square kilometer, Suaq Balimbing shows the highest Sumatran orangutan density of all studied orangutan study areas (van Schaik & Knott, 2001; Husson *et al.*, 2009; Singleton *et al.*, 2009).

Data on infants' behavior were collected during 6 months (from November 2016 until April 2017) by well-trained observers, mainly Caroline Schuppli and myself. There were several full-day follows when Caroline Schuppli and I took simultaneous data of the same infant in order to discuss and define behavioral variants (Inter-observer reliability test: Mean IC- Activity offspring: 0.83). In addition to our own collected data, behavioral data of infants' mothers and of infants themselves, collected by trusted fellow students and volunteers, were incorporated in this study.



Figure 7: Map showing the distribution of the Sumatran orangutans (Pongo abelii). The research area, Suaq Balimbing, is indicated with a black circle. Figure adapted from Dalet, 2007, retrieved from www.d-maps.com.

Data collection

Study subjects and collected data

Focal animal follows were performed on well-known and habituated immature orangutans and their mothers. Behavioral data were collected of different immatures at different stages in their life. In addition, simultaneous behavioral data of the immatures' mothers was collected too. Based on the collected behavioral data, 27 age-individual immature data points were created. I differentiated between two classes of immatures: infants and juveniles. On the one hand, infants are defined as immatures who are still dependent and in permanent association with their mother (0- 9 years of age) (van Noordwijk *et al.*, 2009). On the other hand, juveniles are defined as immatures who are weaned but no longer in permanent association with their mother (>9 years of age) (van Noordwijk *et al.*, 2009). The 27 age-individual data points included 19 age-individual infant data points and 8 age-individual juvenile data points. To be able to create an age-individual data point, following requirements needed to be fulfilled. At least five nest-to-nest follows and a minimum of 60 follow hours had to be collected. In addition, all follow days had to be collected in a period of approximately three months.

Data collected between November 2016 and April 2017

From November 2016 until April 2017, we (Caroline Schuppli and I) collected data on four different infants, ranging from 27 to 78 months of age. In total 602 focal-follow hours in 58 follow days were collected on infants. Total follow days consisted of 8 found-to-nest, 45 nest-to-nest and 5 nest-to-lost follows, ranging from 1h06 minutes to 12h50. Due to the *Neesia* season during December 2016 and January 2017, most of the orangutans left the research area to feed on *Neesia* fruits in the hills outside the study area. Thus, a limited amount of observational data was collected in this period. The minimum requirement of five nest-to-nest follows per individual, with a minimum of 60 focal follow and collected within three months, was achieved for seven age-individual data points. These seven age-individual data points were made of four different infants. Details on the focal infants are summarized in the table below (Table 1, Figure 8). Simultaneously, behavioral data was collected of the infants' mothers.

Focal	Total data points	Estimated birthdate	Sex	Mother	Haplotype	Total follow hours (h:m)	Total N-N follows
Lois	2	01/08/2010	М	Lisa	1	179:16	14
Cinnamon	2	01/04/2012	F	Cissy	1	212:37	15
Frankie	1	01/08/2012	Μ	Friska	2	74:58	5
Eden	2	01/11/2014	F	Ellie	2	136:07	11

Table 1: All infants followed in Suaq Balimbing, during the period of 10 November 2016 -3 April 2017 including information on age, sex, relationships and the total follow hours and nest-to-nest follows.



Figure 8: The four observed infants in Suaq Balimbing during the period from November 2016 – April 2017: Lois, Cinnamon, Frankie and Eden (from top left to bottom right).

Long-term data

Infant data

In addition, behavioral data of infants was used from the extensive long-term database of Suaq Balimbing. From November 2010 until April 2014, different reliable observers collected data on 7 different infants, ranging from 6 to 108 months of age. In total 717 focal follow hours in 72 follow days were collected of the different infants. Total follow days consisted of 15 found-to-nest, 49 nest-to-nest and 8 nest-to-lost follows, ranging from 1h05min to 12h54min. In total, the long-term data was the foundation for 12 extra age-individual infant data points. Details on the focal infants are summarized in the table below (Table 2, Figure 9). Simultaneously, behavioral data was collected of the infants' mothers.

Focal	Total data	Estimated	Sex	Mother	Haplotype	Total selected	Total N-N
	points	birthdate				follow hours (h:m)	follows
Chindy	1	01/01/2003	F	Cissy	1	81:10	5
Fredy	3	01/12/2004	М	Friska	2	150:58	9
Lois	3	01/08/2010	М	Lisa	1	214:34	16
Cinnamon	1	01/04/2012	F	Cissy	1	87:10	8
Frankie	2	01/08/2012	М	Friska	2	100:03	7
Simba	1	01/04/2013	М	Sarabi	1	47:17	4
Rendang	1	18/07/2013	Μ	Raffi	2	35:46	2

Table 2: All infants followed in Suaq Balimbing, during the period of November 2010 - April 2014 including information on age, sex, relationships, the total follow hours and nest-to-nest follows.



Figure 9: The seven observed infants in Suaq Balimbing during the period from November 2010 – April 2014: Chindy, Fredy, Lois, Cinnamon, Frankie, Simba and Rendang (from top left to bottom right).

Juvenile data

Besides, behavioral data of juveniles was also used from the extensive long-term database of Suaq Balimbing. From November 2010 until April 2014, different reliable observers collected data on four different juveniles, ranging from 120 to 157 months of age. In total 467 focal follow hours in 55 follow days were collected of the different infants. Total follow days consisted of 18 found-to-nest, 32 nest-to-nest and 5 nest-to-lost follows, ranging from 1h05min to 12h54min. In total, the long-term data was the foundation for 8 extra age-individual juvenile data points. Details on the focal juveniles are summarized in the table below (Table 3, Figure 10). Simultaneously, behavioral data was collected of the infants' mothers.

Table 3: All juveniles followed in Suaq Balimbing, during the period of November 2010 - April 2014
including information on age, sex, relationships, the total follow hours and nest-to-nest follows.

Focal	Total data	Estimated	Sex	Mother	Haplotype	Total selected	Total N-N
	points	birthdate				follow hours (h:m)	follows
Tina	1	01/01/1998	F	Raffi	2	63:54	5
Shera	2	01/06/1998	F	Chick	2	100:37	7
Ellie	2	01/05/1999	F	Friska	2	131:01	8
Lilly	3	01/03/2001	F	Lisa	1	171:46	12



Figure 10: The four observed juveniles in Suaq Balimbing during the period from November 2010 - April 2014: Tina, Shera, Ellie and Lilly (from left to right).

Protocol

Daily focal sampling was performed by following a mother-infant pair or a juvenile from the morning until the evening nest. Behavioral data was collected of infants, juveniles and infants' mothers. For the infants and juveniles, the exploratory tendency protocol was followed. For the infants' mothers, the standard protocol of collecting behavior was used.

For the immatures (infants and juveniles): exploratory tendency protocol

All occurrence sampling of the performing of any kind of object manipulation behavior (try-feeding and exploration) by an immature was conducted. Try-feeding is defined as a feeding attempt on a food item or other object whereby the item is taken into the mouth but not properly ingested (Power, 2000). Exploration is defined as the usually destructive manipulation of objects without an apparent feeding attempt (Power, 2000). These events were described in detail including context, exact description of the type of manipulation, the manipulated object used and the activity of an immature's mother. Based on this data, an immature's exploratory tendency could be measured. The exploratory tendency, or exploration rate of a focal, was measured based on the number of try-feeding and exploring events a focal performed during a follow day divided by the active period of a focal of the follow day (Formula 1). The exploratory tendency is a field-based behavior measurement technique to determine the cognitive performance of immature Sumatran orangutans and was repetitively used by other researchers (Schuppli & van Schaik, 2012; Schuppli, Meulman *et al.*, 2016).

Formula 1:

Exploration rate of a focal (events/hour) ______Number of try – feeding and exploring events performed

Active period of a focal

An average exploration rate was calculated for both the age-individual infant's and juvenile's data points (N= 27).

For the infants' mothers: general protocol

Behavioral data of the infants' mothers was collected following the standard protocol of the orangutan network for orangutan data collection (van Schaik, 1999; http://www.aim.uzh.ch /research/orangutannetwork/sfm.html), using the focal animal sampling method including instantaneous scan sampling at two minutes' intervals (Altmann, 1974). At every two-minute interval, the activity of the mother was recorded, including a description of what the mother was feeding or about the performing of any other social activity. Further, ad libitum focal sampling was conducted wherefore all social and interesting behaviors (e.g. exploring) were noted separately for the mother. In addition, detailed information about the formation of associations was collected.

Data analyses

Characteristics of the mother

Sociability of the mother Immediate sociability

The sociability of a focal's mother was measured based on the time a focal's mother spent in association with conspecifics (van Schaik *et al.*, 1999). An individual was defined to be in association when another individual was at less than 50 metres (van Schaik, 1999; van Noordwijk & van Schaik, 2005). This border of 50 metres reflects the approximate maximum distance individuals can travel in a coordinated fashion (van Schaik, 1999). The focal, as well as all other dependent infants who were in association with a focal's mother, were not included as association partners when calculating the sociability of a focal's mother. In addition, siblings who were still considered to be in association partner when calculating the sociability of a focal's mother. This would lead to an overestimation of a focal's mother's sociability of a focal's mother.

Thus, the sociability of a focal's mother was determined based on the proportion of time a focal's mother spent in association with conspecifics (van Schaik *et al.*, 1999, 2006). The proportion of time a focal's mother spent in association with conspecifics, reflected the time a focal's mother spends in association during a follow day with at least one association partner divided by the active period of a focal's mother of the follow day (Formula 2). The active period of a focal's mother was calculated as the time between a focal's mother leaving her morning nest until the time the focal entered the focal's mother's night nest. The start and end time an association partner was in and out of association with a focal's mother, was noted down for each association partner. If there were two or more association partners simultaneously in association with a focal's mother, only the association time of one of the association partners was taken into account.

Formula 2:

Sociability of a focal's mother (proportion of time spent in association) $= \frac{\text{Time in association with one or more association partners}}{\text{Active period of a focal's mother}}$

An average sociability of a focal's mother was calculated for each age-individual infant data point (N= 19).

Long-term sociability: sociability of the mother during infancy period of the juvenile

The sociability of a juvenile's mother, during the time a juvenile was still dependent on its mother, was determined based on the mean party size of a juvenile's mother (Setia *et al.*, 2009). A juvenile's mother's party size reflected the number of conspecifics a juvenile's mother associated with during a follow day, including the mother herself. In other words, a solitary individual would have a party size of one (Setia *et al.*, 2009). The party size of a juvenile's mother was calculated for each follow day during the time a juvenile was still in permanent association with its mother. Next, a mean party size over all these follow days was calculated for each age-individual juvenile data point, except for the juvenile Shera since no behavioral data was collected of Chick (Shera's mother) when Shera was still in close association with her mother (N= 6).

Sociability of the juvenile

The sociability of the juveniles was determined in the same way as the immediate sociability of a focal's mother was calculated, namely based on the proportion of time a juvenile spent in association with conspecifics (van Schaik *et al.*, 1999, 2006). An average sociability of a juvenile was calculated for each age-individual juvenile data point (N= 8).

Restrictiveness of the mother

The restrictiveness of a focal's mother was measured based on the number of times a focal was collected by a focal's mother. Therefore, all occurrence data of the collection of a focal by a focal's mother were collected. With the collection of the restrictive behaviors performed by a focal's mother, a rate of restrictive behavior of a focal's mother could be calculated. The rate of restrictive behavior of a focal's mother of times a focal's mother collected a focal during a follow day dived by the active period a focal's mother on that follow day (Formula 3).

Formula 3:

Active period of a focal's mother

However, only for a limited number of follow days, reliable data was collected about a focal's mother restrictiveness. Since only for a small number of follow days the restrictiveness of a focal's mother was calculated, no reliable restrictiveness measure could be calculated per age-individual data point. Only an overall restrictiveness measure for four of the seven focals' mothers was calculated. Therefore, the restrictiveness of a focal's mother was known for only 12 age-individual infant data points (N= 12).

Activity of the mother

The activity of a focal's mother was calculated in two different ways. First, the average daily activity budget of a focal's mother, independent of the activity of the focal, was calculated. Second, it was determined if the activity of a focal's mother, on a specific moment, influenced whether or not a focal performed any kind of object manipulation behavior. For both calculations, the activities of the focals' mothers were divided into three different categories, namely (1) a negative category, which included traveling, (2) a neutral category, which included resting and (3) a positive category, which included feeding, nesting, and exploring.

First, an average daily activity budget of a focal's mother was calculated for each age-individual infant data point. Due to the simultaneous collection of 2-minute activity data of the focals' mothers, by additional (reliable) observers, the daily percentage of time a focal's mother spent on performing activities belonging to either the negative, neutral or positive category could be calculated. However, due to a shortage of observers, for some follow days, no simultaneous (reliable) activity data was collected of a focal's mother. Observers who were considered to have collected reliable activity data of a focal's mother were the following fellow students and research assistants at the Suaq Balimbing research station: Anaïs, Armas, Caroline, Chigusa, Fikar, Izumi, Jacob, Julia, Kevin, Mudin, Saidi, Sofia, Subhan, Syahrul and Toni. Hereby, the daily activity budget of the focals' mothers were calculated for each age-individual infant data point (N= 19).

Second, since the activity of a focal's mother was expected to influence the exploratory tendency of a focal, it was calculated if the activity of a focal's mother, on a specific moment, influenced whether or

not a focal performed any kind of object manipulation behavior. While taking all occurrence data of any kind of object manipulation behavior performed by a focal, the activity of a focal's mother, if possible, was noted down. If a focal's mother activity was unknown while a focal was performing any kind of object manipulation behavior, this data was taken out of the data analysis. Hereby, for each age-individual infant data point, the proportion of time a focal's mother spent on either performing positively-, negatively- or neutrally-influencing activities, while the focal was performing any kind of object manipulation behavior, was calculated (N= 19).

Exploratory tendency of the mother

In the same way as explorative behavior of the focals was collected, it was collected for the focals' mothers. While performing behavioral observation of a focal, in addition, special focus was laid on the collection of all occurrence data of a focal's mother explorative behavior. The explorative behaviors performed by a focal's mother were described in detail, including context and exact description of the type of manipulation and manipulated object. With the collection of the explorative behaviors performed by a focal's mother, a rate of explorative behavior of a focal's mother could be calculated. In general, the rate of explorative behavior of a focal's mother reflected the number of explorative behaviors a focal's mother performed during a follow day divided by the active period of a focal's mother on that follow day (Formula 4).

Formula 4:

Rate of explorative behavior of a focal's mother (exploring events/hour) = $\frac{\text{Total number of explorative behaviors performed by a focal's mother}}{\text{Active period of a focal's mother}}$

Since only for a small number of follow days the rate of explorative behavior of a focal's mother was calculated, no reliable explorative behavior measure could be calculated per age-individual data point. Only an overall explorative behavior measure for six of the seven focals' mothers was calculated. Therefore, the explorative behavior rate of a focal's mother was known for only 15 age-individual infant data points (N= 15).

External and internal factors

Food availability: fruit availability index (FAI)

For every month, a fruit availability index (FAI) was calculated based on phenology monitoring of approximately 1500 trees in a two-ha phenology plot. One of the aspects of tree phenology monitoring was determining the presence of fruits in trees (Appendix A: Tree phenology monitoring protocol). Concrete, for each tree surveyed, it was noted down whether the tree had fruits or not. Based on this data, fruit availability indexes (FAIs) were calculated by the total number of trees that had fruits divided by the total number of trees surveyed (Formula 5). The higher the FAI, the more trees that carried fruits. When calculating FAIs, only the availability and not the abundance of fruits are taken into account. In our data set, the FAIs varied from 5.4 until 14.8. FAIs were calculated for almost every moth, except for December 2010 and January 2011. For these two months, an average FAI was calculated based on the FAIs of the previous and following month. Concrete, the average FAI for December 2010 and January 2011. If observations, belonging to the same age-individual data point, were spread over two or more months, an average of the different FAIs of these months were calculated. An average FAI was calculated for both the age-individual infant's and juvenile's data points (N= 27).

Formula 5: Fruit Availability Index (FAI)

 $= \frac{\text{Total number of trees with fruits}}{\text{Total number of trees surveyed}} * 100$

Family size and composition: number of female related individuals

During previous years, different researchers collected faecal samples as many as possible orangutans habituated in Suaq Balimbing. With these faces samples, DNA analyses could be performed and three clear family clusters aroused. Some of the orangutans, from whom faecal samples were collected, could be placed in one of these family trees (Appendix B: Family trees of the orangutans of Suaq Balimbing). Almost all focals and the focals' mothers were assigned to one of the three family tress. Only one focal and the focal's mother, focal Simba and the focal's mother Sarabi, the relation with the other orangutans in the area is still unclear.

When determining the family size and composition of the focals' mothers, the number of female relatives a focal's mother had, was calculated. The focal itself, as well as all dependent infants of female related individuals, were not taken into account. Based on the same argumentation as for the exclusion of these individuals when determining the sociability of a focal's mother. Further, if evidence for the death of female relatives was found, these were also not taken into account. As mentioned before, for one of the mother-infant pairs (Sarabi and Simba), no genetic data was available. Therefore, the family size and composition could only be calculated for six of the seven focals' mothers. However, to prevent a loss of data, an average of the number of female related individuals a focal's mother has, was calculated for Sarabi, the mother of Simba, by taking an average of the number of female related individuals a focal's mother had. Hereby, the number of female related individuals a focal's mother set of the number of a simbal on an estimation, was calculated for all age-individual infants data points (N= 19).

Sociodemographic factors: age/sex of the focal and maternal age of the focal's mother

Different sociodemographic factors may influence, directly or indirectly, a focal's exploratory tendency. Therefore, the three sociodemographic factors need to be defined: age of a focal, sex of a focal and maternal age of a focal's mother.

First, the age of each focal was determined. Since the exact date of birth is unknown for (most of) the focals, a fixed date of birth had to be determined by observers. The first time observers encountered an orangutan, who was never seen before, a fixed date of birth was determined based on the absolute and relative size of the orangutan. Since only the month and not the day of birth could be estimated, the birthdate of each focal is set on the first day of the month which the focal is expected to be born in. When determining the age of the focals for each age-individual data point, an average age is calculated over the data collection period of an age-individual data point. Thus, for each age-individual data point there is a fixed age of the focal.

Second, a focal's sex was either categorized as male or female.

Third, the maternal age of each focal's mother was determined. However, the date of birth of the focals' mothers, and hereby the exact maternal age of the focals' mothers, was mostly unknown since orangutan studies in Suaq Balimbing only started in 1992. Most focals' mothers were born before this time. Therefore, the maternal age of the focals' mothers was estimated based on the number of infants each focal mother gave already birth to. The focals' mothers were split into different age-classes,

according to how many infants a focal's mother already gave birth to before the birth of the focal itself. Infants who died in the first two years of their life were not taken into account in the calculation of the number of infant a focal's mother already gave birth to. Then, focals' mothers were split into three age-classes. If the focal was the first or second infant a focal's mother gave birth to, a focal's mother gave already birth at 2 to 3 number of infants before the birth of the focal itself. Last, if a focal's mother gave already birth to 4 or more infants before the birth of the focal itself, she was categorized as age-class 3. A less detailed method of categorizing a focal's mother according to her maternal age, was by splitting the focals' mothers only into two different age-classes. All focals' mothers known to give birth to maximal three infants were defined as "young", while all other focals' mothers were defined as "old". Since only one of the focals' mothers could be assigned to age-class 3 (Friska), and therefore no reliable results would be obtained with only one focal mother belonging to age-class 3, it was decided to use the less detailed categorizing method, i.e. with "young" and "old" focals' mothers.

For all 27 age-individual data points, both age-individual infant and juvenile data points, reliable information was present for all of the sociodemographic factors (N= 27). However, the effect of the maternal age of a focal's mother on the sociability of a focal's mother was only calculated for the infant's data points (N= 19).

Maternal dominance rank of the focal's mother

The dominance rank of the focals' mothers was determined by collecting all occurrence behavioral observations of adult females displacing other adult females over the last ten years. Although it is written in the literature that no dominance ranks are existent in orangutans, as seen in other apes (Galdikas, 1995; van Schaik & van Hooff, 1996), over the last years certain adult females had been observed to display or being displaced repetitively by other adult females (Sugardjito, te Boekhorst & van Hooff., 1987; Utami et al., 1997). Based on this anecdotal data, a dominance rank to the adult females could be assigned. Initially, the focals' mothers were divided into three different categories, based on their dominance rank. The focals' mothers with a high dominance rank belonged to category 1, the focals' mothers with an intermediate dominance rank belonged to category 2 and the focals' mothers with a low dominance rank belonged to category 3. Concrete, all focals' mothers placed in category 1, displaced, at least once, all focals' mothers placed in category 2. Further, all focals' mothers defined as category 2, displaced, at least once, all focals' mothers placed in category 3. However, only one of the focals' mothers could be assigned to the highest dominance rank (Friska). Since no reliable results would be obtained with only one individual assigned to the highest dominance rank, it was decided to divide the focals` mothers only in two instead of three different categories, a lower and a higher dominance group. Similar, as if there would be three dominance categories, all focals' mothers belonging to category 1, displaced at least ones, all focals' mothers belonging to category 2. Six of the seven focals' mothers could be assigned to one of the dominance categories. The relation between the dominance rank of a focal's mother and the sociability of a focal's mother was only calculated for all age-individual infant's data points (N= 19).

Presence of an older sibling

Most of the focals have (an) older sibling(s), and the presence of an older sibling is expected to influence a focal's exploratory tendency. Usually, if a mother gives birth to a newly born infant, her older infant still stays in close association for up to two years (Edwards & Snowdon, 1980; van Noordwijk *et al.*, 2012). For each follow day, it was determined whether an older sibling was still in close association with a mother-infant pair. The older sibling was defined to be in close association

with the mother-infant pair when he/she was in association for the entire follow day with the motherinfant pair. If the older sibling was in close association with the mother-infant pair in more than 50% of the follow days, belonging to the same age-individual data point, the older sibling was considered to be in close association with a mother-infant pair. If in less than 50% of the follow days, the older sibling was considered to be not in close association with a mother-infant pair. Whether an older sibling was in close association with a mother-infant was only calculated for all age-individual infant's data points (N=19).

Percentage association partners related with the infant

Besides the number of association partners a focal associated with and the time a focal was in association with each association partner, also the identity and relatedness of the association partners with a focal was determined. Hereby, the percentage of association partners who were related and unrelated with a focal could be calculated for each follow day (Formula 6). Similar as for the calculation of the sociability of a focal's mother, dependent infants of mother-infant pairs, who associated with a focal, were not included as association partners and neither their relatedness was taken into account. Again, the same argumentation for the exclusion of these individuals is valid as for calculating the sociability of a focal's mother.

Formula 6:

Percentage of related association partners (%) = $\frac{\text{Total number of association partners related}}{\text{Total number of association partners}} * 100$

An average percentage of association partners who were related was calculated for (almost) each ageindividual infant data point (N= 16). Due to a lack of reliable data on the identity of the association partners for two age-individual infant data points, no percentage of related association partners could be calculated for these two age-individual infant data points.

Statistics

Residuals of exploration rates

When the immatures' exploration rates were plotted versus the age of the immatures, it became apparent that the relationship between the two variables is non-linear. Therefore, I used a fitted smoothing function to model the non-linear relationship (using the "smooth spline" function of the "stats" package in R). Based on the fitted smoothing function of exploration rates versus the age of the immatures (Figure 11), I calculated the residuals of the immatures' exploration rates. These residuals represent the immatures' exploration rates corrected for age and were used as the new exploratory tendency measure for the immatures in this study.



Residuals of exploratory tendency



Statistical models

All further analyses and plots were done using SPSS.

Multiple linear regression analyses

Since data were collected of the same individuals multiple times, at different stages in their development, the different individual data points were not all independent of each other. Therefore, I used linear mixed models (LMMs), including the individual identity as a random factor. However, in none of the analyses the LMMs were significantly different from the multiple linear regression models (MLRMs), when tested with likelihood ratio tests. Therefore, only the results of the MLRMs are presented here. To be able to perform MLRMs, following assumptions needed to be fulfilled: (1) a linear relationship between the dependent and each independent variable had to be existing, (2) homoscedasticity of the data, (3) multicollinearity of the data and (4) the residuals had to be (approximately) normally distributed. All of these assumptions were fulfilled and MLRMs could be performed.
Results

Factors influencing the sociability of an infant's mother

To assess which factors influenced the sociability of an infant's mother, a MLRM was performed. First, a significant positive effect of the age of an infant on the sociability of an infant's mother was found (p=0.020). This shows that the older an infant becomes, the higher the sociability of an infant's mother (Figure 12). Second, the sex of an infant also had a significant effect on the sociability of an infant's mother (p=0.009). Mothers with female infants are significantly more sociable than a mother with a male infant (Figure 13). For the other factors which were expected to influence an infant's mother's sociability (maternal age, maternal dominance rank, family, food availability and presence of an older sibling), no significant relationships were found (Table 4).



Figure 12: The sociability of the infants` mothers (based on the proportion of time an infant's mother spent in association with conspecifics) plotted versus the age of the infants (in years).



Figure 13: : The sociability of the infants` mothers (based on the proportion of time an infant's mother spent in association with conspecifics) for male and female infants. ** indicates a statistical significant result.

Table 4: Multiple linear regression model with the mother's sociability as dependent variable and (1) characteristics of an infant's mother (maternal age, maternal dominance rank and family), (2) characteristics of an infant itself (age and sex of an infant) and (3) external factors (food availability and presence of an older sibling), as predictor variables. Trends are indicated with * (p<0.05). N refers to the number of age-individual infant data points.

Dependent variable	N	R ²	Predictor variables	Estimates	Std.error	P-value
Sociability of the infant's	19	0.69	Maternal age	0.045	0.29	0.879
mother			Maternal dominance rank	0.46	0.27	0.119
			Family: number of female	0.097	0.11	0.46
			related conspecifics			
			Age of the infant	0.075	0.027	0.020**
			Sex of the infant	0.35	0.11	0.009**
			Food availability	0.037	0.030	0.247
			Presence of an older sibling	0.14	0.143	0.337

Age of the infant

As mentioned before, a significant positive effect of the age of an infant on the sociability of an infant's mother was found. In other words, the sociability of an infant's mother increases with increasing infant's age. Besides an increasing sociability of an infant's mother with increasing independence of an infant, a more specific prediction had been made about the effect of an infant's age on the sociability of an infant's mother. I predicted mothers with very young (0-2 years of age) or older (>4 years of age to have a higher sociability than mothers with mid-aged (2-4 years of age) infants. A positive trend for the effect of an infant's age-class on the sociability of an infant's mothers was found (Kruskal-Wallis, $\chi^{2}(2) = 4,79$, p = 0.091; Figure 14). In a second step, the different age-classes were compared two by two to detect the differences between the age-classes. When the effect of very young infants was compared with the effect of mid-aged infants on the sociability of the infants' mothers, a positive trend was found that infants' mothers with mid-aged infants were more sociable than infants' mothers with very young infants (Mann-Whitney U = 4.00, p=0.087). A similar positive trend was found when the effect of very young infants was compared with the effect of older infants on the sociability of the infants' mothers (Mann-Whitney U = 11, p=0.059). Mothers with older infants tend to be more sociable than mothers with very young infants. When the effect of mid-aged infants were compared with the effect of older infants on the sociability of the infants' mothers, no significant difference between the two age-classes was found (Mann-Whitney U = 13, p=0.440). Thus, mothers with mid-aged infants or older infants do not significantly differ in their sociability (Figure 14).



Figure 14: The sociability of the infants' mothers (proportion of time spent in association) for the different infant age-classes (0-2 years, 2-4 years, <4 years). * indicates a statistical trend.

Family

Percentage related of the association partners

As mentioned before, no significant effect of an infant's mother's family size and composition on the sociability of an infant's mother was found. Thus, the number of female related conspecifics an infant's mother has, does not influence the sociability of an infant's mother. Therefore, it was investigated whether there is a preference to associate with related conspecifics (Figure 15). Based on the average of the 16 age-individual infant data points, no preference to associate with related individuals was found. Instead, on average, only 17% of the association partners were related relative to 83% of the association partners who were unrelated with an infant, or an infant's mother.



Figure 15: Percentage of associations with related and unrelated association partners of the infants` mothers, shown for the age-individual data points (N=16).

Factors influencing an immature's exploratory tendency

Infants

To assess which factors influence the exploratory tendency of infants, a MLRM was performed including the factors (1) sociability of a mother, (2) activity of a mother, (3) sex of an infant, (4) food availability and (5) presence of an older sibling (Table 5). For all tested factors, except for the sex of an infant and the food availability, a significant effect on the exploratory tendency of the infants was found. First, a significant positive effect was found of the sociability of an infant's mother on the exploratory tendency of an infant (p= 0.005, Figure 16). Thus, infants of more sociable mothers have a higher exploratory tendency than infants of less sociable mothers. Second, a significant negative effect was found of the time an infant's mother spent on our previously defined positively-influencing activities (including feeding, nesting and exploring) on the exploratory tendency of an infant (p= 0.003, Figure 18a). Thus, the more time an infant's mother spent on these activities, the lower the exploratory tendency of an infant. Third, a significant positive effect was found of the presence of an older sibling on the exploratory tendency of an infant (p= 0.001, Figure 17). Thus, infants who are in close association with both their mother and an older sibling, have a higher exploratory tendency than infants who grow up without an older sibling nearby. Neither for the sex of an infant and the food availability, a significant effect on an infant's exploratory tendency was found. Thus, the level of food availability does not have an effect on an infant's exploratory tendency. Also, female and male infants do not differ in their exploratory tendency.

Table 5: Multiple linear regression model with an residual exploratory tendency as dependent variable and (1) characteristics of an infant's mother (sociability and activity of a mother), (2) characteristics of an infant itself (sex of an infant) and (3) external factors (food availability and presence of an older sibling), as predictor variables. Trends are indicated with * (p<0.1). The statistical significant results are indicated with ** (p<0.05). N refers to the number of age-individual infant data points.

Dependent	Ν	R ²	Predictor variables	Estimates	Std.error	P-value
variable						
Residual	19	0.80	Sociability of the mother	3.25	0.96	0.005**
exploratory			Activity of the mother	-13.54	3.71	0.003**
tendency of the			Sex of the infant	-0.032	0.55	0.995
infants	Food availability	0.20	0.14	0.159		
			Presence of an older sibling	2.43	0.49	0.001**



Effect of the sociability of an infant's mother on the exploratory tendency of an infant

Figure 16: Residual exploration rate of the infants (corrected for age) plotted versus the sociability of the infants` mothers (based on the proportion of time an infant`s mother spent in association with conspecifics).





Figure 17: Residual exploration rates (corrected for age) for infants with and without an older sibling present.** indicates a statistical significant result.

There are still three other factors which I expected have an influence on infant's exploratory tendency: (1) the restrictiveness of an infant's mother, (2) the explorative behavior of an infant's mother and (3) the percentage of association partners related with an infant. These factors were not included in the MLRM since I did not have these data available for all my age-individual data points. To avoid an overall loss of sample size by including these factors in the overall MLRM, I performed a separate analysis with these factors. To avoid models with too many predictors in relation to sample size, I included the factors individually in separate models. When investigating the effect of the restrictiveness of an infant's mother on the exploratory tendency of an infant, no significant effect was found (Table 6). Similarly, no significant effects were found of (1) the exploratory tendency of an infant's mother and (2) the percentage of association partners related with an infant on the exploratory tendency of an infant (Table 7/8). For the other factors, of which the effects on the exploratory tendency of infants were already tested in the overall MLRM (sociability of a mother, activity of a mother, sex of an infant, food availability and presence of an older sibling, see above), very similar relationships were found in all of these additional analyses.

In the MLRM where the restrictiveness of an infant's mother was included, the effect of the sociability of an infant's mother on the exploratory tendency of an infant was not significant anymore but a trend remained (p= 0.070, Table 6). This could very well be due to the limited sample size of this analysis, especially in relation to the number of predictors included. Interestingly, in two of the MLRMs, a positive trend for food availability on the exploratory tendency of infants was found (p= 0.070, Table 5; p= 0.071, Table 7). In other words, a trend was fund that with increasing food availability, infants' exploratory tendencies increase, just as I predicted initially. To be able to further assess the effect of food availability, more and possibly more fine-grained data of monthly exploration rates are needed. However, to investigate this potential effect of food availability with the available data, the number of predictors was reduced by excluding the clearly non-significant factors (restrictiveness of the mother and sex of the infant). In this reduced model, the sociability of the mother was highly significant again (p= 0.002, Table 6). Also, the other previously found significant factors (activity of the mother and presence of an older sibling) maintained their significance level, suggesting that the data are very robust. However, for food availability, for which a positive trend was found in the previous MLRMs (Table 6/7), became non-significant (Table 9). Overall, the available data suggest that an infant's

Table 6: Multiple linear regression model with residual exploratory tendency as dependent variable and (1) characteristics of an infant's mother (restrictiveness, sociability and activity of a mother), (2) characteristics of an infant itself (sex of an infant) and (3) external factors (food availability and presence of an older sibling), as predictor variables. Trends are indicated with * (p<0.1). The statistical significant results are indicated with ** (p<0.05). N refers to the number of age-individual infant data points.

exploratory tendency is not influenced by changes in food availability.

Dependent variable	Ν	R ²	Predictor variables	Estimates	Std.error	P-value
Residual	12	0.90	Restrictiveness of the mother	-25.12	15.58	0.168
exploratory			Sociability of the mother	2.68	1.17	0.070*
tendency of the			Activity of the mother	-15.60	4.27	0.015**
infants	Sex of the infant	-1.77	1.42	0.226		
			Food availability	0.65	0.23	0.070*
			Presence of an older sibling	2.31	0.52	0.007**

Table 7: Multiple linear regression model with residual exploratory tendency as dependent variable and (1) characteristics of an infant's mother (explorative behavior, sociability and activity of a mother), (2) characteristics of an infant itself (sex of an infant) and (3) external factors (food availability and presence of an older sibling), as predictor variables. Trends are indicated with * (p<0.05). N refers to the number of age-individual infant data points.

Dependent variable	Ν	R ²	Predictor variables	Estimates	Std.error	P-value
Residual exploratory	15	0.86	Explorative behavior of the mother	-0.24	9.58	0.981
tendency of the			Sociability of the mother	3.25	0.96	0.006**
infants			Activity of the mother	-13.54	3.71	0.004**
			Sex of the infant	-0.032	0.55	0.963
			Food availability	0.20	0.14	0.071*
			Presence of an older sibling	2.43	0.49	0.003**

Table 8: Multiple linear regression model with residual exploratory tendency as dependent variable and (1) characteristics of an infant's mother (sociability and activity of a mother), (2) characteristics of an infant itself (sex of an infant) and (3) external factors (food availability, presence of an older sibling and **percentage of association partners related with an infant**), as predictor variables. Trends are indicated with * (p<0.1). The statistical significant results are indicated with ** (p<0.05). N refers to the number of age-individual infant data points.

Dependent variable	Ν	R ²	Predictor variables	Estimates	Std.error	P-value
Residual	16	0.88	Sociability of the mother	2.36	0.93	0.032**
exploratory			Activity of the mother	-16.68	3.67	0.001**
tendency of the			Sex of the infant	0.066	0.51	0.90
infants			Food availability	0.21	0.14	0.18
			Presence of an older sibling	3.20	0.62	0.001**
			Percentage of association partners related with the infant	-0.20	1.38	0.89

Table 9: Multiple linear regression model with residual exploratory tendency as dependent variable and (1) characteristics of an infant's mother (sociability and activity of the mother), (2) external factors (food availability and presence of an older sibling), as predictor variables. Trends are indicated with * (p<0.1). The statistical significant results are indicated with ** (p<0.05). N refers to the number of age-individual infant data points.

Dependent variable	Ν	R ²	Predictor variables	Estimates	Std.error	P-value
Residual	19	0.78	Sociability of the mother	3.23	0.87	0.002**
exploratory	Activity of the mother	-13.63	3.23	0.001**		
tendency of the			Food availability	0.20	0.12	0.118
infants			Presence of an older sibling	2.42	0.47	0.001**

Activity of the mother

Positively-, negatively- and neutrally-influencing activities

Average daily activity budgets for the infant's mothers were calculated for each age-individual data point. Concrete, the proportions of time the mothers spent on activities which were expected to positively (feeding, nesting and exploring), negatively (traveling) and neutrally (resting) influence her offspring's exploratory tendency, were calculated for each age-individual infant data point.

I was especially interested in the effects of "positively- and negatively-influencing activities" (previously defined) of the mothers on the exploratory tendencies of the infants. Since the "positivelyand negatively-influencing activities" of an infant's mother are significantly negatively correlated with each other (Pearson correlation, r = -0.74, n = 19, p < 0.001), only one of the two measures could be included in the overall MLRM. It was decided to include the "positively-influencing activities" of an infant's mother to assess the overall effect the activity of an infant's mother has on the exploratory tendency of an infant.

As mentioned before, a significant negative effect was found of the proportion of time an infant's mother engaged in "positively-influencing activities" on an infant's exploratory tendency (Figure 18a). In other words, the more time an infant's mother spent on feeding, nesting and exploring, the lower the exploratory tendency of an infant. As predicted due to the significant negative correlation between "positively- and negatively-influencing activities" of an infant's mother, the opposite effect of the proportion of time an infant's mother performed "negatively-influencing activities" on infants exploratory tendencies was found (Figure 18b): The more time an infant's mother spent on traveling, the higher the exploratory tendency of an infant.

In addition, I performed a visual inspection of the graphical relationship of the effect of the "neutrallyinfluencing activities" of the mother on infants' exploratory tendencies. Visual inspection suggests that there is no effect of "neutrally-influencing activities" of an infant's mother on infants' exploratory tendencies (Figure 18c).



Figure 18a: Residual exploration rate of the infants (corrected for age) plotted versus the proportion of time a mother engaged in "positively-influencing activities" (feeding, nesting and exploring).



Figure 18b: Residual exploration rate of the infants (corrected for age) plotted versus the proportion of time a mother engaged in "negatively-influencing activities" (traveling).



Figure 18c: Residual exploration rate of the infants (corrected for age) plotted versus the proportion of time a mother engaged in "neutrally-influencing activities" (resting).

Activity budget of an infant's mother while an infant was exploring and/or try-feeding

In order to find out which activities of a mother proximately facilitate explorative events in infants, the activity budget of an infant's mother, while the infant was exploring and/or try-feeding was calculated. Valid for each age-individual (infant) data point, an infant performed the most exploring and/or try-feeding events when an infant's mother was feeding, nesting or exploring, less when an infant's mother was resting and the least when an infant's mother was traveling (Figure 19). Therefore, I expected that the more time an infant's mother spends of her daily time on feeding, nesting and exploring, the higher the exploratory tendency of an infant. However, as described above, the opposite effect was found (MLRM: p=0.003, Table 5).



Figure 19: Proportion of time the mothers engage in different activities (traveling, resting and feeding/nesting/exploring,) while the infant was exploring and/or try-feeding, represented for all age-individual infant data points (N=19), as well as an average calculated over all mothers. On average, an infant's mother is 13% of her time traveling, 18% of her time resting and 69% of her time feeding, nesting and exploring while an infant is exploring ad/or try-feeding.

Activity budgets

The average activity budgets of orangutans may differ depending on the habitat they live in and on their age-sex class. Different average activity budgets were found in the literature, depending on which factors were taken into account when calculating the average activity budget of orangutans. In my thesis, I wanted to compare these different average activity budgets, found in the literature, with the average activity budget of the infants` mothers in this study (Table 10).

Table 10: Representation of the average activity budgets of orangutans from different studies. Differences in the average	age
activity budgets of orangutans are due whether or not habitat and/or the age-sex classes of the orangutans are inclua	led

	Specifications	% Traveling	% Resting	% Feeding	% Other activities	Total
1	All orangutans (Knott, 1999)	13	44	40	3	100
2	Sexually active females (Morrogh-Bernard <i>et al.,</i> 2009)	14	37	47.5	1.5	100
3	Sexually active females & peat swamp forest (Morrogh- Bernard <i>et al.</i> , 2009)	14.5	27.9	55.5	2.1	100
4	Suaq Balimbing (Morrogh- Bernard <i>et al.,</i> 2009)	16.9	25.9	54.9	2.3	100
5	This study	20	16	61	3	100

Based on visual comparisons, the activity budgets seem to differ substantially dependent on the habitat they are living in and to which age-sex class they belong. The infants' mothers in this study overall spent less time on resting and more time on feeding and traveling compared to all other average activity budgets of orangutans found in the literature. The differences in the average activity budgets of orangutans, between this study and what was found in the literature, become smaller when more specific characteristics are taken into account. For instance, if the average activity budget of all orangutans (1) is compared with the average activity budget of the infants' mothers in this study (5), the differences are enormously. In contrast, if the average activity budget of sexually active females living in a swamp forest (3) and/or the average activity budget of orangutans living in Suaq Balimbing (4) are compared with the average activity budget of the infants' mothers in this study (5), the differences are clearly less pronounced.

Juveniles

Even though the main focus of this study was on infants, also data on juvenile animals were collected which resulted in 8 age-individual juvenile data points. I investigated whether the exploratory tendency of juveniles is influenced by the same factors as the exploratory tendency of infants. However, only the effect of three factors on the exploratory tendency of juveniles could be investigated, i.e. (1) the sociability of an infant's mother during the infancy period of a juvenile, (2) the immediate sociability of a juvenile and (3) the food availability. For the other factors, either no data was available or was applicable for the juveniles. Using an MLRM, I found no significant effect of any of these three factors on the exploratory tendency of the juveniles (Table 11). However, the absence of a statistically significant results was probably due to the small sample size. Therefore, it was decided to perform visual inspection of the graphical relationships. First, visual inspection suggests a positive effect of the sociability of a juvenile's mother, during the infancy period of a juvenile on exploratory tendency. The higher the sociability of a juvenile's mother during the infancy period of a juvenile, the higher the exploratory tendency of a juvenile (Figure 20). Second, visual inspection suggests a positive effect of the immediate sociability of a juvenile on its exploratory tendency. The higher the immediate sociability, the higher the exploratory tendency of a juvenile (Figure 21). Last, visual inspection provided no evidence for an effect of food availability on the exploratory tendency of a juvenile (Figure 22). However, to be able to test the statistical significance of these relationships, a larger sample size is needed.

Table 11: Multiple linear regression model with residual exploratory tendency as dependent variable and (1) characteristics of a juvenile's mother (sociability of a juvenile's mother during the infancy period of a juvenile), (2) characteristics of a juvenile itself (immediate sociability of a juvenile), (3) external factors (food availability), as predictor variables. Trends are indicated with * (p<0.05). N refers to the number of age-individual infant data points.

Dependent variable	Ν	R ²	Predictor variables	Estimates	Std.error	P-value
Residual exploratory tendency of	7	0.53	Sociability of the mother during the infancy period of the juvenile	-0.16	0.14	0.36
the juveniles			Immediate sociability of the juvenile	0.53	0.65	0.50
			Food availability	-0.057	0.078	0.54





Figure 20: Residual exploration rate of the juveniles (corrected for age) plotted versus the sociability of the juveniles' mothers during the infancy period of the juveniles. The sociability of the juveniles' mothers is calculated based on the mean party size (N = 6, see material and methods).

Figure 21: Residual exploration rate of the juveniles (corrected for age) plotted versus the immediate sociability of the juveniles. The sociability of the juveniles is calculated based on the proportion of time a juvenile spent in association with conspecifics (N= 8).



Figure 22: Residual exploration rate of the juveniles (corrected for age) plotted versus the food availability (N=8).

Discussion

The main aim of my project was to investigate which factors influence the exploratory tendency of infant Sumatran orangutans. Based on the results of previous research, the sociability of an infant's mother was expected to be one of the most important factors influencing an infant's exploratory tendency (Schuppli, Forss, Meulman, Atmoko *et al.*, 2016). The orangutans at Suaq Balimbing show individual differences in their levels of sociability. Since factors influencing the sociability of an infant's mother indirectly influence an infant's exploratory tendency, it was relevant for the aim of this project to investigate the factors influencing an infant's mother's sociability. Therefore, I investigated which factors influence the sociability of an infant's mother. Factors that were hypothesized to have an effect were (1) food availability, (2) family size and composition, (3) age of the infant, (4) sex of the infant, (5) dominance rank of the mother, (6) age of the mother and (7) the presence of an older sibling.

However, besides the sociability of an infant's mother, I hypothesized that more factors may have an effect on an infant's exploratory tendency. These factors can be divided into three different categories, namely (1) characteristics of the infant's mother, such as the sociability, restrictiveness and the activity of the mother (2) characteristics of the infant itself, such as age and sex, and (3) external factors, such as food availability, whether or not the infant lives together with an older sibling and the relatedness of the association partners with the infant.

Research question I: Which factors influence the sociability of an infant's mother? Sociability of the mother

For the effect of the sociability of an infant's mother on an infant's exploratory tendency, I expected that infants with more sociable mothers have a higher exploratory tendency than infants with less sociable mothers. I found evidence for the hypothesis in this study. Since mothers differed remarkably in their levels of sociability, factors which may influence the sociability of an infant's mother, and thus indirectly the exploratory tendency of an infant, were investigated.

Environmental factor: food availability

Firstly, the effect of food availability on an infant's mother's sociability was investigated. I expected that in periods with a higher level of food availability, an infant's mother would be more sociable than in periods with a lower level of food availability (Sugardjito, te Boekhorst & van Hooff, 1987; Knott, 1998, 1999). However, no effect of food availability on the sociability of an infant's mother was found. In other words, no significant difference in the time an infant's mother spent in association with conspecifics, between periods with a low or a high level of food availability, was found. This result implies that mothers with dependent offspring do not change their association patterns dependent on the food availability. Similar results were reported in previous studies performed in Suaq Balimbing and other study areas (van Schaik, 1999; Utami, 2000; Harrison et al., 2010). The absence of effects of food availability on association patterns can be explained by the exceptional high level of food availability in Suaq Balimbing, due to the unusual high habitat productivity and relatively constant production of the peat swamp forest (van Schaik, 1999; Delgado & van Schaik, 2000; Fragaszy & Perry, 2008). In most forests where orangutans are habituated, orangutans are more sociable during periods with a high level of food availability since food competition decreases and hereby the energetic constraints linked to the formation of associations are limited (Delgado & van Schaik, 2000; Fragaszy & Perry, 2008). However, even in periods with a low level of food availability in Suaq Balimbing, the food availability will still be relatively high compared to most other forests where orangutans are habituated. Therefore, at Suaq Balimbing, irrespective of food availability, associations will be formed.

Family size and composition

Secondly, I investigated whether size and/or composition of an infant's mother's family influences the sociability of an infant's mother. It was expected that there would be a preference of the infants' mothers to form associations with female related conspecifics (Singleton & van Schaik, 2002; Russon et al., 2009; Singleton et al., 2009; van Noordwijk et al., 2012). Following this, infants' mothers with a higher number of female related conspecifics were expected to have more opportunities for association and hereby be more sociable. However, no preference of the infants' mothers, to associate with female related conspecifics, was found. The absence of such kin-biased association patterns was recorded before in Suaq Balimbing and can be linked, similar as for the absence of any effect of food availability on the formation of associations, with the high habitat productivity and relatively constant production of the peat swamp forest in Suaq Balimbing (van Schaik, 1999; Fragaszy & Perry, 2008; Kunz, 2015). As mentioned before, contrary to most study areas where orangutans are habituated, food competition, and hereby the costs for associating, is relatively low in Suaq Balimbing (Knott, 1999; van Schaik, 1999). Since being social goes hand in hand with multiple potential benefits, the formation of associations, even with unrelated individuals, may overall be beneficial (van Schaik, 1999; Delgado & van Schaik, 2000). Hereby, the orangutans at Suag Balimbing have been reported to be more social and tolerant towards both related and non-related conspecifics, e.g. various mother-infant pairs have been recorded to form associations with unflanged males without any mating purpose (van Schaik, 2000). Such relationships have only been rarely documented in orangutans living in other habitats (Kunz, 2015). Since no kin-biased association patterns were recorded in this study, I neither expected to find an effect of the size nor composition of an infant's mother's family. In other words, based on the first finding of an absence of a preference for related association partners, I did not expect the number of female related individuals an infant's mother has to affect the sociability of a mother. Indeed, no relationship between the number of female related individuals and the sociability of an infant's mother was found.

To conclude, the absence for a relationship between the size and composition of an infant's family on the sociability of an infants' mother could be explained by the unusual high habitat productivity and relatively constant production of the peat swamp forest in Suaq Balimbing. This lead to an overall high sociability of the population of Suaq Balimbing (van Schaik *et al.*, 1999; van Schaik, 2000).

Sociodemographic factors

Age of the infant

Thirdly, I looked at the effect of an infant's age on the sociability of an infant's mother. Based on the differences in energetic requirements between infants of different age-classes, I expected that mothers would be more sociable when having either a very young (0-2 years of age) or already an older infant (>4 years of age). In contrast, when having a mid-aged infant (2-4 years of age), I expected the sociability of an infant's mother to be the lowest (van Schaik, 1999), because energetic constraints for mothers with mid-aged infants are higher than for mothers with either very young or older infants (van Schaik, 1999). In this study, I found that infants' mothers become increasingly sociable when their infants become more independent. However, no evidence was found for a higher sociability of mothers of very young or older infants compared to mothers with mid-aged infants. In contrast, an opposite trend was found, i.e. infants' mothers are more sociable when having a mid-aged infant than when having a very young or older infant.

Performing a cost-benefit analysis about the formation of associations, may explain the opposite effect found in this study. The benefits linked with the formation of associations are different for all age-sex classes of orangutans (Galdikas, 1995; Delgado & van Schaik, 2000). First, for adult females, the main direct benefits for the formation of associations is the protection for male sexual coercion (Rijksen, 1978; Fox, 1998; Delgado & van Schaik, 2000). By associating with flanged males, adult females will be protected against e.g. sexual harassment by unflanged males (Fox, 2002; Knott et al., 2010). However, evidence was found that mothers with either very young or mid-aged infants rarely experience male sexual coercion (Knott et al., 2010). Knott, Thompson, Stumpf & McIntyre (2010) studied mating frequencies between non-periovalutory, pregnant and periovulatory females. (Non-)periovulatory females are females who are (not) ready to conceive (Dictionary, 2008). In this study, almost no mating encounters were reported in non-periovualtory and pregnant females. In other words, sexual harassment of adult females seems to be very limited when infants are still fully dependent on the mother. Therefore, only mothers with older infants, and not with either very young or mid-aged infants, may benefit by associating as a protection against male sexual coercion. In terms of benefits associations impose for the infants, as mentioned before, by associating with conspecifics, a number of opportunities for social learning are created which ultimately may have a positive effect on the infant's cognitive development (van Schaik, 1999; van Schaik et al., 1999; Delgado & van Schaik, 2000). However, since very young infants spend most of their time in body contact with their mother, drinking mother milk and resting, very young infants are unlikely to pay much attention to the activities of association partners. Thus, it is questionable how much very young infants engage in social learning from association partners other than the mother. Therefore, very young infants are unlikely to benefit from the formation of associations. In contrast, mid-aged infants and older infants will benefit more from the formation of associations. Since most social learning occurs between the ages of 2 to 4 years of age, the benefits of socializing for mid-aged infants are expected to be higher than these of older infants. Therefore, the positive effects of associations on an individual's cognitive development may be highest for the mid-aged age-class, which explains the pattern of increased sociability of mothers of mid-aged infants I found in this study.

Sex of the infant

Fourthly, I investigated whether the sociability of an infant's mother changes dependent on the sex of her infant. As mentioned above, when an infant's mother is more sociable, more opportunities for social learning are created, which is expected to have a positive influence on an infant's cognitive performance (van Schaik, 1999; van Schaik et al., 1999; Delgado & van Schaik, 2000). Since having a smart, highly cognitive male infant is expected to be more beneficial for the maternal fitness (Trivers, 1972) and female infants are longer dependent on their mother than male infants (Miller, 2013), it was hypothesized that an infant's mother will be more sociable when raising a male infant than when raising a female infant. However, a reverse relationship was found, namely infants' mothers were significantly more sociable when having a female infant than when having a male infant. Thus, it seems more beneficial for the maternal (indirect) fitness to be more sociable when having a female infant instead of when having a male infant. This may be based on the difference in dispersion distance between both sexes when reaching independency. While female orangutans are philopatric and stay close to their natal area (van Noordwijk et al., 2009), male orangutans tend to move away from their natal area (van Noordwijk et al., 2009). This difference in dispersion distance may influence an infant's mother's motivation to form associations. By forming associations, mothers introduce their infants to the community of neighbouring orangutans. A socially well-integrated infant may later experience less difficulties when establishing an own home range in the neighbouring area. Since female orangutans stay around their natal area and male orangutans disperse (van Noordwijk *et al.*, 2009), it is more important for female than for male orangutans to be well integrated in the neighbouring population during infancy. This may explain the result of this study that an infant's mother is more sociable when having a female instead of a male infant. A similar, opposite relationship was found in a study performed in chimpanzees (Lonsdorf, Anderson *et al.*, 2014). In chimpanzees, females migrate to neighbouring communities while males stay in their natal group (Lonsdorf, Anderson *et al.*, 2014). Thus, in apes it seems as if the philopatric sex benefits from higher sociability during infancy.

Maternal dominance rank of the infant's mother

Fifthly, I investigated whether the dominance rank of an infant's mother had an effect on her sociability. Previous studies did not consider female dominance rank as a possible factor influencing the sociability of an infant's mother due to two main reasons. First, as a consequence of a rather solitary life style of orangutans (Wich *et al.*, 2004, 2010), it is difficult to assign a reliable dominance rank to each individual. Second, the presence of a clear dominance hierarchy in female orangutans has been doubted (Roman, 1977; Rijksen, 1978; Tuttle, 1986; Tuttle & Cortright, 1988; Kaplan & Rogers, 1994; Galdikas, 1995) (Appendix C: Absence of linear dominance hierarchy in orangutans). However, based on anecdotal data of females displacing other females, collected over different years in Suaq Balimbing, a crude two-step dominance rank of the different adult females could be calculated in this study.

Since in a variety of species, adult females with a higher dominance rank establish their home ranges in higher quality habitats than adult females with a lower dominance rank (e.g. chimpanzees: Williams et al., 2002; Murray, Eberley & Pusey, 2006; Thompson et al., 2007; Kahlenberg et al., 2008; red-winged blackbirds: Eckert & Weatherhead, 1987; northern spotted owl: Franklin et al., 2000). I hypothesized that a similar pattern would be present in adult female orangutans. Hence, adult females with a higher dominance rank will have more and better access to food resources (Williams et al., 2002; Murray, Eberley & Pusey, 2006; Thompson et al., 2007; Kahlenberg et al., 2008). Therefore, I expected that adult females with a higher dominance rank would have a higher sociability than adult females with a lower dominance rank. However, no effect of the dominance rank of an infant's mother on the sociability of an infant's mother was found, which is in line with previous studies performed in Suaq Balimbing (Manuel, Harrison & Thorpe, 2012). This result could also be a consequence of the crudeness with which dominance rank of the different adult females was assigned. Social relations might have changed over these couple of years and not all displacements between adult females reflect a difference in dominance rank. Instead, the observed pattern may be the result of a core area defence mechanism (Knott et al., 2008; Singleton et al., 2009). Each adult female has her own established stable home range with a core area (Singleton et al., 2009). The core area of an adult female is defined as the most intensively used part of an adult female's home range. Although home ranges of adult females often overlap with each other, overlap of core areas is rather limited. Since home ranges mainly exist to avoid food competition, each adult female is expected to stay loyal and be dominant in her own home range, especially in the core area of her home range (Singleton et al., 2009). Evidence has been found that adult females contest more for resources and win encounters more often when they are in their own core areas, undetermined the dominance rank of the visitor and resident orangutans (Knott et al., 2008; Singleton et al., 2009). The outcome of encounters between two adult females may be more dependent on the position where the encounter takes place than on their dominance rank. Based on the GPS data, collected every 30 minutes when following an orangutan, and the details known about the displacements, it could be determined whether the observed encounters were a result of a core area defence mechanism. However, this was beyond the scope of my project.

However, a core area defence mechanism may not be existent for the adult females in Suaq Balimbing due to the strong overlap of the adult females home ranges and their core areas. Even though, evidence for the existence of a core area defence mechanism in Suaq Balimbing was found in a previous study (Singleton, 2000). Therefore, it may have affect the results of this study.

To conclude, whether the absence of an effect of a mother's dominance rank on her sociability is a real result or a consequence of the crudeness in the determinations of the adult female dominance ranks is unknown. This hypothesis should be investigated again once more data on female dominance rank is available and hereby a more detailed dominance hierarchy can be established.

Maternal age of the infant's mother

Sixth, the effect of the maternal age on the sociability of an infant's mother was investigated. As suggested by the 'Terminal Investment Theory', I expected an increase in sociability of an infant's mother with increasing maternal age (e.g. Hirschfield & Tinkle, 1975; Morrow, Arnqvist & Pitnick, 2003; Fessler et al., 2005). However, no significant effect of the maternal age on the sociability of an infant's mother was found. Multiple factors might explain the absence of such a relationship. Firstly, in terms of the 'Terminal Investment Theory', studies in general provided mixed results. On the one hand, studies performed in long-lived birds and Barbary macaques, found positive evidence for the 'Terminal Investment Theory' (california gull: Pugesek, 1981; Pugesek, 1995; collared flycatcher: Part et al., 1992; Barbary macaque: Paul, Keuster & Podzuweit, 1993). On the other hand, a study performed on rhesus macaques and long-lived seabirds found negative evidence for the 'Terminal Investment Theory' (rhesus macaque: Berman, 1984; long-lived seabird: Sæther et al., 1993). Therefore, it might be that the 'Terminal Investment Theory' is not valid in orangutans. Secondly, conflicting results have been found about the average life span of wild orangutans. In a recent study of wild Sumatran orangutans, researchers estimated an average life span for orangutans of approximately 58 years (Wich et al., 2004). However, based on DNA analyses, which revealed the estimated number off infants an adult female gave already birth to, certain adult females in our research area are estimated to be notably older than the estimated average life span. For instance, Friska gave birth to at least 6 children and is estimated to be at least in her late sixties (Figure 22). Therefore, since there is still some uncertainty about the average life span of wild Sumatran orangutans, it is unclear from which age a higher investment in the infant, as a consequence of a decline in future survival chances, is expected. For this reason, it is difficult to test the 'Terminal Investment Theory'. Thirdly, the absence of differences found in sociability between infants' mothers with a different age, might be due to a confounding factor. For instance, the maternal style or personality of infants' mothers (Fairbanks, 1996). An infant's mother might be more or less sociable due to her maternal style or personality. However, there was no measure for maternal style and/or personality in this study. Therefore, the maternal style and/or personality could not be taken into account in the analyses. Fourthly, the exact maternal age of the infants' mothers was unknown. Therefore, the maternal age of the infants' mothers was estimated based on the (known) number of infants a mother already gave birth too. However, since male infants disperse from their natal area (van Noordwijk et al., 2009), it is assumed that these males will not be in the study area anymore. In other words, no DNA analyses could be done on these males. Hereby, a significant number of male infants a mother gave birth to may be missed based on DNA analyses. In this way, for some of the adult females, an underestimation of the number of infants an adult female gave already birth too is possibly made. Hereby, the age of an infant's mother will be underestimated. In addition, this is a less precise way compared to when the exact age of the infants' mothers would be known. Therefore, this could also have had an effect on the absence of a relationship found between the dominance rank and the sociability of a mother. To conclude, multiple factors can explain the absence of a relationship found between the maternal age and the sociability of an infant's mother.

Presence of an older sibling

Last, the effect of the presence of an older sibling on the sociability of an infant's mother was investigated. I expected that if an older sibling was still in permanent association with the mother-infant pair, the sociability of the mother would be higher. However, no support for this hypothesis was found.

The hypothesis was based on the idea that social play with conspecifics is highly important for older siblings (Groos, 1898; Fagen, 1981; Kunz, 2015). Due to an older sibling's need to associate for social play, the older sibling is expected to "pull" the mother-infant pair into association when the older sibling initiates an association. Therefore, an infant's mother was expected to be more sociable when an older sibling is still in permanent association. The lack of evidence found for a positive effect of the presence of an older sibling on an infant's mother sociability, may (partly) be due to the method used to define an older sibling in permanent association with a mother-infant pair. As described in the method section, an older sibling was considered to be in permanent association with a mother-infant pair when it was in more than 50% of the follow days, belonging to the same age-individual data point, for a full day in association with the mother-infant pair. This means that in less than 50% of the follow days, the older sibling could go on short-term excursions to associate with other conspecifics by himself/herself, and come back to the mother-infant pair later on the day. Therefore, the idea that whenever an older sibling initiates an association the mother-infant pair automatically will follow the older sibling was not supported by the data of this study. Instead, the mother does not seem to be bothered by the older sibling leaving the mother-infant pair for some time. It may be more beneficial for an infant's mother not to invest in constantly following the older sibling. Because of the high energetic constraints the mother already experiences through her newly born offspring, she may have to limit the energy spent on traveling (Gittlean & Thompson, 1988). Therefore, it would be interesting to investigate the same relationship when an older sibling is defined to be in permanent association with a mother-infant pair when the older sibling is in all follow days, belonging to the same ageindividual data point, a complete day in association with the mother-infant pair. In addition, it would also be interesting to determine from which age on older siblings start making these short-term excursions to associate with conspecifics, without the mother following the older sibling.

Research question II: Which factors influence an infant's exploratory tendency?

Influence of the mother

Sociability of the mother

I found evidence that infants of more sociable mothers have a higher exploratory tendency than infants of less sociable mothers. This result is in line with the previous reported result by Schuppli, Forss, Meulman, Atmoko *et al.* (2016). In humans, it has been widely reported that the higher the quality and quantity of social inputs an individual receives during childhood, the higher an individual's later cognitive development (Nelson *et al.*, 2007). Since the number of social inputs an infant orangutan receives mainly depends on the sociability of an infant's mother, this result implies that there is a high similarity between the development of cognition in humans and orangutans. Therefore, it is suggested that the evolutionary roots for the sensitivity for social inputs on an individual's cognitive performance may be inherited from our great ape ancestor (Schuppli, manuscript). To be able to state this hypothesis, it is important to investigate which other factors influence an infant's exploratory tendency and whether these factors can also be linked to the number of social inputs an individual receives during its development.

Restrictiveness of the mother

Besides the effect of the sociability of an infant's mother on the exploratory tendency of an infant, I investigated whether the restrictiveness of an infant's mother had an effect on the exploratory tendency of an infant. I expected that the higher the restrictiveness of an infant's mother, the lower the exploratory tendency of an infant. However, restrictiveness of an infant's mother did not have an effect on the exploratory tendency of an infant. The absence of a relationship may be explained by the lack of reliable data collected. Since this data does not belong to the standard data collection protocol, most observers did not consequently write down this behavior. Therefore, for future research in this direction, it would be necessary to have a separate sheet to write down in detail when, why and how restrictiveness events occur. In this way, more precise data analyses may be performed.

Activity of the mother

Average daily activity budget of the infants' mothers

I investigated whether the average daily activity budget of the infants' mothers, in this study, was comparable with the results found in the literature about the average daily activity budget of orangutans (MacKinnon, 1974; Rodman, 1979; Mitani, 1989; Knott, 1999). According to the literature, orangutans spend approximately 44% of their time resting, 41% of their time feeding, 13% of their time traveling and 3% of their time nest building and engaging in other activities, such as fighting, vocalizing, mating and socializing (MacKinnon, 1974; Rodman, 1979; Mitani, 1989; Knott, 1999). In this study, I found that an infant's mother approximately spends 16% of her time resting, 61% of her time feeding, 20% of her time traveling, and 3% of her time nest building and engaging in other activities such as fighting, vocalizing, mating and socializing. Thus, the average daily activity budget of the mothers differed clearly from what was found in literature. Multiple explanations can be given for the differences found between the average daily activity budget of orangutans in this study and the average daily activity budget reported in the literature.

First, the average daily activity budget of an orangutan, found in the literature, was calculated based on the results of three different studies performed in orangutans (MacKinnon, 1974; Rodman, 1979; Mitani, 1989; Knott, 1999). However, these three studies performed observations on different subspecies of orangutans. MacKinnon (1974) calculated the average activity budget based on data collected of both Sumatran and Bornean orangutans while in the studies performed by Rodman (1979) and Mitani (1989), an orangutan's average activity budget was calculated based on data collected only on Bornean orangutans. However, the different (sub)species of orangutans differ notably between each other in certain characteristics. Firstly, one of the main differences between Sumatran and Bornean orangutans, which is expected to influence an orangutan's average activity budget, is the productivity of their habitat (Morrogh-Bernard et al., 2009). Sumatran forests are assumed to be of better quality for orangutans than Bornean forests due to a higher and more stable food availability (Delgado & van Schaik, 2000; Fox et al., 2004; Marshall et al., 2009; van Schaik, Marshall & Wich, 2009). Consequently, Sumatran orangutans are thought to spend less time feeding and more time engaging in other activities compared to Bornean orangutans (van Schaik, Marshall & Wich, 2009). Therefore, it would be more conclusive to calculate average activity budgets or each species separately instead of making an average daily activity budget for both orangutan species together. Secondly, besides the variation in habitat productivity between Sumatran and Bornean forests, there is also local variation in orangutans' habitats (Morrogh-Bernard et al., 2009). Basically, there are two main types of habitat were orangutans are habituated, namely (1) non-masting forests, where the habitat is predominantly peat swamp forest and a regular supply of fruit is present and (2) masting forests, where the habitat is predominantly mixed-dipterocarp forest and an irregular supply of fruit is present only (Rodman & Mitani, 1987; Knott, 1999; Morrogh-Bernard et al., 2003, 2009). Orangutans are expected to allocate their time differently, depending in which habitat type they are living (Wich et al., 2008 Morrogh-Bernard et al., 2009). Recently, a comparison study of the average daily activity budgets of orangutans living in 9 different study areas, spread over the Sumatran and Bornean islands of Indonesia, was performed (Morrogh-Bernard et al., 2009). It was found that orangutans living in non-masting forests, or predominantly peat swamp forests, spend more than 50% of their time feeding while orangutans living in masting forests, or predominantly mixed-dipterocarp forests, spend less than 50% of their time feeding (Morrogh-Bernard et al., 2009). The differences in the average activity budgets, dependent on the habitat type orangutans are living in, is a consequence of their strategy they use for obtaining enough food (Wich et al., 2008; Morrogh-Bernard et al., 2009). There are two different strategies orangutans use, especially in periods with low food availability; namely (1) the 'search and find' strategy or (2) the 'sit and wait' strategy (Knott, 1998). When using the 'search and find' strategy, orangutans aim to maximize their energy intake by resting little and mainly feeding or traveling in search for the few fruit species which are fruiting. This strategy is mainly used by orangutans in nonmasting, peat swamp forests. With the 'sit and wait' strategy, orangutans aim to minimize their energy expenditure by spending long periods of time resting and relatively short periods of their time traveling. This strategy is mainly used by orangutans living in masting, mixed-dipterocarp forests (Knott, 1998; van Noordwijk et al., 2013). Based on this, I expected that the daily activity budget would not only differ between the Sumatran and Bornean orangutans, but also between individuals living in masting or non-masting forests. Since Suaq Balimbing is a non-masting, peat swamp forest (Knott, 1999), it explains why the time an orangutan spends on feeding and traveling is higher, and the time an orangutan spends on resting is lower, relatively to what was reported as an overall average across populations in the literature by Knott (1999).

Second, besides the inter-population variation, due to habitat productivity (van Schaik, Marshall & Wich, 2009) and forest type (Morrogh-Bernard *et al.*, 2009), influencing the daily activity budget of orangutans, individual variation was also not taken into account by Knott (1999) (Morrogh-Bernard *et al.*, 2009). When Knott (1999) determined the average activity budget of orangutans, all age- and sex-

classes were included in the analysis: unflanged males, non-sexually active females, sexually (non-) active females and flanged males (Knott, 1999; Morrogh-Bernard *et al.*, 2009). However, this study only calculated the activity budget of sexually active females, the infants' mothers. Previous research found clear differences between individuals of different age- and sex-classes. Non-sexually active females are known to feed the longest and rest the least, flanged males rest the longest and feed/travel the least and unflanged males travel the longest (Morrogh-Bernard *et al.*, 2009). Therefore, comparing the average activity budget of mothers of our study with the average activity budget reported by Knott (1999), it is not entirely valid (Morrogh-Bernard *et al.*, 2009). Instead, the activity budgets of the mothers from this study should be compared with the average activity budget of the sexually active females at other populations. When I calculated the average activity budget of the sexually active females only, over the 9 different research areas, I found that they spend 47.5% of their time feeding, 37% of their time resting, 14% of their time traveling and 1.5% of their time engaging in other activities (Morrogh-Bernard *et al.*, 2009). Comparing my results with this data, a less pronounced difference to what was found in the literature was found.

To conclude, it is important to take (1) inter-population variation, as a consequence of habitat type and forest productivity, and (2) individual variation, such as the age-sex class of the orangutans, into account when calculating an orangutan's average activity budget. Therefore, I calculated the average activity budget of the sexually active females over the 5 different study areas located in a peat-swamp forest. I found that they spend 55.5% of their time feeding, 27.9% of their time resting, 14.5% of their time traveling and 2.1% of their time engaging in other activities (Morrogh-Bernard *et al.*, 2009). If the comparison between the average daily activity budget of the infant's mothers in this study and the average daily activity budget of the sexually active females living in peat swamp forests was made, a less pronounced difference is found. The remaining variation present may be a consequence of the exceptional high level of food availability in Suaq Balimbing (van Schaik, 1999; Delgado & van Schaik, 2000; Fragaszy & Perry, 2008).

The effect of the activity of an infant's mother on an infant's exploratory tendency

Besides the sociability and the restrictiveness of an infant's mother, I also investigated the effect of an infant's mother's activity on an infant's exploratory tendency. Three different hypotheses about the effect of the activity of an infant's mother on an infant's exploratory tendency were made. First, I expected that infants will perform most object manipulation behavior while their mother is feeding, nesting or exploring (Jaeggi *et al.*, 2010; Kunz, 2015). Second, based on the first hypothesis, I expected that an infant's exploratory tendency would be influenced by the daily activity budget of an infant's mother (Jaeggi *et al.*, 2010; Kunz, 2015). The more time an infant's mother spends on traveling and/or resting, and hereby the less time an infant's mother spends on feeding, nesting and/or exploring, the lower an infant's exploratory tendency was expected to be (van Noordwijk & van Schaik, 2005; Jaeggi *et al.*, 2010; Kunz, 2015). Third, I expected that the level of exploratory tendency of the mother would have a positive effect on the exploratory tendency of the infant (Lonsdorf, 2006).

Activity of an infant's mother while an infant is performing any kind of object manipulation behavior

First, I expected that an infant would perform most object manipulation behaviors while an infant's mother was feeding, nesting or exploring herself, less when an infant's mother was resting and the least when an infant's mother was traveling (Jaeggi *et al.*, 2010; Kunz, 2015). Evidence for this hypothesis was found for all the age-individual data points separately. Thus, as expected feeding, nesting and exploring have a positive influence on the exploratory tendency of an infant, traveling has

a negative influence on the exploratory tendency of an infant and resting has a neutral influence on the exploratory tendency of an infant.

Daily activity budget of an infant's mother

Second, based on the finding that infants perform most object manipulation behavior during the time an infant's mother is feeding, nesting or exploring, less during the time an infant's mother is resting and the least during the time an infant's mother is traveling, I expected that an infant's exploratory tendency would be influenced by the daily activity budget of an infant's mother (Jaeggi *et al.*, 2010; Kunz, 2015). Concrete, the more time an infant's mother spends on negatively-influencing activities, and hereby the less time an infant's mother spends on positively- or neutrally-influencing activities, the lower an infant's exploratory tendency was expected to be (van Noordwijk & van Schaik, 2005; Jaeggi *et al.*, 2010; Kunz, 2015). However, the opposite effect of the effect of positively- and negatively-influencing activities on the exploratory tendency of an infant was found. Only resting had, as expected, a neutral influence on the exploratory tendency of an infant engaged the most in the performing of object manipulation behaviors when a mother was performing positively-influencing behaviors.

Exploratory tendency of an infant's mother

Third, I expected that the exploratory tendency of the mother would be correlated with the exploratory tendency of the infant (Lonsdorf, 2006). However, no effect of a mother's exploratory tendency on an infant's exploratory tendency was found. This result implies that it is more beneficial for the infants' exploratory tendencies to receive inputs of a larger number of different role models than to receive more varied inputs of their strongest role model, their mother.

However, to be able to state this argument, a higher number of reliable data needs to be collected. Only one, highly trained observer (Caroline Schuppli) collected consequently, during certain time periods, the explorative behaviors performed by an infant's mother while observing infants. Thus, only for a limited number of age-individual data points, a reliable exploration level of an infant's mother could be calculated. In addition, despite being a highly trained observer, it may be possible that some of the exploratory behaviors, performed by an infant's mother, were missed since the observer was supposed to pay close attention to an infant's activity. If more exploratory behaviors are missed from mothers of a certain age-class, it is possible that the exploratory tendency data of the mothers was biased. Therefore, it would be interesting to investigate whether there is bias in the collected exploratory behaviors and whether the same results are obtained with a larger data set.

Influence of the infant

Age of the infant

I expected that the age of an infant would be one of the most important characteristics affecting an infant's exploratory tendency. The exploratory tendency of an infant was expected to be the highest between the ages of one to four years, followed by a quite abrupt ceasing of an infant's exploratory tendency around four to five years of age (van Adrichem *et al.*, 2006; Kunz, 2015). Indeed, a similar relationship between exploratory tendency and age was found in this study. The exploratory tendency of infants was the highest between the ages of two to four years followed by a quite abrupt ceasing of their exploratory tendency around four years of age.

Sex of the infant

I expected that female infants have a higher exploratory tendency than male infants. However, the data did not supported this hypothesis. I argued that female infants were expected to engage more in object manipulation behavior than male infants due to their difference in future interests (Galdikas, 1985; Gittlean & Thompson, 1988). However, one could also argue that "male infants are expected to engage more in object manipulation behavior than female infants". Firstly, since adult males move away from their natal area, in contrast with adult females who stay close to their natal area, adult males will have to able to cope with and survive in a new environment (Rodman, 1973; MacKinnon, 1974; Rijksen, 1978; Galdikas, 1985, 1988; Mitani, 1989; van Schaik & van Hoof, 1996; Utami et al., 1997; Knott, 1998, 1999; van Noordwijk et al., 2002, 2012; Singleton & van Schaik, 2002; Setia et al., 2009; Morrogh-Bernard et al., 2011; Arora et al., 2012). By engaging more in any kind of object manipulation behavior during infancy, an adult male will be able to use these previously gained experiences and transfer them to new situations, e.g. new food resources (Nisbett, 2009; van Schaik & Burkart, 2011). Therefore, males may have a higher incentive to be more exploratory and thus inventive than females. Secondly, as reported before, male infants have been found to stay in close association with their mother for a shorter time period than female infants (Miller, 2013). Therefore, male infants have less time available than female infants to learn the same number of essential cognitive skills, to be able to survive independently. However, this second line of argumentation may not be valid for Sumatran orangutans at Suaq Balimbing since so far, no study investigated whether there is a difference in the length of dependency between male and female orangutans at Suaq Balimbing. Thus, it may be that both sexes have a similarly high motivation, even though most likely for different underlying reasons, to engage in object manipulation behavior. This would explain the absence of any sex differences found.

Influence by external factors

Environmental factor: food availability

Besides the characteristics of the mother and the infant itself, I expected that an increased level of food availability would have a positive effect on an infant's exploratory tendency. Food availability was expected to have both an indirect and a direct influence on an infant's exploratory tendency. As previously mentioned, I did not find evidence for an indirect effect of food availability on an infant's exploratory tendency. For the direct effect of food availability on an infant's exploratory tendency, I expected that during periods of a high level of food availability, the exploratory tendency of infants would increase (van Noordwijk & van Schaik, 2005; van Noordwijk et al., 2013; Kunz, 2015). However, no effect of food availability on an infant's exploratory tendency was found. A similar explanation, as given for the absence of an indirect effect of food availability on the exploratory tendency of an infant, may be given for the absence of a direct effect of food availability on the exploratory tendency of an infant. Due to the unusual high habitat productivity and relatively constant production of the peat swamp forest, there is an exceptional high level of food availability in Suaq Balimbing (van Schaik, 1999; Delgado & van Schaik, 2000; Fragaszy & Perry, 2008). Hereby, even in periods of lower food availability, energetic constraints are limited and the infants may still have enough time and energy available to perform any kind of object manipulation behaviors. However, the absence of an effect found in Suag Balimbing does not exclude that effects may be present in other study areas with an overall lower level of food availability.

Presence of an older sibling

I expected that infants living together with an older sibling would have a higher exploratory tendency than infants living without an older sibling (Jolly, 1985; Barr & Hayne, 2003). In other words, an older sibling was expected to stimulate an infant to perform more object manipulation behaviors, such as try-feeding and exploration. I found strong support for this hypothesis in this study such as that the presence of an older sibling had a significant positive effect on the immediate exploratory tendency of an infant. However, it may be more interesting to investigate the developmental effect of the presence of an older sibling on an individual's later cognitive performance during adulthood. This can only be investigated when both the cognitive performance of a number of adolescents as well as the total period the adolescents spent in association with both their mother and an older sibling is known. I expect that the longer an adolescent spent in close association with both their mother as well as an older sibling during infancy, the higher an adolescent's cognitive performance will be.

Percentage association partners related with the infant

Last, I expected that infants have a higher exploratory tendency when they spend more time in association with related than with unrelated conspecifics. However, no evidence for this hypothesis was found. This result suggests that at Suaq Balimbing the same social learning benefits arise for an infant, independent whether they are together with related or unrelated with the association partners. Besides the relatedness of the association partners, it would be also interesting to investigate whether the identity (mother-infant pairs, juveniles, adolescent, unflanged males, flanged males) of the association partners have differing effects on the exploratory tendency of an infant.

Extension of research question II: Which factors influence a juvenile's exploratory tendency?

I also performed a small side research project where I investigated whether the same factors, which were hypothesized to influence an infant's exploratory tendency, also influenced a juvenile's exploratory tendency. No significant results were found. However, the absence of statistically significant results was probably due to the small sample size. Therefore, it was decided to perform visual inspection of the relationships. Based on the visual inspection, I found that food availability did not seem to have an effect on exploratory tendency in juveniles, just as it has been found in infants. Most likely, the same arguments are valid to explain the absence of a positive effect of food availability on a juvenile's exploratory tendency. For both, the sociability of a juvenile's mother during infancy and the immediate sociability of a juvenile, a positive effect seems to be present on the exploratory tendency, a very similar pattern to what I had found for infants. Thus, sociability has both a positive immediate and developmental effect on the exploratory tendency of a juvenile. Further, it would be interesting to perform a study with a stronger focus on juveniles and see whether the outcomes are comparable between infant and juvenile Sumatran orangutans. For the performance of such a study, more juvenile data would be needed.

Conclusion: from Sumatran orangutans to humans

The aim of this study was to shed light on the evolutionary roots of cognitive development in humans. In humans, it is known that, in addition to genetic predispositions, developmental inputs determine an individual's cognitive development (Plomin & Spinath, 2004). Individuals, who receive a higher quantity and quality of social inputs during childhood, will have a higher cognitive performance (Nelson *et al.*, 2007). Even small differences in the frequency and quality of social inputs, such as the number of social interactions, have shown to affect an individual's cognitive development (Maggi *et al.*, 2010). Therefore, social inputs are considered the main factor influencing an individual's cognitive development (Maggi *et al.*, 2010).

Multiple studies have shown that cognition is not uniquely present in humans (e.g. pigeons: Blough, 1989; cattle: Fernandes et al., 2015; horses: Schuetz, Framet & Kreuger, 2016). Contrary, different animal species have been reported to have a certain level of cognition (e.g. pigeons: Blough, 1989; cattle: Fernandes et al., 2015; horses: Schuetz, Framet & Kreuger, 2016). Assuming evolutionary continuity, it is expected that the main factor that influences the development of cognition in humans, the sensitivity for social inputs, can also be found in humans' closest living relatives, the great apes (Schuppli, manuscript). Therefore, I focused on determining the role social inputs have on the development of cognition in Sumatran orangutans (Pongo abelii). The effect of different factors on the exploratory tendency, a behavioral measure of cognitive performance, of wild infant Sumatran orangutans was analysed. Most importantly, evidence was found that the immediate sociability of an infant's mother had a significant effect on an infant's exploratory tendency. Thus, as for humans, an increased number of social interactions had a positive effect on an infant's exploratory tendency. In addition, also evidence was found that the activity of an infant's mother, the age of an infant and the presence of an older sibling had an effect on an infant's exploratory tendency. The effect of these factors could also be linked to the quantity and quality of social inputs an infant Sumatran orangutan received. Thus, the more social inputs an infant Sumatran orangutan received, the higher its exploratory tendency.

Due to the high similarity between humans and Sumatran orangutans, for the sensitivity of social inputs on an individual's cognitive development, it can be concluded that human sensitivity to opportunities for social learning, which provided a critical foundation for the evolution of the unique skill-transmission system we see in humans, was inherited from our great ape ancestors.

Future research questions

Factors influencing an infant's mother's sociability

I investigated the effect of different factors on an infant's mother's sociability. However, I did not include the possibility of a genetic effect influencing the sociability of a mother: there may be an innate predisposition as a mother to be less or more sociable. To be able to investigate this genetic effect, cortisol values have to be measured which was beyond the scope of my project. However, I would be interested to investigate this in a following research project.

Innate predisposition to be less or more sociable: measuring cortisol values

In a comparison study performed between Bornean and Sumatran orangutans in captivity, it was found that Bornean orangutans tend to have higher cortisol values than Sumatran orangutans when housed in groups. Cortisol is a well-known biomarker used to measure psychological stress (Elder & Menzel, 2002; Lee et al., 2012). When the same individuals were housed alone, no significant differences in cortisol values, between the Sumatran and Bornean orangutans, were found. Basically, it was found that Bornean orangutans, independent of the food availability (since in captive situations no food competition is expected), will have more stress when being in association. Therefore, Bornean orangutans have an innate predisposition to be less sociable than Sumatran orangutans (Weingrill et al., 2011; Amrein et al., 2014). Although no comparison between Sumatran and Bornean orangutans is made in this study, I am interested to investigate whether similar individual variation in innate sociability between orangutans of the same population exists. By measuring the level of cortisol of the different infants' mothers in Suaq Balimbing, it could be determined whether there is variation in how stressful associations are experienced by each infant's mother. Since the orangutan population in Suaq Balimbing seems to be rarely suffering of food competition, due to the unusual high habitat productivity and relatively constant production of the peat swamp forest (van Schaik, 1999; Delgado & van Schaik, 2000; Fragaszy & Perry, 2008), they would be the ideal wild population to investigate whether intra-population variation is existing in the innate predisposition to be less or more social.

Factors influencing an infant's exploratory tendency

I also investigated the effect of different factors on the infants' exploratory tendencies. However, I was not able to investigate the effect of all factors that could be explored. Following are three factors, (1) the personality of both the infants as well their mothers, (2) the identity of association partners and the motivation for the formation of associations and (3) the genetic predisposition to have a higher exploratory tendency, which may have an important effect on an infant's exploratory tendency. Due to time limitations, I was not able to collect all data and include these factors in my analyses. However, I would be very interested to investigate these factors in a future research project.

Personality

Personality may very well influence an infant's exploratory tendency (Carere & Locurto, 2011). I hereby expect that the personality of the mother as well as the personality of the infant itself may be an important source of variation causing differences in exploratory tendencies between infants (Carere & Locurto, 2011). Personality is defined as consistent inter-individual differences in correlated behavior traits, which are stable over time and/or across different situations and/or contexts (Gosling, 2001; Gladden, Figueredo & Jacobs, 2009). Many species show a great level of individual variation in personality within populations (Réale *et al.*, 2007; Smith & Blumstein, 2013). This can be theoretically presented on e.g. a Proactive-Reactive axis (Wilson *et al.*, 1994; Koolhaas *et al.*, 1999). Proactive

individuals are considered more aggressive, active, exploratory and bold while reactive individuals are considered to be more peaceful, reactive, avoidant and shy (Koolhaas *et al.*, 1999; Groothuis & Carere, 2005). First, concerning an infant's personality, some studies showed that reactive individuals learn slower than proactive individuals as a consequence of reactive individuals' avoidance behavior towards novel stimuli (Sih *et al.*, 2004). Therefore, I expect that proactive individuals will have a higher exploratory tendency than reactive individuals. Second, I also expect that the personality of an infant's mother may influence indirectly an infant's exploratory tendency. Since the activity of an infant's mother is expected to influence the activity of an infant, proactive mothers are expected to have a more positive influence on the exploratory tendency of an infant than reactive individuals (Koolhuis *et al.*, 1999; Groothuis & Carere, 2005). For the restrictiveness of an infant's mother, reactive individuals are expected to be more anxious and become more restrictive towards their infants than proactive individuals (Maner *et al.*, 2008; Meyer & Hamel, 2014). Therefore, I hypothesize that infants of proactive mothers will have a higher exploratory tendency than infants of reactive mothers.

Unfortunately, because of the limited time available and the complexity of personality experiments in the wild, I was not able to consider personality in my study. However, the idea on how to perform a personality experiment and how to determine the personalities of wild Sumatran orangutans was thought about and previously tested (Forss *et al.*, 2015). Following are briefly some ideas given on how to perform the personality experiment.

Personality experiment in a population of wild Sumatran orangutans

The best way to measure personality is by looking at an individual's reaction to a novelty, such as a novel object or environment (Carter et al., 2012). Individuals, which are first in line to explore a novel object or environment, are considered proactive and vice versa for the individuals who are the last to investigate a novel object or environment (Wilson et al., 1994). To measure personality in wild orangutans, novel food items can be placed in their environment, such as durian or bananas. It is important that the focal sees the observers manipulating the novel object since previous tests, performed by Forss (2015), have shown that there is a higher chance that the focal will approach the novel object if the focal saw the observer manipulating the object first (Forss et al., 2015). Once the novel object is placed in the focal's environment and noticed by the focal, the observer can measure the focal's latency to approach or touch the novel object. Focals with the shortest latency will be considered the most proactive, whereas focals with the longest latency are considered the most reactive. However, based on previous observations not all focals may participate in exploring the novel object (Schuppli, pilot experiment 2014; Forss et al., 2015). In addition, it may take a number of trials before a focal is exploring the novel object (Schuppli, pilot experiment 2014; Forss et al., 2015). Therefore, it would be conclusive to also look at other measure, such as observing (1) if a focal is coming closer or going away from the novel object (approach-retreat) and (2) whether or not a focal is looking to the novel object.

Identity of association partners and motivation for association

I determined the sociability of an infant's mother based on the proportion of time an infant's mother spent in association with conspecifics. However, I did neither take into account the identity of the association partners nor the motivation for the formation of associations. Although, these are factors which likely determine the quality of an association and thus may have important effects on the exploratory tendency of an infant First, although different benefits and motivations are associated with the formation of associations dependent on the age-sex class of the association partners, I did not take into account with whom a mother-infant pair formed associations (Table 12). Depending on the benefits linked with and the motivation of an individual to socialize, associations are likely to differ in their quality. So far, orangutans have been reported to form three types of associations: (1) travel bands, (2) temporary associations and (3) consorts (Utami *et al.*, 1997). Firstly, during a travel band, individuals feed together within a food patch, leave and stay together for a certain time period, and sometimes even visit the next food patch together. Secondly, during a temporary association, individuals feed together within a food patch and leave separately (Sugardjito, te Boekhorst & van Hooff., 1987). Lastly, during consorts, a receptive female and an adult male (flanged or unflanged) travel together for a certain time period (Schurmann & van Hooff, 1986; Utami *et al.*, 1997). The motivation for an individual to form an association can partly be deduced by analysing which type of association took place. Therefore, the type of association is a first important distinction, which I should make, when analysing the different associations.

orangutans.		
Age-sex classes of orangutans	Main benefits for the formation of associations	

Table 12: The main benefits linked to the formation of associations for the different age-sex classes of

Age-sex classes of orangutans	Main benefits for the formation of associations
Infants	Social learning (i.e. peering)
Juveniles & adolescents	Social learning (i.e. peering)
	Social play
Adult females	Protection against male sexual coercion
Adult males	Opportunities for mating

Second, I would be interested in performing a detailed analysis about the specific behaviors and activities taking place during an association (Table 13). As for the type of association, each of these behaviors and activities may (partly) reflect the motivation for an individual to associate and thus the quality of the association. In addition, different activities may stimulate infants to varying extents. Therefore, I expect that these behaviors and activities may influence an infant's exploratory tendency differently. This can be best illustrated by some examples of behavioral observations in the field. For instance, when two mother-infant pairs associate with each other, the infants often engage in social play. When social play occurs, this association is expected to have a positive influence on the cognitive development of an infant. Since socio-cognitive abilities are needed during play to be able to adjust to the play partner and the environmental circumstances, social play is expected to develop such sociocognitive skills (Kunz, 2015). Another example, when a mother-infant pair is being chased by an unflanged male and the mother keeps on running away from this unflanged male, it is not expected that this association will positively influence an infant's exploratory tendency. In contrast, since the mother is constantly traveling and the only thing the infant is focused on is trying to keep up with its mother, the infant will have (almost) no time to perform any kind of object manipulation behavior. Therefore, dependent on the type of association and specific activities and behaviors, which take place during an association, an infant's exploratory tendency is expected to be positively, negatively or neutrally affected by the association. To conclude, not all associations will be equally beneficial for an infant's exploratory tendency.

Table 13: A list of possible behaviors and activities that may take place during associations. These behaviors and activities may reflect the motivation of an individual to associate.

List of factors which may have an effect on the exploratory tendency level of an infant

- 1. Agonistic interactions
- 2. Social play
- 3. Social learning (i.e. peering and/or begging)
- 4. (Forced) copulations
- 5. Feeding tolerance
- 6. Food sharing/ Co-feeding

Last, it may be important to determine which association partners performed these specific behaviors and between which association partners social interactions took place, e.g. between a mother and her infant, between a mother and the association partner etc. Possibly, whether an infant was directly or indirectly involved in a certain interaction, will also have an influence an infant's exploratory tendency.

Genetic predispositions to be more exploratory

In a study performed in humans, it was shown that genetic influence accounts for approximately 50% of the variance between individuals' cognitive performances (Plomin & Spinath, 2004). However, developmental inputs are expected to be even more important in the development of an individual's cognition (Plomin & Spinath, 2004). For orangutans, the importance of genetic influence on an infant's exploratory tendency is vague. Therefore, it would be interesting to determine whether there is a heritable innate predisposition of exploratory tendency in Sumatran orangutans.

Different measure to include the environmental factor food availability

In my study, no information was included about the infants' mothers' home ranges, more specifically about the quality or productivity of their home ranges. Only the monthly food availability (FAI) was taken into account as a measurement to represent the changes in food availability in the study area. However, it would be interesting to have more detailed information about the quality and food availability of each infant's mother home range separately. Therefore, in a future research project, I would like to determine the home range sizes, the position of the home ranges and/or travel distances of the infants' mothers, to see whether these factors can be linked with the quality and food availability of the infants' mothers' home ranges. The data on these factors is already available.

Measurement techniques: home range size, position and travel distances

I could use three possible techniques to assess the quality and food availability of an individual's home range.

A first possible technique to assess the quality and food availability of an individual's home range is via determining an individual's home rang size. It is expected that the larger an individual's home range is, the lower the quality and food availability of the home range will be (van Schaik, Marshall & Wich, 2009; Singleton *et al.*, 2009). However, due to very large home ranges of orangutans and a rather small study area in Suaq Balimbing, there may be a bias when determining individuals' home range sizes (Singleton *et al.*, 2009; Utami *et al.*, 2009).

A second possible technique to assess the quality and food availability of an individual's home range is via determining the position of an individual's home range in the study area. As mentioned before,

every month the phenology of the study area is determined. Concrete, approximately 1500 trees are checked for the presence and abundance of flowers, fruit and young leaves. In this way, the temporal (monthly) variation in food availability and forest productivity is assessed. The study area is divided into two phenology plots, one going from west to east, and one going from south to north. In this way, gradients of food availability throughout the study area can be determined. By assessing which individuals live more to e.g. the north or the south of the study area, which can easily be done through the collected GPS data, an estimation can be made about the quality and food availability of an individual's home range (Figure 23).

A third possible technique to assess the quality and food availability of an individual's home range is via daily travel distances of individuals (van Schaik, Marshall & Wich, 2009). Dependent on which habitat type orangutans are habituated in, they use a different tactic to cope with lower food availability (Knott, 1998). Since Suaq Balimbing is a peat swamp forest where orangutans aim to maximize their energy intake by resting little and increase feeding or traveling in search for the fruit species which are fruiting (Knott, 1998), I expect that in periods with lower fruit availability, the travel distances will be longer compared to periods with higher fruit availability. Since orangutans are usually followed from their morning until their evening nest, and observers collect every 30-minutes GPS data about the individual's daily traveling, travel distances can be calculated for each follow day for each individual. Therefore, I expect that individuals, who overall have shorter travel distances, will have a better quality home range with higher fruit availability. To conclude, all three techniques could be used to assess the quality and food availability of an individual's home range.



Figure 23: The position of individuals' home ranges in the study area of Suaq Balimbing, as a measurement technique to determine the quality of individuals' home ranges.

Conclusion for future research questions

In my study, I investigated different factors, which were expected to influence (1) an infant's mother's sociability and (2) an infant's exploratory tendency. However, there are still a number of other factors, which may influence these two characteristics.

First, the innate predisposition of an infant's mother to be more or less sociable may have an important effect on an infant's mother's sociability. Second, the personality of both the infants as well their mothers, the identity of association partners and the motivation for the formation of associations and the genetic predisposition to have a higher exploratory tendency may have an important effect on an infant's exploratory tendency.

In addition, I also summarized three techniques that could be used to determine the quality of an individual's home range. By making use of these techniques, more detailed information about the quality of an infant's mother home range could be determined. Also, the effect of the quality of an infant's mother's home range on an infant's mother's sociability and an infant's exploratory tendency could be investigated.

However, as a consequence of time limitations, these factors and techniques could not be included in my study. Therefore, I would be interested to investigate these factors in a following up research project.

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Appendix Appendix A: Tree phenology monitoring protocol.

Tree phenology monitoring

To assess temporal variation in food availability and forest productivity in a study site c. 1500 trees in a 2ha phenology plot are checked monthly for the presence and abundance of flowers, fruit and young leaves. In Tuanan, for example, the plot is situated along two transects in the center of the study area. ALL trees within 5 m on either side of the transects and with a diameter at breast height (dbh) of \geq 10 cm have been labeled with a number, measured and identified.

Phenology Crop Sizes

Young leaves (daun mudah)

Estimate the percentage of the leaves on a tree that are new in that month. Try to score new leaves only once! (Thus check current crop against that of last month).

0% = 0

0 < YL < 5% = 2.5 5 < YL < 25% = 15 25 < YL < 50% = 37.5 50 < YL < 75% = 62.5 75 < YL < 100% = 87.5



Flowers (bunga)

Estimate the number of flowers in the tree. This scale is deliberately crude because numbers can change from day to day, and once-a-month monitoring cannot be more precise.

None (tidak ada) = 0 Few (sedikit) = 1 Medium (sedang) = 2 A lot (banyak) = 3



Fruits (buah) Estimate the number of fruits in a tree and indicate ripeness: M = ripe (masak); m = unripe (mentah)

0 = 0 1 - 10 = 1+ 10 - 100 = 10+ 100 - 1000 = 100+ 1000 - 10000 = 1000+ Etc...

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Appendix B: Family trees of the orangutans of Suaq Balimbing.



Haplotype 2



Haplotype 2







These two figures explain why no female dominance linear hierarchy can be existent in a population of wild orangutans. This is a hypothetical example of 4 adult females with each an established home range in an area in Suaq Balimbing. As seen in the first figure, the home ranges of the 4 adult females partly overlap with each other. When home ranges overlap, encounters will occur. Hereby, each adult female "knows" with whom their home range overlaps and their dominance rank relative to the other adult females. However, as seen in the second figure, the home ranges of these 4 adult females overlap with more adult females. For instance, the home range of adult female 1 also overlaps with the home range of adult females 2, 3 and 4. In other words, adult females 2,3 and 4 will never encounter with adult female 5, and hereby no dominance relationship is existent between these individuals. The same is true for adult female 6. Therefore, since orangutans do not live in social groups, no linear dominance rank can be existing in a population of wild orangutans.