

Skill learning in immature Sumatran orangutans
(*Pongo abelii*)

When and how do immature orangutans reach adult levels of skill competence?



Master's Thesis

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Abstract

Sumatran orangutans (*Pongo abelii*) show the latest age of first reproduction and longest nutritional dependence of any nonhuman primate. They also live in a highly skill intense foraging niche including extractive foraging and tool use. The aim of this study was to investigate whether skill acquisition (as predicted under the skill learning hypothesis) or energetic constraints (as predicted by the energetic brain hypothesis) determine the age of first reproduction in Sumatran orangutans. I further looked at which learning mechanisms are involved in the process of skill acquisition. I collected data on different measures of ecological competence of immature Sumatran orangutans at Suaq Balimbing, Indonesia and compared my results with data on Bornean orangutans previously collected by other students at the Tuanan research station. I found that immature Sumatran orangutans reach adult-like levels of ecological competence long before age of first reproduction. It is therefore very likely that rather than skill acquisition, energetic constraints act as limiting factor on their development.

In terms of learning mechanisms, my results suggest that immature orangutans learn most foraging skills socially from their mothers but also show a high tendency to explore object in their environment independently from their mothers. Furthermore, I found evidence that social learning continues after the age of weaning, mainly in the form of horizontal transmission between immatures and adult animals other than the mother as well as among peers. The comparison of the two orangutan populations showed that the skill learning trajectories are very similar. However, immatures at Suaq Balimbing seem to have more opportunities for social learning and I found some preliminary evidence that this might have resulted in distinct exploratory tendencies among the two populations. Consequently, consistent with the cultural intelligence hypothesis my findings have provided evidence that opportunities for social learning might be a determining factor for the intelligence of a species. Social transmission of knowledge and skills or in other words culture might have be an important ingredient that made us humans smart.

1 Introduction

1.1 Research background and objective

One characteristic that we humans share with our closest relatives the great apes is a remarkably slow life history in form of a long life span, slow paced development and expanded period of immaturity. In most primates including humans, the developmental period (birth until age at first reproduction) takes around a quarter of the total life span (Jerison, 1973; Gurven et al., 2006; Jones and Marlowe, 2002). A further characteristic of humans is their unmatched brain size and intelligence expressed in an immense behavioral repertoire. Like any other mammal, humans acquire most skills and knowledge for survival during immaturity. In humans this developmental period is longer than in any other extant mammal. After weaning around the age of three it takes at least 14 more years until modern hunter-gatherers start to reproduce at around the age of 17-20 (Jones and Marlowe, 2002; Gurven et al., 2006). The reason for the slow development and delayed adulthood of humans has not yet been resolved. Previous studies could show that a slow life history for most species correlates with the development of larger brains (Barrickman et al., 2008; Deaner et al., 2003; Allman and Hasenstaub, 1999). Larger brains are associated with higher cognitive abilities and therefore better survival prospect but they also impose higher developmental costs (Isler and van Schaik, 2009; Barrickman et al., 2008; Allman and Hasenstaub, 1999).

Among many others, the skill learning hypothesis and the expensive brain hypothesis are two main life history hypotheses to explain the length of the juvenile period of a given species and its correlation with brain size. According to the skill learning hypothesis large brained animals mature slowly because they need time to learn skills that are essential for adult survival and reproduction. The age of first reproduction is consequently set by the number and complexity of the skills a species has to learn (Ross and Jones, 1999; Janson and van Schaik, 1993). Contrarily, the expensive brain hypothesis suggests that the pace of maturation is primarily determined by energetic constraints. Accordingly, high energetic investment into brain growth of large brained species results in a delay in the physical development of the body (Isler and van Schaik, 2009).

Studies on different primate species provided mixed evidence for the two hypotheses (e.g. Stone 2006 (Squirrel monkeys (*Saimiri sciureus*)); Fragaszy and Boinski 1995 (Capuchin monkeys (*Cebus olivaceus*)); Gurven 2006 (Humans)). Orangutans (*Pongo spp.*) are an especially interesting species for research in this area as they show a very derived life history. This includes a late age of first reproduction and the longest nutritional dependence of any primate species (van Noordwijk and van Schaik, 2005). Further, they live in a complex foraging niche and rely on a variety of complex skills (van Noordwijk et al., 2009; van Noordwijk and van Schaik, 2005). Unlike other great apes, orangutans show a fairly solitary life style: adult and juvenile animals range mostly

solitarily. Consequently, orangutans depend more on their own ecological knowledge and acquired skills than more gregarious species (for whom individual skills are harder to measure as they could potentially rely on the skills of other, more experienced group members), which makes them especially suitable to test the different hypotheses.

The aim of this project was to investigate to what extent different life history hypotheses (e.g. skill learning or expensive brain) apply to orangutans. For this purpose I investigated skill competence and development of wild immature Sumatran orangutans. I put special focus on skill acquisition of independently ranging, weaned immatures in order to gain insight into learning behavior during the period between weaning and first reproduction. The collected data was compared with data from previous projects on skill acquisition in the same population as well as in a population of Bornean orangutans. Data of individuals of different age classes, collected during different study periods helped to refine the understanding of the slow development of orangutans during immaturity. Furthermore, in form of a literature review parallel to this project I investigated whether one of the different established life history hypotheses can be generally applied over different mammal and bird species or if a new model can be developed that explains the observed variance more accurately (e.g. in the form of a fusion of different established theories). Investigating when and how orangutans and other species reach skill competence is expected to help to understand their unique life history. This may also help to achieve a better understanding of the evolution of the human life history.

1.2 Hypotheses explaining the length of the developmental period

Earlier studies could show that life history parameters including the length of the developmental period (birth till first reproduction) are tightly linked to brain size. Large-brained species have a slow life history: they commonly show an expanded life span, late age of first reproduction and prolonged developmental periods (Deaner et al., 2003; Isler and van Schaik, 2009; Barrickman et al., 2008). On the one hand, large brains are associated with high energetic costs. Brain tissue is very expensive to grow and maintain: In a resting state, an animal's brain uses more energy per unit weight than most other tissues of the body (Mink and Blumenschine, 1981; Isler and van Schaik, 2009). Therefore, larger-brained species need a longer developmental period to grow and differentiate their brains, which results in a delayed maturity and reproduction (Barrickman et al., 2008). On the other hand, large brained species show an expanded life span including prolonged reproductive periods: large brains are connected with high cognitive performance (Deaner et al., 2007) including an increased learning ability and higher behavioral flexibility which leads to better adult survival (Allman and Hasenstaub, 1999; Deaner et al., 2003). In sum, large brains impose immense developmental costs, but also benefits in form of an increased cognitive performance resulting in a longer reproductive life span.

So far, several hypotheses have been developed to explain the relationship between

life history parameters, in particular the length of the developmental period and brain size.

The *skill learning or needing to learn hypothesis* (Ross and Jones, 1999; Janson and van Schaik, 1993) proposes that large-brained animals mature slowly because they need to acquire skills and knowledge essential for adult success. According to this hypothesis, the acquisition of skills needed for successful adult performance such as certain foraging- or social skills determines the age of sexual maturity. The skill learning hypothesis suggests that the need to acquire information imposes long periods of learning and consequently late maturation. Species that face complex social or ecological problems are thought to show a slow postnatal growth rate, which then leads to an extended infant or juvenile period. The prolongation of these developmental periods finally results in more time for learning.

The skill learning hypothesis predicts that species improve their ecological and social performance gradually during the whole period of immaturity and delay reproduction until a sufficient skill level is reached (figure 1.1, (Dunkel, 2006)). In general, under the skill learning hypothesis it is expected that skill competence is reached around or after the age of first reproduction (figure 1.1, scenario b & c). A scenario where skill competence is reached long before the age of first reproduction (figure 1.1, scenario a) would speak against the skill learning hypothesis. The delay in first reproduction is compensated by better adult survival and reproduction. However, different body size and strength imply different optimum foraging strategies. So, to fully confirm the skill learning hypothesis, adult levels of ecological competence have to be reached due to increased skills rather than body size or strength. Thus, trajectories of skill acquisition should to a certain extent vary from that predicted by the development of physical growth and strength (Janson and van Schaik, 1993).

Furthermore, immature individuals are expected to spend more time practicing the skills in which they have not reached adult level of competence yet, even though the energetic returns might be very low (Stone, 2006). In general, species that live in complex foraging niches including various extractive and processing techniques of resources or in a complex social environment are expected to show longer periods of immaturity than species that live in cognitively undemanding habitats.

The *embodied capital hypothesis* is very similar to the skill learning hypothesis but focuses on the evolution of the extended human life history during the emergence from a common ancestor with chimpanzees (*Pan troglodytes*) (Kaplan et al., 2000). This hypothesis sees the transition to learning-intensive foraging strategies, including high quality, difficult to acquire food sources as cause for the extension of the life history parameters (Kaplan et al., 2000, 2003; Barrickman et al., 2008). The shift to these cognitively more demanding and therefore more learning intense feeding strategies dragged along an elongated period of immaturity with low productivity. This is paid off by higher adult performance which includes provisioning of the younger generation. Similarly, the investment in developing a large brain is compensated by decreased mortality and consequently longer reproductive periods and thus possible success as an adult. Further, the specialization in hunting with big, valuable food packages is

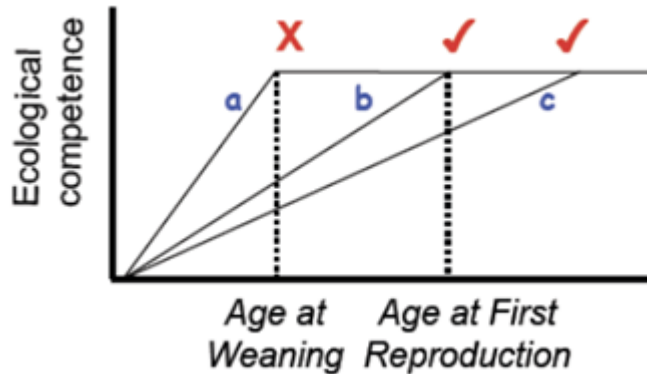


Figure 1.1: **Predictions of the skill learning hypothesis about the timing of full ecological competence.** Scenario b and c support the skill learning hypothesis, a rejects it (Dunkel, 2006).

thought to have lead to increased cooperation between men and women which facilitated provisioning of offspring. Provisioning results in reduced child mortality and higher reproductive rates. Hunting also promoted food sharing between families which reduces the risk of food shortages and therefore leads to a lower mortality (Kaplan et al., 2003).

The *maturational constraint hypothesis* suggests that the slow maturation of large brained animals is determined by the time it takes to develop the brain up to functional maturity (van Schaik et al., 2006; Deaner et al., 2003). This hypothesis assumes that certain behaviors rely on a mature nervous system. Furthermore, complex behaviors require long, fixed maturation periods and cannot emerge immediately. The pace of development of the brain and behavior then affects life history, in particularly the onset of sexual maturity (Deaner et al., 2003). Additionally, larger brains are associated with more complex patterns of neural connectivity. Consequently, it takes more time to develop a large brain than a small one (Gibson, 1991). As differentiation of the brain continues after mass growth has been completed it is likely that brains imply high energetic costs even after adult brain size has been reached. This hypothesis can also explain why many motor patterns develop progressively during juvenility, independently from training and of a given species at approximately the same age for all individuals (reviewed by Parker and McKinney 1999). A delay in brain maturation should consequently result in a deferment in overall development of these motor patterns (van Schaik et al., 2006). The maturational constraint hypothesis assumes that the nervous system of immatures develops progressively throughout the whole developmental period and adult levels of function are not reached before age of first reproduction. Consequently, neuroanatomical and behavioral markers of maturity are reached just before age of first reproduction (Deaner et al., 2003). Thus, the pace of maturation of the nervous system or in other words the time to fully differentiate the brain and not the number of skills to learn or the physical development of the body determines the length of the immature period and consequently age at first reproduction.

The *expensive brain hypothesis* differs from the other hypotheses as it focuses on energetic, rather than on time constraint. According to the expensive brain hypothesis, the pace of development is mainly determined by energetic trade-offs. Under conditions where energy is limiting, high energetic investment into brain growth results in a delay of the physical development of the body (Isler and van Schaik, 2009; Deaner et al., 2003). Brain tissue is among the most expensive tissues to develop and maintain. Further, unlike for other organs, the energy flow to the brain needs to be held constant and cannot be temporally reduced (Isler and van Schaik, 2009; Deaner et al., 2003; Tanner, 1986). In resting state warm-blooded vertebrates use 2-8% of their metabolism for maintenance of the central nervous system. Primates and some other large brained mammals are an exception to this rule as they invest a higher proportion of their resting body metabolism into the central nervous system (Mink et al. 1981: humans 20%, orangutans 11%, chimpanzees 13%, baboon 12.9%). This value is likely to be even higher for immature animals, as they have larger brains in relation to their body mass (Holliday, 1986). The expensive brain hypothesis proposes that this high investment into brain development during infancy and early juvenility imposes limitations on body growth. Sacher and Staffeldt (1974) suggested that during mammalian ontogeny the brain is the slowest growing organ in the fetus and determines the growth pace of other tissues. Further, it has already been proposed that because at the beginning of the immature period much energy is needed to develop the brain, fast somatic growth is delayed and can only be finished after the brain is fully developed (Deaner et al., 2003). The expensive brain hypothesis concludes that these energetic constraints on brain development directly lead to a slowdown of the somatic growth rate and consequently to an extended period of immaturity and later age of first reproduction. The expensive brain hypothesis states that those energetic constraints have such a severe effect that they set the age of maturity whereas the time needed to reach adult competence is not limiting as skill competence is reached before age of first reproduction.

The expensive brain hypothesis makes the following predictions. First, large brained species are expected to show a prolonged period of immaturity whereby somatic growth (and possibly brain development) is not completed until the age at first reproduction. This effect is expected to be stronger for species that live in a poor habitat with limited resource availability. In species with additional external energy flows to the mother or the immature, such as in altricial and more pronounced in cooperatively breeding species, those effects are expected to be less distinct. Second, among species with big litter sizes, the correlation between brain size and length of the immature period should be weaker as they are known to adjust their litter size instead of life history parameters to reduce their cost of reproduction (Isler and van Schaik, 2009). Third, adolescent growth spurts, following a period of low juvenile growth, should also become more pronounced as relative brain size increases.

The *malnutrition avoidance hypothesis*, which again focuses on energetic constraints sees the prolonged period of immaturity as a mean to avoid brain starvation during development (van Schaik et al., 2006; Janson and van Schaik, 1993; Deaner et al., 2003). In early growth and development brains are highly sensitive to starvation (Nowicki et al., 1998; Levitsky and Strupp, 1995). Brain growth rates in mammals are very

Table 1.1: **Hypotheses on the correlation between the length of the developmental period and brain size.** AFR= age of first reproduction.

hypothesis	limiting factor, determining AFR		expected correlation brain size AFR	
			normal conditions	extra enegery
needing to learn	time	to reach skill competence	yes	yes
embodied capital		to reach skill competence	yes	yes
maturational constraint		to differentiate brain to maturity	yes	yes
expensive brain	energy	to develop brain and body	yes	no
malnutrition avoidance		to assure brain maintenance during growth	yes	no

inflexible: in contrast to body growth, brain development cannot adjust to temporary energy shortages (Tanner, 1986; Deaner et al., 2003). Brain starvation during immaturity is very dangerous for the organism as it often drags along severe cognitive impairments and reduced adult performance later in life (Nowicki et al., 1998; Levitsky and Strupp, 1995). A slow-paced brain growth helps to avoid brain starvation and enhances the probability to survive to maturity while fully competent (van Schaik et al., 2006). As somatic growth is thought to be partly linked to brain growth (Deaner et al., 2003), the growth rate of the body is consequently also slowed down. This then leads to an overall extension of the developmental period. According to the malnutrition avoidance hypothesis, species that live in a poorer habitat or in a habitat with fluctuating resource availability are expected to show a slower development than species that live in a rich and temporally stable habitat. The brain malnutrition avoidance hypothesis is consistent with the expensive brain hypothesis: both hypotheses predict a slowdown of development in large brained species, caused by the costs of brain development, which then results in a prolonged immature period. Whereas the expensive brain hypothesis states that energetic constraints in general determine the length of the immature period, the brain malnutrition avoidance hypothesis focuses on one way to explain how energetic trade-offs may work to affect the pace of development.

The five presented hypotheses each focus on one factor as having the main limiting effect on the development and finally determines age at first reproduction. They can be divided into two categories: needing to learn, embodied capital and maturational constraint propose that time limitations set age of first reproduction (time hypotheses) whereby expensive brain and malnutrition avoidance focus on energetic constraints (energy hypotheses) 1.1. All the hypotheses predict that brain size and age of first reproduction are correlated with large brained species having a late age of first reproduction. However, in species with additional energy flows (such as cooperatively breeding species), other than the time hypotheses, the energy hypotheses do not expect such a correlation any more. The later was confirmed in a study across different mammal species (Isler and van Schaik, 2009).

The life history hypotheses presented above are not mutually exclusive and it is likely that several of them apply in different species, since they postulate different factors

(such as the number of skills to learn, the energy available or the brain mass to differentiate) that limit the timing of maturity. Each hypothesis presents one factor as a limiting principle that sets the pace of development in all species. Therefore, they can all be encompassed under a general developmental constraint model (GDCM), as it takes into account that the limiting factors may have different relevance for various species (Schuppli et al. in preparation). In a side project parallel to this thesis, the GDCM was developed and tested with a data set of approximately 60 different mammal and bird species. In the following section the model and its predictions will be described briefly and the main results of the comparative study will be summarized.

1.3 The general developmental constraint model (GDCM)

According to the GDCM, the energy that species living in energetically limiting habitats need to grow and differentiate its brain tissue, is the main constraint on the length of the developmental period. As brains are energetically very expensive to develop, somatic growth is constrained by the need to fully differentiate brain tissue (Isler and van Schaik, 2009; Deaner et al., 2003). Taking energy supply as a general constraint that sets the pace of development, other factors such as amount of skills to learn may influence developmental pace under certain circumstances.

In species with additional external energy flows to the mother or the immature, such as in species with biparental provisioning like in many birds, this kind of energetic affect is expected to be less distinct. A similar (and more extreme) scenario is cooperative breeding: in such species the energy flow to the developing immature is so high that energetic trade-offs may hardly affect the developmental pace. Consequently, other factors are thought to determine the time to reach adult competence. These factors may include skill acquisition in the foraging context but also in the social domain. In a comparative study on primates Joffe (1997) has found that species that rely on higher social skills have evolved an extended juvenile period. However, to test the GDCM the main focus was put on the development of foraging skills as those are directly related to fitness (Stephens and Krebs 1986) and easier to measure than social skills.

The GDCM predicts that if species with additional energy subsidies live in habitats with complex foraging niches, (including various extracting and processing techniques of resources) the length of the developmental period should be determined mainly by the time to acquire foraging skills (figure 1.2). In species that permanently live in social groups with extensive sharing of resources, the performance in various essential skills may reach the highest values even long after the age of first reproduction given that individuals can rely on support from group members. This includes hunting skills social carnivores, where kills are shared and individuals do not have to rely on their own hunting performance.

In sum, the GDCM predicts that in most mammals age of skill competence is reached long before age of first reproduction whereas in species with additional energy flows to the developing young (such as birds or cooperatively breeding mammals), age of skill

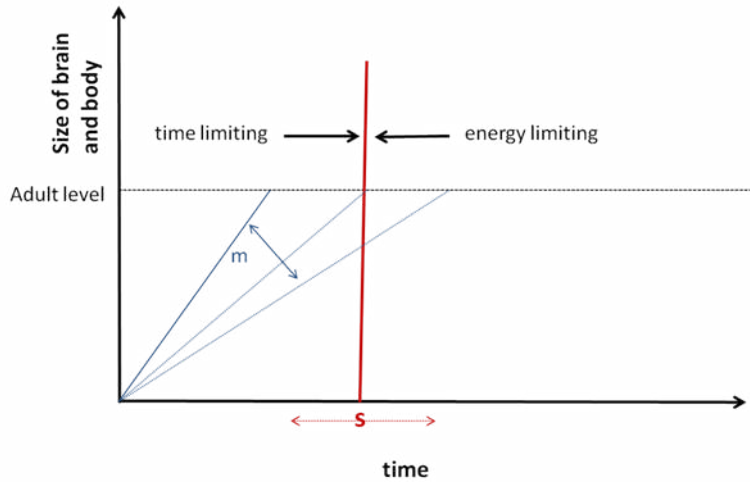


Figure 1.2: **The general developmental constraint model.** m = pace of development: determined by energy supply (eg. richness of the habitat) and brain mass the species has to develop; s = adult like skill competence: dependent on niche complexity; AFR= age of first reproduction.

competence may be reached around age of first reproduction, depending on the complexity of the niche the species lives in. In species with obligate sharing of resources (such as in cooperative hunters), skill competence may be reached long after age of first reproduction.

The GDCM was tested with a data set comprising 35 mammal and 23 bird species. Data on age of first reproduction was retrieved from an established data base (Isler unpublished data). As measure of competence for foraging skills data on food processing rates and capture rates from the published literature were taken (Schuppli et al. in preparation).

Consistent with the GDCM's predictions it was found that in most mammals, competence in foraging skills is reached before the end of the juvenile period. Contrarily to mammals, most birds, which are known for the complexity of their niche (Ricklefs 2004) reach adult skill competence around the age of first reproduction (figure1.3). Within mammals the relative age of skill competence was found to increase with increasing niche complexity figure1.4). This shows that species that live in complex foraging niches need indeed longer to acquire their skills than others. Furthermore, cooperatively breeding mammals were shown to reach skill competence on average later than independent breeders (figure1.5 a). Cooperative hunters reach peak values of skill competence later than independent foragers (figure1.5 b) and often after age of first reproduction.

Agreeing with the GDCM's main assumptions, these results provide strong evidence that not exclusively skill acquisition or energetic constraints determine age of first reproduction but that both factors have a different relevance for various species.

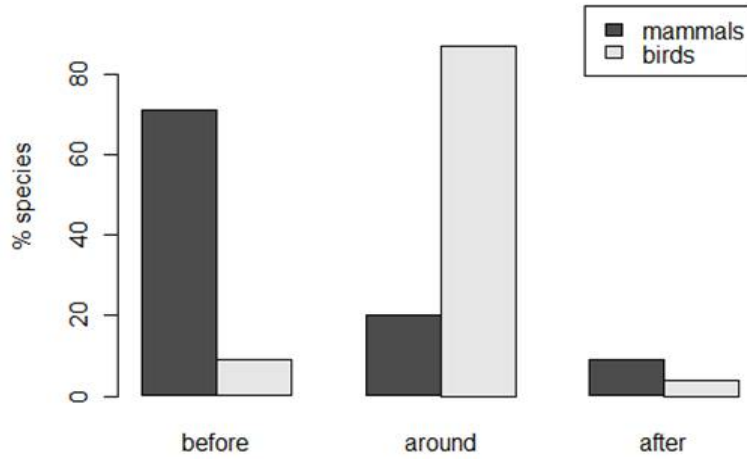


Figure 1.3: **Age of skill competence relative to age of first reproduction.** Percentage of bird and mammal species that reach skill competence before (before 85% of the developmental period is completed), around (after 85% and before 115% of the developmental period is completed) and after (after 115% of the developmental period is completed) age of first reproduction.

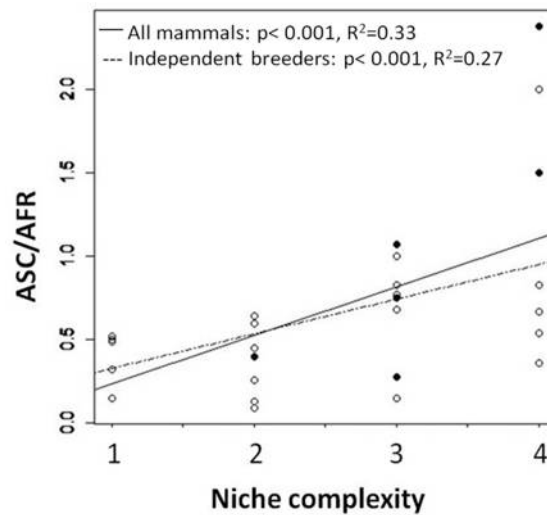


Figure 1.4: **Relative age of skill competence and niche complexity.** Relative age of skill competence (age of skill competence (ASC) divided by age of first reproduction (AFR)) as a function of niche complexity (PGLS regression).

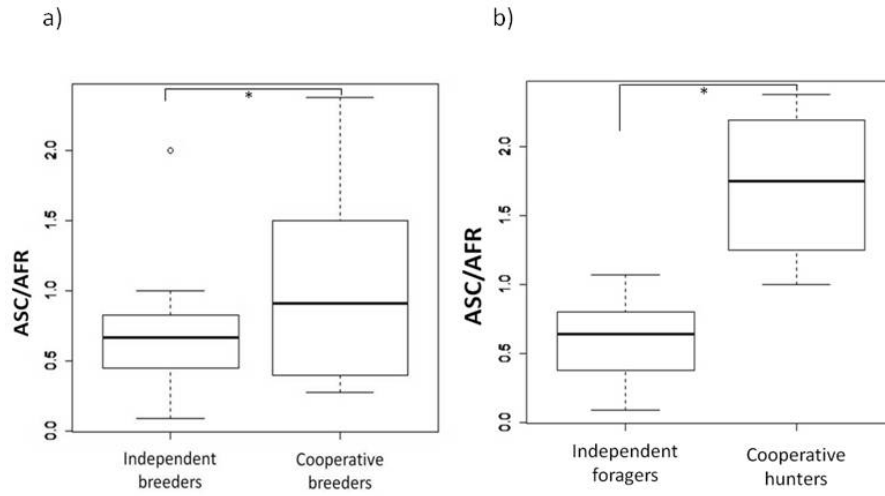


Figure 1.5: **a) Relative age of skill competence: Independent versus cooperative breeders.** Relative age of skill competence (age of skill competence (ASC) divided by age of first reproduction (AFR)) of independent and cooperative breeders. **b) Relative age of skill competence: Independent foragers versus cooperative hunters.** Relative age of skill competence (age of skill competence (ASC) divided by age of first reproduction (AFR)) of independent foragers and cooperative hunters. * $p < 0.05$.

1.4 Orangutans as study species

Orangutans, the only Asian great apes are found on the Islands of Sumatra and Borneo (figure1.6). Nowadays, orangutans are divided into two different species: *Pongo abelii* on Sumatra and *Pongo pygmaeus* on Borneo, whereby the latter are subdivided into three subspecies: *P.p. pygmaeus*, *P.p. wurmbii* and *P.p. morio* (Goosens et al., 2009; Zhi et al., 1996, figure1.6).

Orangutans are a very interesting species to test the different life history hypotheses about the length of the juvenile period for several reasons. Pontzer et al. (2010) could show that free living orangutans use less energy (daily energy expenditure), relative to body mass, than nearly any eutherian mammal ever measured. Orangutans have a long life span and the longest inter birth intervals of all extant mammals. Furthermore, they show a late age at first reproduction (15-16 y for Sumatran females, 12-14 y for Bornean females) and the longest nutritional dependence of any nonhuman primate (van Noordwijk and van Schaik, 2005; Wich et al., 2009, van Noordwijk, personal communication). This slow development provides orangutans with an extended period of learning during which they acquire a variety of complex skills. Unlike the other great apes, orangutans show a solitary life style. Adult and juvenile orangutans (immature animals that are weaned but haven't reach age of first reproduction), range widely solitarily and have to rely more or less completely on their own ecological knowledge (Byrne, 2007; van Noordwijk and van Schaik, 2005). Like chimpanzees, orangutans live in a so-called cognitive foraging niche: their diet consists of many difficult to process food items and adult animals show numerous extracting and food processing

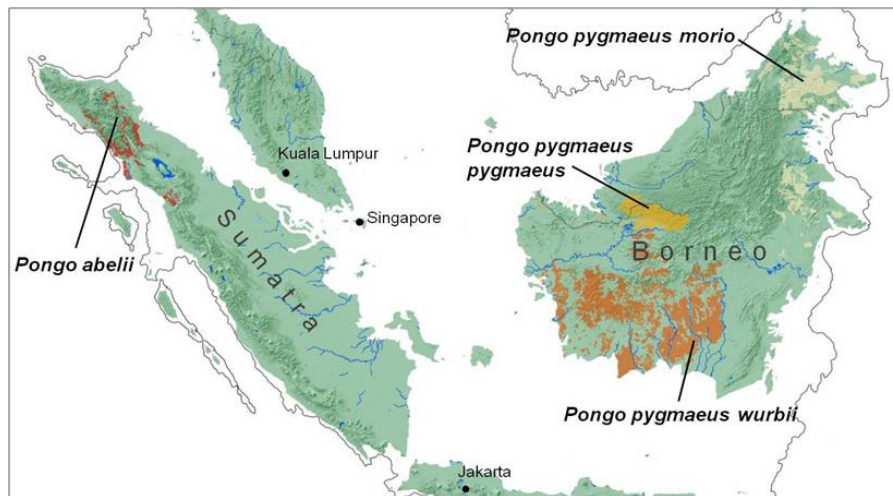


Figure 1.6: **Relative age of skill competence and niche complexity.** Distribution of *Pongo abelii* (red) on Sumatra and the three subspecies of *Pongo pygmaeus* (yellow, orange and white) on Borneo. (Map by Eric P. Willems).

techniques (Byrne, 2007). Some orangutan populations even use tools to get access to embedded food (van Schaik and Knott, 2001; van Schaik et al., 2003).

1.4.1 Orangutans skills

During the developmental period immature orangutans have to learn all the skills necessary to survive and reproduce. In general, one can divide the skills orangutans need to survive into the following categories: ecological competence, non-food related technological skills, social skills and loco-motor skills.

Ecological competence is thought to be a key factor of the development of independence as the foraging ability is directly related to fitness (Stephens and Krebs 1986). Accordingly, most studies about skill development in mammals have focused on foraging or hunting efficiency (e.g. Gunst et al. 2008; Holekamp and Smale 1997; Stone 2006). The ecological competence can be divided into the following aspects Galef2001:

1. What to eat
2. How to eat
3. Where and when to eat

What to eat includes diet composition and food selection competence; *How to eat* processing competence such as processing techniques and foraging efficiency; and *Where and when to eat* the ability to find foods in appropriate proportions and time intervals or more general: range use competence.

The most prominent *non-food related technological skill* of orangutans is nest building. Orangutans build a new nest out of leaves and twigs every night in the trees. They also

frequently build day nests for short naps or play during the day. The category further includes head and nest covers, usually made of leaves and used for protection against the rain or the sun (van Schaik et al. 2003). Adult animals have also been observed to construct so called bee swatters out of leaves to protect their face when foraging for honey (van Noordwijk and van Schaik, 2005). Former studies could show geographic variations between study sites in several of these behaviors (van Schaik et al., 2003). This includes presence and absence of certain behavior patterns that cannot be linked to any ecological differences (for example building a nest just above the real nest as protection against the rain) and therefore strongly suggests the presence of cultural differences between the orangutan populations (van Schaik et al., 2003, 2009).

Even though the orangutan is mainly known as a solitary species, *social skills* needed for social relationships, mating and parenting are important elements of their behavioral repertoire.

Loco-motor skills include all skills used for travelling independently in the canopy and also to do so in an efficient way. One important loco-motor skill that immature orangutans have to learn is the crossing of gaps in the canopy (Phillips et al. in preparation). Gap crossing is acquired gradually during development and the learning process relies heavily on maternal assistance (see below) (Phillips et al. in preparation).

1.4.2 Physical and skill development of immature orang-utans

Orangutan newborns are helpless and completely rely on their mothers (van Noordwijk and van Schaik, 2005). Mothers provide their infants with milk, help them to travel in the canopy and protect them from the elements and from conspecifics. During immaturity young orangutans must then gradually learn all the skills and acquire all the knowledge necessary to survive without the support of their mothers. So far, apart from age of first reproduction on, no sex differences in the timing of physical and skill development of immature orangutans have been reported. Therefore, the developmental patterns described in the following section in general apply for females and males. For the rest of this thesis immature animals up to the age of weaning will be called infants whereas immature between weaning and age of first reproduction will be referred to as juveniles.

Orangutan infants spend the first few months of their lives in almost constant body contact with their mothers and are carried whenever the mother travels. This contact time declines to around 50% by the infants second birthday. Immatures stay in close proximity to their mothers even when they are not carried any more. Up to six years of age immatures stay within ten meters of their mothers for more than 50% of their time (van Noordwijk et al., 2009). The timing of weaning differs between the study sites. At the Sumatran study sites Suaq and Ketambe, nursing can be observed until the offspring is seven and a half years old. In the Bornean study sites (Tuanan, Sabangau and Kinabatangan) infants are weaned one to two years earlier at five and a half to seven years of age (van Noordwijk, personal communication). Mean inter birth intervals also differ between the study sites: the Sumatran populations show higher

values (8.2 y and 9.3 y) than the Bornean populations (6.1-7.7 y) (Wich et al., 2009; Knott et al., 2009).

For Sumatran and Bornean infants the amount of time spent close to the mother (<10 m) suddenly starts to decrease around the age of seven to eight. Juveniles then start to leave their mothers for longer time spans but stay in visual and auditory contact until they are nine to ten years old. During this period, juveniles occasionally visit their mothers or associate with peers. At the Sumatran sites animals of these age classes have been seen to travel around in peer groups of two to five animals whereas Bornean immatures at Tuanan associate with peers less frequently (van Schaik, personal communication). However, at another Bornean site, Tanjung Puting, Galdikas (1995) reported that independently ranging juvenile ("adolescent") females spent a lot of their time in association with other individuals. Finally, ranging seems to become completely independent of the mother around the age of 12 years. (van Noordwijk et al., 2009; van Noordwijk and van Schaik, 2005).

In terms of *ecological competence* a lot is known for the development of Bornean but less about Sumatran orangutans. For food selection competence (What to eat) it has been shown for Bornean infants that by weaning (around the age of six) their diet is identical to the mother's diet (Jaeggi et al., 2010; Dunkel, 2006). Food selection competence also includes recognizing edible food items from a close range. Evidence has been found that in Tuanan immatures between 3-6 years of age are not able to recognize and collect termite rich pieces of wood on their own whereas slightly older infants seem to have reached full competence (van Noordwijk and van Schaik, 2005; Jaeggi et al., 2010).

For the food processing competence (How to eat) it has been shown that 3-5 year old infants in Tuanan could already process everything their mothers ate (Dunkel, 2006). At the same study site Dunkel (2006) found that feeding rates of young immature Bornean orangutans are lower than the ones of their mothers. However, the three oldest immatures (estimated age 8-10 years), achieved adult levels of feeding efficiency. Furthermore, infants and juveniles ate foods of similar hardness and toughness like their mother. For the Sumatran study sites, less data on the development of food processing competence is known. The population of Suaq is known for its tool use to gain access to seeds in fruits or insects in tree holes. Seven years old animals have been observed to successfully use such tools (van Noordwijk and van Schaik, 2005).

The third important aspect of ecological competence is the ability to locate food patches in the forest (Where to eat). Only very few data on these skills has been collected so far. In a study on Bornean orangutans Latscha (2008) provided evidence that range use competence might develop later than other aspects of ecological competence. However, by the age orangutans start to range completely independently from their mothers, when they are around 11-12 years old, they should have reached a certain level of competence in finding food (van Noordwijk et al., 2009). This is supported by the fact that there is hardly any evidence for mortality after infancy and no evidence for increased mortality during the juvenile period of life (van Noordwijk, personal communication).

The development of *non-food related technological skills* has been documented at the Sumatran as well as at the Bornean sites. Sumatran and Bornean infants can build their own nests around three years of age but share night nests with their mothers at least up to the time of final weaning (seven to eight years of age at Suaq and six to seven years of age at the Bornean sites) (van Noordwijk and van Schaik, 2005; van Noordwijk et al., 2009). The time at which immature finally stop sleeping in their mothers nest seems to be variable: in Tuanan (a Bornean study site) immatures have been seen to occasionally share the night nest with their mothers even after the birth of their younger sibling (van Noordwijk, personal communication). At all study sites orangutans have been observed to make covers for the head and nest against the rain. Infants as young as one year have been observed to construct such protections even though they do not need them as they cling to their mothers during rain until they are 3-5 years old (van Noordwijk et al., 2009; van Noordwijk and van Schaik, 2005).

For the *loco-motor development* it is known that infants in Sumatra and Borneo are carried 80% of the time the mother travels until the age of two (van Noordwijk and van Schaik, 2005; van Noordwijk et al., 2009). Mothers frequently assist their infants when moving in the canopy, especially when crossing gaps between trees. Various forms of maternal travel assistance have been described whereby bridging (mother makes a bridge between two trees, waits for the offspring and lets it travel across her body or at a newly continuous path between the trees) and riding together in one tree during tree sway (mothers sways a tree in order to deform it to reach the next tree, while offspring travels in the same tree, usually above the mother so that it reaches the next tree first) belong to the most frequently observed forms (Phillips et al. in preparation; van Noordwijk et al. 2009). For Bornean immatures it has been shown that the amount of maternal travel assistance reaches almost 0% around the age of weaning (Phillips et al. in preparation). It therefore seems as if complete loco-motor independence is reached before weaning (Phillips et al. in preparation; van Noordwijk et al. 2009).

Very little is known about the development of *social competence* in orangutans. As in many other primate species, orangutan mothers act as mediators when their infants start to interact with conspecifics (Nowell and Fletcher 2007 (gorillas (*Gorilla gorilla gorilla*)); van Noordwijk et al. 2009 (orangutans)). Even after juvenile orangutans have seemingly started to range independently their mothers have been observed to approach and intervene, whenever they encounter conspecifics (van Noordwijk, personal communication). So far, association preferences and time spent in theses associations have not been explicitly investigated for Sumatran juveniles. For the Bornean Juveniles it is known that they sometimes visit familiar adult females with their offspring within their natal area. However, some Bornean juveniles seem to actively avoid encounters with their conspecifics of all age and sex classes what can be seen either as lack of interest or social confidence to interact with conspecifics (van Noordwijk et al., 2009).

To my knowledge no longitudinal data has been collected on the physical development of wild orangutans. However, some mixed longitudinal data on the ontogeny

of captive orangutans is available. Leigh and Shea (1995) developed trajectories for body weight ontogeny of *Pongo pygmaeus*. They concluded that female orangutans stop growing around the age of 18 whereby no clear growth spurt could be established. Male orangutans can increase their body weight throughout their whole life whereby they grow at a relatively constant rate till the age of five but then gain weight at an increasing rate until they are 13 years old (Leigh and Shea, 1995).

To sum up, until now it seems that young orangutans acquire all their skills necessary for survival until the age of weaning or shortly after weaning when they begin to range independently from their mothers. However, females reach adult body size and start to reproduce around the age of 15-16 (Sumatran individuals) respectively 12-14 (Bornean individuals) (van Noordwijk and van Schaik 2005; Wich et al. 2009; van Noordwijk personal communication), several years after they have started to range independently. Very little is known about the period between the two developmental milestones of weaning and first reproduction. When they leave their mothers, and join groups of peers, juvenile orangutans mostly also leave their natal home range (van Noordwijk et al. 2009). In a group of peers that come from different mothers and home ranges, it is likely that the juveniles differ individually in their skills or diet compositions. Entering a new home range possibly also means that the juveniles gain access to resources that have not been present in their natal home range. It may be that to a certain extent social learning in such peer groups occurs, and juveniles learn new skills from each other or acquire new skills through independent exploration. So far, it has remained unresolved whether and how orangutans acquire skills after they have started to range independently (figure 1.7), whereby with this study I intended to shed some light on the skill development in this period of the life.

1.4.3 Learning mechanisms during orangutan development

Galef and Laland (2005) define learning as "a set of complex ontogenetic processes that allow animals to acquire, store and subsequently use information about the environment". In general, learning is subdivided into social learning and asocial (individual) learning.

According to Heyes (2011) asocial learning is "learning about other agents or the inanimate world that is not influenced by observation of, or interaction with another individual or its products". Asocial learning by trial and error may be the basis to learn about novel food items in primates (Milton 1993; Gustafson et al. 2010). When an individual discovers a skill independently by asocial learning this is commonly classified as independent exploration. Independent exploration is thought to come along with costs as it bears the risk of intoxication, injury or simply a loss of time. Consequently, young animals might use social information to avoid those costs (Galef and Giraldeau, 2001).

Heyes (2011) defines social learning "learning about other agents or the inanimate world that is influenced by observation of or interaction with, another individual or its products" (based on Heyes 1994; Hoppit and Laland 2008). Social learning has been

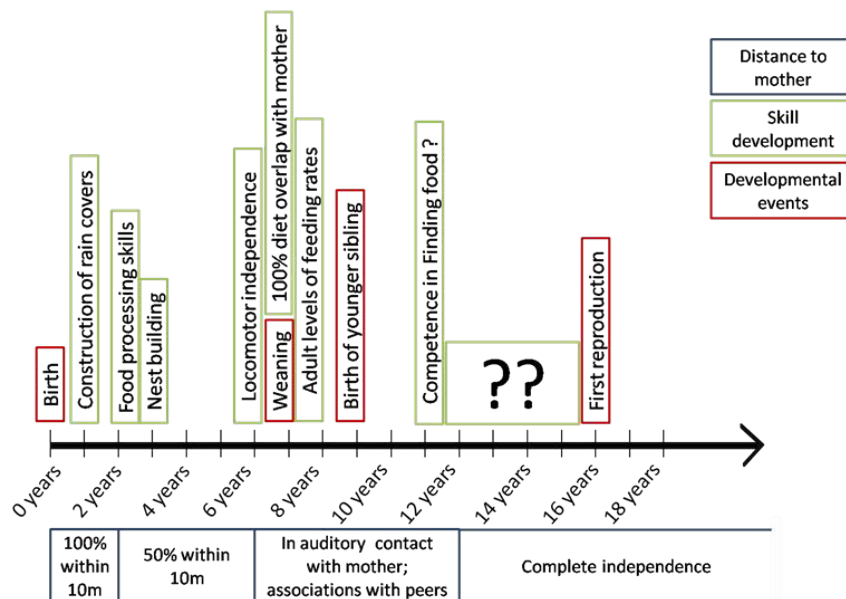


Figure 1.7: **Orangutan development.** Developmental milestones during orangutans' infancy (birth until weaning) and juvenility (weaning until first reproduction). Age of first reproduction refers to (Sumatran) female animals whereas the remaining data applies to males and females.

found in a variety of species such as fish, birds, rodents and primates (reviewed by Galef and Laland 2005). Rapaport and Brown (2008) categorize social learning into 7 different classes 1.2. Social learning can further be divided into vertical (such as skill transmission from mother to infant) and horizontal (skill transmission among other group members) transmission. In a recent review Heyes (2011) proposes that social and none social learning includes the same basic learning mechanisms being mostly based on associative processes.

Former studies could show that infant orangutans learn many of the above presented complex foraging skills socially from their mothers (Forss, 2009; Jaeggi et al., 2010). Forss (2009) also found evidence that infant orangutans show explorative behavior that is not a direct outcome of social learning but based on independent exploration. However, to what extent immature orangutans learn from individuals other than their mothers and to what extent social learning takes place after weaning remains unresolved. One of the aims of this study was to fill this gap in our knowledge.

1.4.4 Sumatran versus Bornean study sites

The study sites of Sumatra and Borneo differ in several aspects. In general Sumatren forests are more productive than Bornean ones, and thus availability of edible food is lower in the Bornean habitats (reviewed by Russon et al. 2009). In Sumatra and Borneo food abundance fluctuates over the year. Additionally, caused by the El Niño, severe fruit scarcities occur in 2-12 years intervals. This phenomenon is less pronounced in Sumatra than in Borneo (Delgado and van Schaik C.P., 2000). In Sumatra, orangutan densities are higher than in Borneo in comparable habitats (reviewed by Husson et al.

Table 1.2: **Social learning mechanisms:** from Rapaport and Brown 2008, p. 191.

Term	Definition
Social facilitation or response facilitation	The presence of an individual increases another's foraging behavior or the foraging act of one individual may make the same act more likely to occur in another individual.
Stimulus enhancement or local enhancement	An individual may learn to orient its efforts to a food item or location by virtue of another's activities, from which learning then occurs via individual experience.
Observational conditioning	An individual gathers foraging information by drawing a link between some aspect of the environment with which a demonstrator interacts and the food; for example by watching another individual eat a novel food, a naive animal may learn to recognize the item as food.
Imitation	The naive individual learns a new behavior such as foraging technique, by matching the detailed sequence of actions exhibited by another.
Teaching	Individual a modifies its behavior only in the presence of naive observer B at some cost or at least no immediate benefit, thereby encouraging or punishing B's behavior and providing B with experience, or setting an example for B; as result B acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than would otherwise be the case.
Opportunity teaching	A type of teaching in which individual A puts individual B in a situation conducive to learning a new skill or acquiring knowledge.
Coaching	A type of teaching in which individual A directly alters the behavior of B by encouragement or punishment.

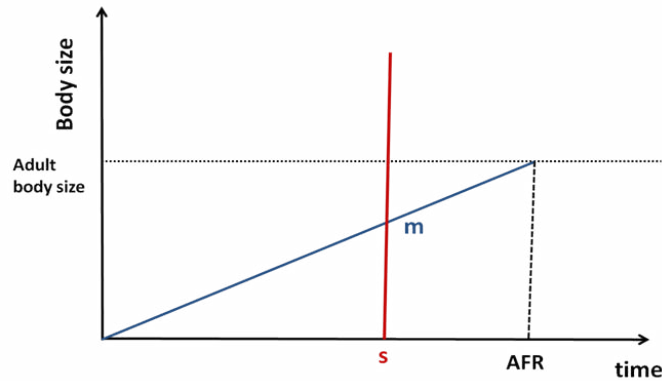


Figure 1.8: **The general developmental constraint model for orangutans.** m = pace of development: determined by energy supply (e.g. Richness of the habitat) and brain mass the species has to develop; s = adult like foraging skill competence: dependent on niche complexity; AFR= age of first reproduction.

2009). In terms of sociality it is known that Sumatran orangutans are more gregarious than the Bornean ones, thus they have a higher tendency to associate with each other (van Schaik 1999). Further, Sumatran orangutans, in particular the population at Suaq Balimbing, exhibit a very broad and complex foraging repertoire. This includes also tool use: orangutans at Suaq frequently use twigs to extract honey and insects out of tree holes. They also process twigs to use them as tools to get access to seeds in fruits with sharp hair (van Schaik et al., 2003; Fox et al., 1999; van Schaik and Knott, 2001; Forss, 2009).

1.5 Questions and Hypotheses

The main purpose of this project was to test whether the general developmental constraint model applies for Sumatran orangutans. Orangutans are relatively large brained, the brain volume of Sumatran orangutans (*Pongo abelii*) is around 388 ccm (Taylor and van Schaik, 2007). Furthermore, orangutans live in an extreme habitat: Asian forests have a low plant productivity and the availability of orangutan food fluctuates over the year and over the course of different years (van Adrichem et al., 2006; Wich et al., 2009). As a physiological adaptation for minimizing energy throughput, free-living orangutans have very low daily energy expenditures relative to body mass (Pontzer et al., 2010). Accordingly, the General Developmental Constraint Model (GDCM) predicts that their developmental time in orangutans is determined energetic rather than time constraints: the energy to reach adult constitution and not the time to acquire skills but sets the pace of development in orangutans (figure1.8).

In order to test this hypothesis I tested the following predictions (for definitions of specific behaviors see section 3.2.2):

1. For the *developmental skill trajectories* I expect that immature orangutans reach adult levels of competence in all skills that do not depend on size or strength well

before the age of first reproduction. Based on former studies that have looked at skill development in infant orangutans, I expect the following timing for the different dimensions of ecological competence:

By the time of weaning adult levels of food selection competence will be reached:

1a) The immatures' diets will overlap to nearly 100% with the ones of their mothers.

1b) The number of independent feeding patch discoveries will have reached adult values.

Between weaning and age of first reproduction adult levels of food processing and range use competence will be reached:

1c) Processing techniques and foraging efficiency (including tool use) will reach adult levels: Intake rates and processing times for all food items will be equal to the ones of adult animals.

1d) Adult competence in locating food patches in the forest will be reached: straightness values of the travel routes will reach adult values before age of first reproduction.

2. For the *learning mechanisms* I expect that infants and juveniles learn through independent exploration and socially from their mothers (vertical transmission) and other role models (horizontal transmission) if available. After leaving their mothers juveniles will acquire additional skills and knowledge by independent exploration and socially from their peers and adult individuals (horizontal transmission).

2a) Infants and juveniles show selective peering at short range role models. Peering rates are increased for items that are complex to process or rare in the mother's or in their own diet.

2b) Young infants show the highest peering rates because they are the least knowledgeable. Thereafter, with increasing age peering rates of immatures decrease and reach adult values before age of first reproduction.

2b) If individuals other than the mother are close by, older immatures (which have reached a certain level of skills) will peer more frequently at these role models than at their mothers. This is expected because these individuals may have additional skills to the ones the immature already learned from their mothers. Consequently, immatures which have already acquired most skills from their mothers and have the locomotor capacity to choose between different potential role models will show more interest in foreign role models.

2c) Young infants show the highest rates of object play and explorative behavior because they are the least knowledgeable. With increasing age rates of those behaviors

decrease.

2d) Try feeding rates are higher for food items that require a high level of processing skills and for items that are rare in the mothers' diet.

2e) Explorative behavior and object play mainly follows the immatures peering pattern as it is an outcome of social learning. However, some of it can't be linked to the infants peering pattern as it is based on independent exploration. This includes that immatures are expected to try feed on items that are not part of their mother's diet.

2f) Juveniles that have just started to range independently will show a great overlap in diet composition with their mother whereas in older juveniles the overlap with their mothers decreases with age because the juveniles include new foods in their repertoire.

2 Methods and Material

2.1 Study site and study period

Data was collected in a six month period between October 2010 and April 2011 on a population of Sumatran orangutans at the Suaq Balimbing research station $3^{\circ}42'N$, $97^{\circ}26'E$, Aceh selatan, Indonesia). The Suaq Balimbing research area consists of 500 ha coastal peat swamp forest, with adjacent areas of mixed dipterocarp, riverine, and seasonally flooded freshwater swamp. The orangutans at Suaq Balimbing have been object to behavioral observations between 1992 and 1999 and from 2007 on. At Suaq Balimbing an orangutan density of seven individuals per square kilometer has been recorded, which is currently the highest known number of wild orangutans (Singleton and van Schaik, 2001; Husson et al., 2009).

2.2 Data collection

2.2.1 Procedure

Data was collected daily by following focal animals from their morning nest to the evening nest. To collect behavioral data, standardized methods of focal animal sampling including instantaneous scan sampling with two minutes intervals and ad libitum focal animal sampling following an established protocol for orangutan data collection ([www.aim.uzh.ch/orangutannetwork/Field Guidelines.html](http://www.aim.uzh.ch/orangutannetwork/Field%20Guidelines.html)) were used. Every two minutes the activity of the focal animal and its distance to all party members (see definitions of distance classes below) was recorded. Special attention was given to social interactions, feeding techniques and explorative behavior. These behaviors were recorded ad libitum so as to get a complete record. Ranging data (exact GPS locations with a precision of 5-10 m) were collected throughout the focal follows at half hours using a GPS device (Garmin GPS map 60CSx). Data collection was conducted by me, Sofia Forss (a PhD student working on a similar project) and five well trained field assistant. Additionally, data collected from 2007 to 2009 by Ellen Meulman, Sofia Forss and field assistants formed part of the analysis. This data was collected in the same way, following identical protocols and using the same definitions of behaviors. The two data collection periods will be referred to as the first (2007-2009) and the second study period (2010-2011).

2.2.2 Definitions of activities

Definitions of different kinds of activities such can be found in the standardized protocol for orangutan data collection ([www.aim.uzh.ch/orangutannetwork/Field Guidelines.html](http://www.aim.uzh.ch/orangutannetwork/Field%20Guidelines.html)). Classifications and definitions of behavioral elements especially relevant for this study are listed below.

Developmental stages of study subjects:

Immatures: All immature animals between birth and age of first reproduction.

Infants: Immature animals before the age of weaning.

Juveniles: Immature animals between the age of weaning and age of first reproduction.

Feeding context:

Food item: Different edible items (e.g. leaves, fruits, flowers) of the same plant species are considered as different food items. The term "food item" usually refers to a unique species item combination.

Food patch: within one tree or trees with the same food item within 10 m distance.

Processing steps: depending on the complexity of the technique needed to ingest the item the following processing steps were defined (See Forss2009 for examples): Processing step 0: Items that are picked and ingested as a whole.

Processing step 1: Items that need one step of processing such as breaking up, spitting out or peeling off item parts in order that they can be ingested.

Processing step 2: items that need two of the above described steps of processing combined.

Processing step 3: items that need three of the above described steps of processing combined.

Processing step 4: items that need four of the above described steps of processing combined.

Processing step 5: whenever tool use is involved in the foraging process.

Tool use: Foraging that includes the use of tools (e.g. broken off sticks) to access the food item. Two forms of tool use were observed during the course of this study: inserting sticks into tree holes to seize insects or their product (tree hole tool use) or inserting sticks into Neesia fruits to obtain the nutritious seeds that are protected by an extremely hard fruit shell with itchy hairs (seed extraction tool use)(figure2.7).

Explorative behavior:

Object play (APO): Manipulation of objects with no apparent immediate goal, including repetitive movements(figure2.5).

Try feeding: Feeding attempt on a food item or other object whereby the item is taken into the mouth but not properly ingested(figure2.5).

Exploration: Non repetitive, usually destructive manipulation of objects without apparent feeding purpose (figure 2.5).

Sampling: Eating something for the first time (this cannot be recognized as such during data collection but only be detected retrospectively, when analyzing the data).

Associations with conspecifics:

Party: Association of two individuals within 50 m distance from each other. A party size of one means the focal animal was on its own, party size two that it was in association with one other individual and so on.

Distance classes: the following distance classes were used (m):

0: individuals are in body contact.

< 2: individuals are within less than two meters distance from each other but not in body contact.

< 5: individuals are within two and five meters distance from each other.

< 10: individuals are within five and ten meters distance from each other.

< 50: individuals are within ten and 50 meters distance from each other.

Feeding tolerance: Party members were feeding in the same feeding patch: in the same tree or within ten meters from each other, feeding on the same type of food item.

Co-Feeding: Party members feeding from one and the same item close together or taking turns.

Peering: An individual is directly looking at the action of another individual sustained over at least five seconds and at a close enough range that enables the peering individual to observe the details of the technique used by the other (figure 2.6).

2.2.3 Observed skill classes and measures of competence

In terms of ecological competence (according to the definition of Galef and Giraldeau (2001)), data on diet composition and *food selection competence* (What to eat), *processing competence*: processing techniques and foraging efficiency (How to eat) and *range use competence* (When and where to eat) was collected:

To investigate food selection competence, I looked at diet composition of the juveniles in terms of relative overlap with the mother's diet. I assessed levels of food selection competence by looking at the amount of independent feeding bouts of immatures (e.g.

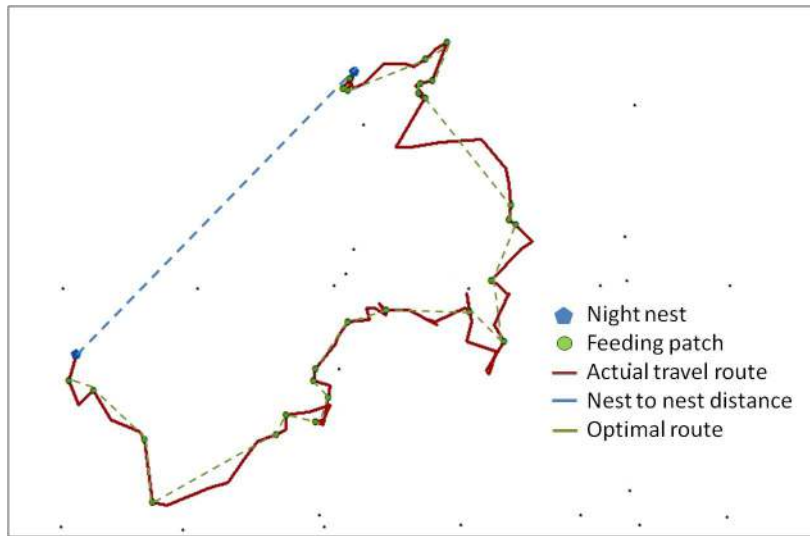


Figure 2.1: **Ramble ratios calculations.** GPS data of an example full day follow including the exact actual travel route of the focal animal, positions of night nests and feeding patches. Only feeding patches in which the focal animal was observed eating for more than 5 min were recorded.

bouts in which the immature starts to eat before the mother does or eats all alone) and the amount of try feeding of inedible food items.

To asses food processing competence I compared processing techniques between the individuals. As a measure of level of competence I used the similarity to the mother's techniques. Foraging efficiency was estimated by the intake- and processing rates (e.g. average time to collect, open, handle and eat) of the different food items as in Dunkel (2006).

Range use competence is the ability to find foods in correct proportions and time intervals. To investigate range use competence, the path traveled by the focal individual during an observation day was recorded with the help of a GPS device. Every 30 minutes the exact location of the focal animal was recorded. In order to get more precise data on the actual travel route of the focal animals we additionally took GPS data every five minutes. However, this was only possible on certain days as it required the presence of an additional observer. Sinuosity values (ramble ratios) were calculated by dividing the length the actual route traveled on a given day (daily path length) by the distance between the two successive night nests (nest to nest distance; figure2.1). In addition, so called feeding ramble ratios were calculated by dividing the daily path lengths by the length of the direct route from feeding patch to feeding patch (optimal route; figure2.1). Consequently, a higher ramble ratio value implies a more straight ranging pattern.

2.3 Focal animals

I focused data collection on two mother infant pairs, five juvenile animals and additionally on one adult female which is the mother of one of the juveniles (figure2.2, figure2.3, figure2.4). The three adult females in the sample were mothers of all but two of the immatures 2.1. Of the latter the mothers are not known. Genetic analysis showed that there are most likely two different mitochondrial DNA lineages (mtDNA lineages) in Suaq Balimbing. Five of the immature focal animals could be assigned to mtDNA lineage, whereas for the others the genetic data is not available yet. Of all but two of the focal animals data from July 2007 until April 2009, collected by Sofia Forss and Ellen Meulman was available and included in the analyses 2.1. Of one mother-infant pair (Raffi and Ronaldo) only data collected in the period 2007-2009 could be included in the analysis as they could not be followed long enough in 2010-2011. Dates of birth for the focal individuals are widely unknown. Ages of the immature animals were estimated absolutely and relatively to each other before commencement of the data analysis. I obtained relative ages of the juveniles by body size comparison whenever two of them were observed within less than two meters of each other. This enabled to six direct size comparisons (each comparison was done by at least two observers individually) from which we obtained the complete size hierarchy. These relative ages were translated into absolute estimates by recorded timing of the entry at different life stages and dates of birth of younger siblings. Juveniles that were in party with their mothers for more than 30% of the observation time were classified as semi-independently ranging, the others as independently ranging. Ages of infants were determined by body size comparisons and by the amount of time spent in body contact with their mothers and based on the amount of travel assistance they received from their mothers when ranging through the canopy. Infants were classified into clinging or non-clinging infants: based on Forss (2009) infants were classified as clinging infants when they spent less than 10% of their moving time in body contact with their mothers.

Depending on the location of their home range and therefore traceability, the amount of follow hours differs between individuals 2.1. To avoid sampling biases I only considered individuals with a minimum of approximately 100 follow hours in this study. For each separate analysis I determined a different amount of minimal follow hours and therefore not all individuals could be included in all analyses (see results).

2.4 Comparison to data collected at Tuanan

I compared the collected data with data from previous projects on skill acquisition of immature orangutans at the Tuanan study site in Borneo ($2^{\circ}09'06''.1''S$, $114^{\circ}26'26''.3''E$, Kalimantan tengah, Indonesia). The habitat at Tuanan consists of partly logged peat swamp forest. Orangutans at Tuanan have been object to behavioral observations since 2003. Tuanan has an orangutan density of 3.84 animals per square kilometer (Husson et al., 2009). Data collected on Bornean orangutans (*P. pygmaeus wurmbii*) by Lynda



Figure 2.2: **Adult focal animals.** Lisa, Friska, Cissy and Raffi (from left to right).



Figure 2.3: **Juvenile focal animals.** During the second study period: Tina (14-15 y), Shera (13-14 y), Ellie (12-13 y), Lilly (10 y) and Chindy (9 y) (from top left to bottom right).



Figure 2.4: **Infant focal animals.** Fredy (5-6 y) and Lois (0.5-1 y) of the second study period (2010-2011) and Ronaldo (1-2 y) during the first study period (2007-2009) (from left to right).

Table 2.1: **Focal animals and follow hours.** Estimated age, relatedness and assigned developmental class for all focal animals during the first (2007-2009) and the second study periods (2010-2011). Red and blue colored names indicate different mtDNA lineages. For animals without a colored name the genetic data is not available yet. Follow hours of each of the focal animals are given for the first and second study period. The last column shows how many full follow days with GPS data were available (second study period only) whereby in the brackets the number of follow days on which GPS data was collected at five minutes intervals is given (*).

Name	Sex	Mother	Estimated age 2010-2011	Developmental class 2010-2011	Estimated age 2007-2009	Developmental class 2007-2009	Follow hours 2007-2009	Follow hours 2010-2011	Total follow hours since 2007	Number of GPS full-day follows*
Lois	m	Lisa	0.5-1y	clinging infant				111	111	
Ronaldo	m	Raffi			1-2y	clinging infant	92		92	
Fredy	m	Friska	5-6y	non-cl.infant	2-3y	clinging infant	389	154	542	
Chindy	f	Cissy	9y	1/2indep.juvenile	6-7y	non-cl.infant	97	120	217	8 (5)
Lilly	f	Lisa	10y	indep.juvenile	7-8y	non-cl.infant	292	111	403	7 (6)
Ellie	f	Friska	12-13y	indep.juvenile	9-11y	1/2indep.juvenile	243	227	469	12 (6)
Shera	f	unknown	13-14y	indep. juvenile		indep. juvenile		197	197	11 (4)
Tina	f	unknown	14-15y	indep. juvenile	11-12y	indep. juvenile	169	150	319	6 (4)
Lisa	f	Cissy	unknown	adult female	unknown	adult female	300	111	411	11 (5)
Friska	f	unknown	unknown	adult female	unknown	adult female	420	153	573	12 (6)
Cissy	f	unknown	unknown	adult female	unknown	adult female	93	64	158	3 (3)
Raffi	f	unknown	unknown	adult female	unknown	adult female	92		92	

Dunkel and Adrian Jaeggi (2006) were used for the comparison.

2.5 Inter observer reliability

I calculated inter observer reliabilities using special follow days during which one or more observers were following the same individual. During these follows no verbal exchange about the activity of the focal between the observers took place. For the instantaneous scan sampling the mean index of concordance for the recorded activities was 84.86 ± 3.37 . Daily rates of the different activities reached an even higher level of accordance and no difference in the daily rates of the different activities was found between the observers (Wilcoxon: $n = 5$, $p = 0.955$). For all behaviors that were collected ad libitum (including try feeding, object play, exploration and peering) only data collected by Sofia Forss and me was included in the data analyses. Because we did not have enough simultaneous follows to calculate exact inter observer reliabilities, I calculated hourly rates for each follow day for the two infant focal animals (which showed all behaviors on a daily base) and compared them between the two observers. To limit environmental influences I matched the days between the observers in a way that only successive days were compared. I found some evidence for a difference between Sofia Forss and me 2.2. For each of the two infants only three or four days for each observer could be compared. Furthermore, there was a lot of variation in the frequency of occurrence of these behaviors between days and therefore, the comparisons may not be very accurate. However, as for both infants the relative proportions of follow hours for each observer were approximately the same, the difference between the observers should not affect the difference between the focal animals.

Table 2.2: **Inter observer reliabilities of ad libitum data.** Mean frequencies and standard deviations of peering, object play (APO), try feeding (TF) and exploration rate (events per feeding hour of the mother, as these behaviors occur mainly when the mother is feeding), recorded by Caroline Schuppli (CS) and Sofia Forss (SF).

Focal	Obser- ver	mean peer- ing rate	stdev	mean APO rate	stdev	mean TF rate	stdev	mean ex- plo- ration rate	stdev
Fredy	CS	0.45	0.15	1.27	0.56	0.64	0.82	0.09	0.08
Fredy	SF	0.52	0.74	0.83	0.30	0.47	0.45	0.13	0.19
Lois	CS	2.92	0.44	2.26	1.29	1.62	0.60	0.08	0.17
Lois	SF	1.59	0.49	0.79	0.34	0.93	0.36	0.03	0.06



Figure 2.5: **Different forms of explorative behavior.** Try feeding, exploration and object play (from left to right).



Figure 2.6: **Peering.** A juvenile peering at an unflanged male, a juvenile peering at another juvenile and an infant peering at his mother (from left to right).



Figure 2.7: **Different forms of tool use.** Tree hole tool use (left) and seed extraction tool use (right).

3 Results

3.1 Ecological competence

3.1.1 What to eat: Food selection competence

To investigate food selection competence (the ability to recognize food items), I calculated diet overlaps between mother and offspring. By the end of the second study period 52-72 different food items were recorded for each of the three adult focal animals that were followed in both study periods. However, between the two study periods the diets of all three females grew drastically 3.1 and so it could well be that we do not have a complete record of the diet repertoires yet. Therefore, with likely constraints of the current data set conclusions about diet selection competence have to be drawn very carefully. To best avoid potential sampling biases in terms of different amounts of follow hours, I always compared the immatures directly to the recorded state of their mothers of the given study period.

Table 3.1: **Diet spectra of adult females.** Number of different food items recorded in both study periods for each adult female (mother).

Mother	number of recorded food items 2007-2009	number of recorded food items 2007-2011
Friska	51	71
Lisa	54	68
Cissy	33	52
Raffi	20	

With increasing age the immatures ate an increasing proportion of their mother's food items (Spearman: $n = 10$, $r = 0.94$, $p < 0.001$, figure 3.1 a). Around the age of weaning they ate approximately 80% of their mothers' food items whereby this value did not seem to increase after the age of weaning. Shortly before the age of weaning immatures started to include food items in their diets that their mothers had never been observed eating. The large majority of those items were known to be part of other adult individuals' diets. The proportion of those items increased significantly with advancing age (Spearman: $n = 10$, $r = 0.97$, $p < 0.001$, figure 3.1 b). Neither the overlap with mother's diet nor the proportions of items that exclusively offspring had been observed eating correlated with the follow hours (Spearman: $n = 10$, $r = 0.26/0.288$, $p = 0.467/0.419$), which provides reassurance that this result is not simply driven by a sampling bias. Furthermore, I investigated diet spectrum sizes (the sheer number of items in an individuals' diet) whereby I compared the number of different food items of the immature animals to the number of food items of the adult female with the most comparable amount of follow hours (for all immatures with known relatedness this was their mother). I found that spectrum size increased with age (Spearman: $n = 13$,

$r < 0.001$, $p = 0.04$, figure3.1 c). It also seemed that adult spectrum size was reached around the age of 12 and that older juveniles might have had slightly bigger spectrum sizes than adult animals with comparable amount of follow hours (figure3.1c).

For infants, food selection competence can also be measured in the proportion of independent food patch discoveries. This is distinct from the ability to locate food patches in the forest (which is discussed below): food patch discoveries are thought to show the competence to discover edible food items at close range whereas locating food patches works over a wider range. Based on Forss (2009) I counted all feeding bouts in which the infant started feeding before its mother did or fed completely independently (while the mother was feeding on something different or performing another activity) as independent discoveries. With increasing age the number of independent food patch discoveries increased significantly (Spearman: $n = 5$, $r = 0.90$, $p = 0.037$, figure3.2). Shortly before the age of weaning the proportion of independent feeding patch discoveries reached around 50% of all feeding bouts. This strongly suggests that at this age, infants are equally competent in discovering food patches as their mothers.

To sum up, even though I have to draw conclusions prudently because diet repertoires are most likely incomplete at the current state of this research, I found evidence that food selection competence reaches adult rates latest around the age of twelve. With increasing age infants show an increasing diet overlap with their mothers. Shortly before the age of weaning immatures are equally competent as their mothers in recognizing food patches at a close range. Around the same time they start to add food items to their diets that their mothers do not seem to eat. Older juveniles have similar sized or even slightly bigger diet repertoires than adult animals and therefore seem to have reached full food selection competence.

3.1.2 How to eat: Food processing competence

I assessed the ability to process food by comparing feeding rates of the immatures with the ones of adult females. As feeding rates are potentially influenced by different ecological factors I only included data for which exact information about ripeness and abundance of the fruits in the tree was available in the following analyses. Because developmental trajectories might vary for items of different complexity, I analyzed the development of feeding rates separately for items that needed different steps of processing.

In the first place, I compared feeding rates of adult females (Friska, Cissy and Lisa) for items with different processing steps. Feeding rates of items that require one step of processing were significantly higher than of items with two or three processing steps (Mann-Whitney U: $n_1 = 4$, $n_2 = 8$, $n_3 = 4$, $p_{1,2} = 0.004$, $p_{1,3} = 0.029$, figure3.3), whereby I found no difference in feeding speed between items that required two or three processing steps (Mann-Whitney U: $n_{2,3} = 8, 4$, $p = 0.8$; figure3.3). To find out whether fruit size rather than processing complexity drove this result I used a stepwise multiple linear regression model with feeding rate as a dependent and processing steps as well as fruit size (diameter of the widest part of the fruit) as independent variables.

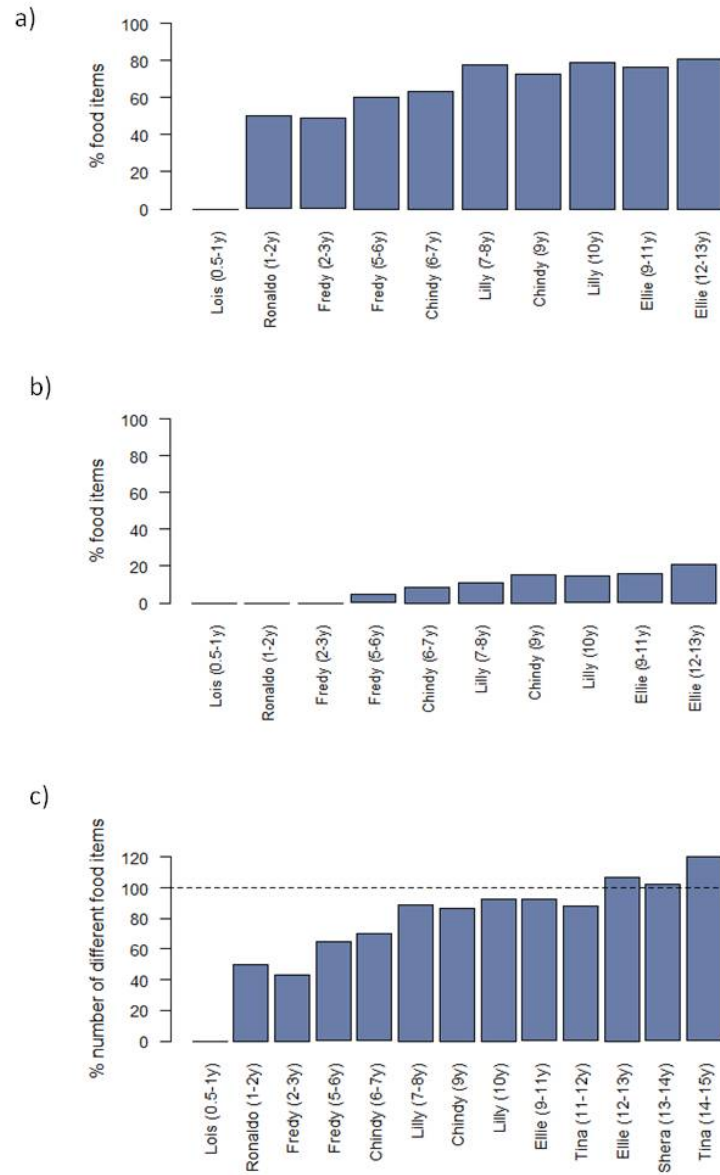


Figure 3.1: **a) Diet overlap with mother.** The proportion of mothers' food items eaten by offspring. **b) Food items which only offspring eats.** Proportion of food items in offspring's diet that mother has never been observed to eat. **c) Diet spectrum size.** Number of different food items in percentage of spectrum size of the adult female with the most similar number of follow hours.

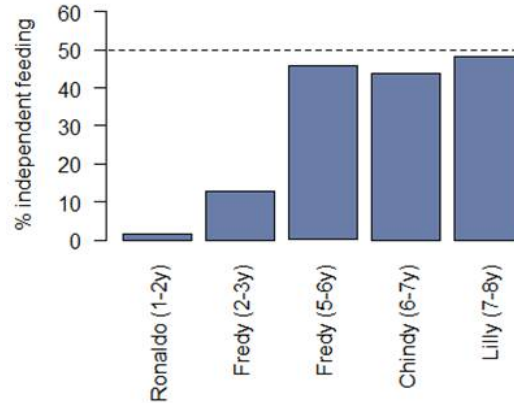


Figure 3.2: **Independent discoveries of food patches.** Percentages of all feeding bouts in which the infant started feeding before the mother did or fed completely independently (while the mother was feeding on something different or was engaged in another activity).

The most powerful model ($n = 16$, $R^2 = 0.61$, $p = 0.008$, $AIC = 116.712$) included processing complexity, fruit size and the interaction between these two factors. The models showed that processing complexity had a significant negative effect on feeding speed ($p = 0.015$, slope = -0.49) whereby fruit size only showed a trend for such an effect ($p = 0.092$, slope = -3.30). The interaction term showed that with decreasing processing complexity fruit size had a stronger negative effect on feeding speed ($p = 0.038$, slope = 2.94).

This confirms that with increasing processing complexity of the food item feeding rates become lower, whereas fruit size influences feeding speed only for items of low processing complexity. This justifies the processing steps we had defined before the analysis as it shows that they indeed manifest in the behavior of the animals.

For every food item, I expressed feeding rates of the immatures in percentage of the average adult females feeding rate. I did this for ten different food items of which we had feeding rates of several individuals (3 for processing step one, 4 for processing step two and 4 for processing step three). For each individual I only included a given food item in the analysis when a sample of at least five single measurements was available. Therefore, not for all of the food items I could use data of every individual: for each item data of 4 to 10 individuals was available. A multiple linear regression model ($n = 33$, $p < 0.001$, $R^2 = 0.35$, $AIC=373.75$, figure3.4) revealed a significant effect of age ($p = 0.001$, slope = 2.14) and processing steps on feeding speed ($p = 0.041$, slope = -7.78), whereby the interaction between the two factors was not significant ($p = 0.206$). This suggests not only that feeding speed gradually increased with age but also that developmental trajectories differed depending on the level of processing an item requires: adult feeding speed seemed to be reached earlier for less complex items. However, adult like feeding speed for all classes of items seemed to be reached around the age of twelve (figure3.4).

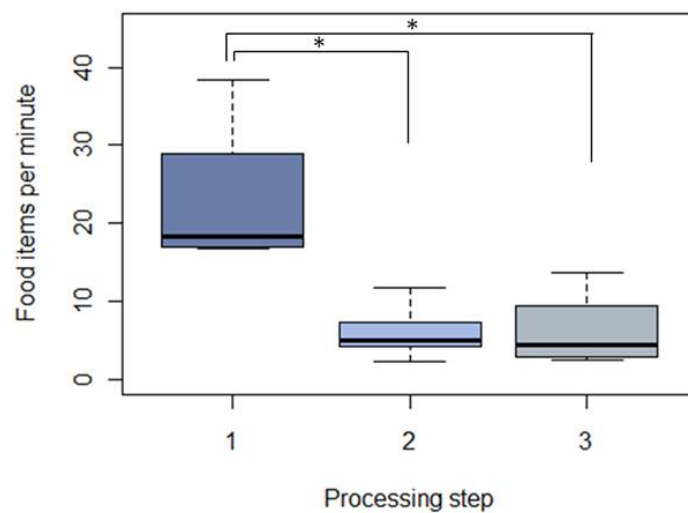


Figure 3.3: **Feeding rates of adult females.** Average feeding rates (food items per minute) of three adult females (Cissy, Friska and Lisa) for items requiring different steps of processing. * $p < 0.05$.

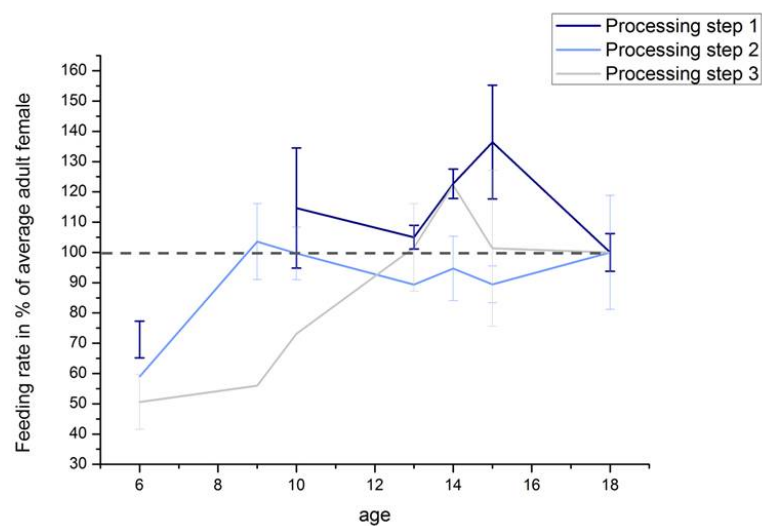


Figure 3.4: **Development of feeding rates.** Feeding rates in percentage of the average feeding rate of the adult females across differently aged individuals.

I did not observe any systematic difference in the feeding techniques between adult and juvenile animals. Only adult and juvenile animals (but never infants), were observed to use tools successfully. Unfortunately, we could collect only limited tool use data in the second study period: my observation period did not coincide with a *Neesia* fruiting season and therefore, I could not observe any seed extraction tool use. However, in a former study van Noordwijk and van Schaik (2005) have found that seven year olds are competent *Neesia* tool users. During the second study period we observed Tina, Ellie and Lilly doing insect tool use. For Ellie we recorded four incidents of insect tool use whereas Tina was observed using tools twice. They both seemed equally competent as adult females: they acted very goal directed and successfully extracted the food items. For Lilly we recorded more than 30 incidents of insect tool use whereby all but one of them happened on a single day. Lilly still seemed to struggle a bit when using tools: she often discarded her tool after very short time, mostly without being successful and immediately made new tools.

In sum, by comparing the immatures' feeding rates and techniques with the ones of adult animals I found strong evidence that juveniles around the age of twelve years are as competent as adults in processing all food items using the same techniques (including tool use).

3.1.3 When and where to eat: Range use competence

To investigate range use competence (the ability to locate food patches in the forest) I calculated different sinuosity values of the travel route: ramble ratios and feeding ramble ratios (see Material and Methods for definitions), whereby only data taken in the second study period (2010-2011) was available. For the juveniles I only included days on which they ranged independently from their mothers in the analysis. I used data of the three adult females Friska, Lisa and Cissy to get an adult reference.

In the first place I used all data of full follow days (during which the focal animal was followed from the morning to the evening nest) for which the GPS data at 30 min intervals was available. This led to a sample size of 6 to 12 follow days per individual. Standard deviations of the daily ramble ratios of all individuals overlapped and I found no effect of age on the ramble ratios (Spearman: $n = 6$, $r = -0.49$, $p = 0.329$, figure 3.5 a). To correct for differences in food availability over time that might influence the ranging patterns I assigned each follow day to one of five different time periods (each of approximately four weeks). For each time period I then calculated the average adult female daily ramble ratio and expressed each ramble ratio of the juvenile animals in percentage of this adult reference. Again, I found no relationship between age and ramble ratio (Spearman: $n = 6$, $r = 0.26$, $p = 0.623$, figure 3.5 b).

In the second place I redid the same analysis with the more precise ranging data which was based on GPS data collected at five minutes intervals. This data also allowed the calculation of the feeding ramble ratios. I found no correlation between age and daily ramble ratios (Spearman: $n = 6$, $r = -0.46$, $p = 0.544$, figure 3.6 a) or between age and daily feeding ramble ratios (Spearman: $n = 6$, $r = -0.46$, $p = 0.544$, figure 3.6 b).

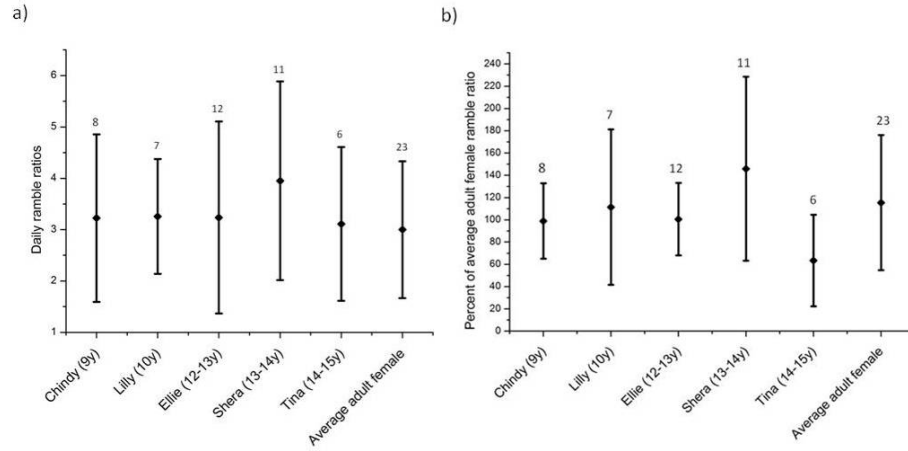


Figure 3.5:) **a) Daily ramble ratios.** Means and standard deviations of daily ramble ratios (actual travel route divided by direct nest to nest distance) of juveniles on days they ranged independently, compared to adult females based on GPS data taken at 30 min intervals. Numbers above the variance bars indicate sample size (number of follow days). **b) Daily ramble ratios in percentage of average adult female per time period.** Daily ramble ratios of juveniles on days they ranged independently expressed in percentage of the average adult female daily ramble ratio within the same four weeks period.

b). Interestingly, all juveniles, even the youngest one (Chindy) showed ramble ratios and feeding ramble ratios which partly overlapped with the range of adult females. However, Chindy showed the highest variation in both ramble and feeding ramble ratios. This could be seen as indication that she still had some problems locating food patches in the forest. Lilly which we estimated to be only about a year older than Chindy showed constantly low ramble and feeding ramble ratios.

To sum up, the comparison of ramble ratios of juveniles with the ones of adult females suggests that the competence to locate food patches in the forest emerges around or shortly after the age at which immature orangutans start to range independently.

3.2 Learning mechanisms: Social learning or independent exploration

Orangutans are assumed to acquire skills via two mechanisms: social learning and independent exploration (Jaeggi et al., 2010). For social learning I investigated time spent in association with other individuals and peering rates. For independent exploration I looked at object play, try feeding and exploration. For many of the results I present in this section Sofia Forss conducted similar analyses on the same population in 2009 for her Master's thesis on independent exploration and social learning in immature Sumatran orangutans. In the meantime sample size has grown: follow hours of all focal animals have increased and furthermore new individuals could be included in the analysis. One of the goals of the current study is to review and clarify the old results by redoing some of the analyses and by conducting analyses that have formerly

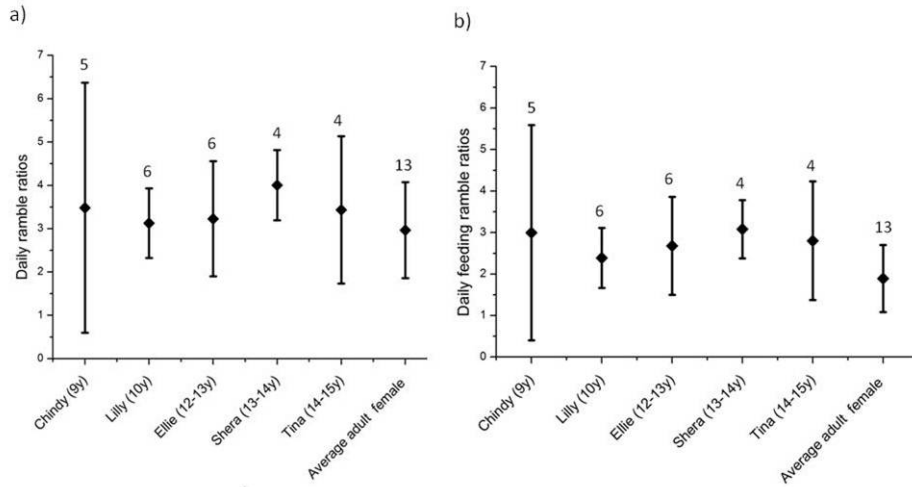


Figure 3.6: **a) Daily ramble ratios.** Means and standard deviations of ramble ratios (actual travel route divided by direct nest to nest distance) of juveniles on days they ranged independently, compared to adult females, based on GPS data taken at 5 min intervals. Numbers above the variance bars indicate sample size (number of follow days). **b) Daily feeding ramble ratios.** Means and standard deviations of feeding ramble ratios (actual travel route divided by the direct route from feeding patch to feeding patch) of juveniles on days they ranged independently, compared to average adult female.

not been possible due to the limited sample size.

3.2.1 Time spent in association with others

To investigate opportunities for social learning I looked at the time spent in party with other individuals and the distances between individuals when in party. The total amount of time immature orangutans at Suaq Balimbing spent in party with other individuals decreased with age (Spearman: $n = 13$, $r = -0.88$, $p < 0.001$, figure3.7).

For the association time with different classes of individuals I found that the proportion of time spent with the mother decreased steeply from the age of weaning on (Spearman: $n = 13$, $R^2 = -0.90$, $p < 0.001$, figure3.8). No age effect was found for the time spent in party with individuals other than the mother (Spearman: $n = 13$, $r = -0.16$, $p = 0.596$, figure3.8).

Consistent with a former study on the same population (van Noordwijk and van Schaik, 2005) I found that the proportion of total party time the offspring spent within two meters of the mother decreased with age (Spearman: $n = 8$ (infants and semi-independently ranging juveniles), $r = 0.99$, $p < 0.001$,) whereas the proportion of total party time spent between 10 and 50 meters of the mother increased during infancy (Spearman: $n = 8$, $r = -0.97$, $p < 0.001$, figure3.9a). For the associations with other classes individuals I observed no such age effect (Spearman: $n = 13$ (all immatures), $r = 0.12 / -0.03$, $p = 0.694 / 0.915$, figure3.9b). However, it seemed that older infants might have spent a slightly higher proportion of total party time than younger infants

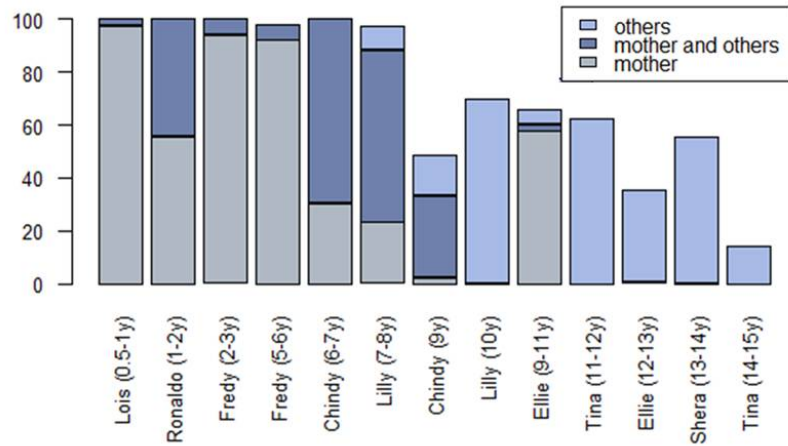


Figure 3.7: **Time spent in party.** Percentage of total follow time the immatures spent in party with *only the mother* (including older and younger sibling), *the mother and other individuals*, and *only other individuals*.

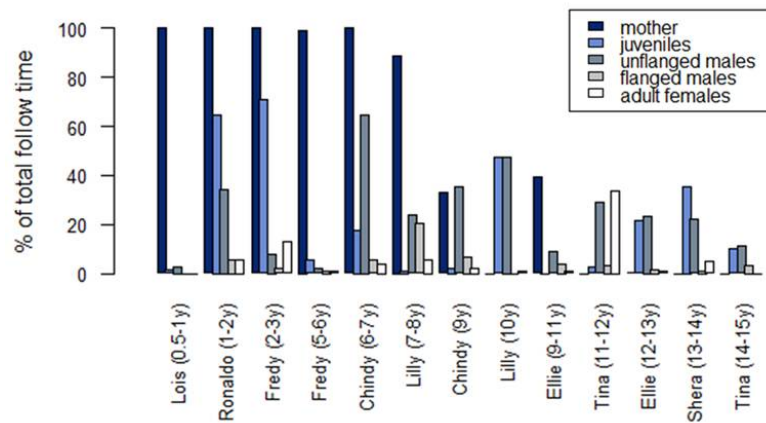


Figure 3.8: **Time in party with different classes of individuals.** Percentage of total time the immature spent in party with their mothers (including younger (infant) sibling), juveniles (females and males), unflanged males, adult females (mother-infant pairs and adult females without offspring) and flanged males.

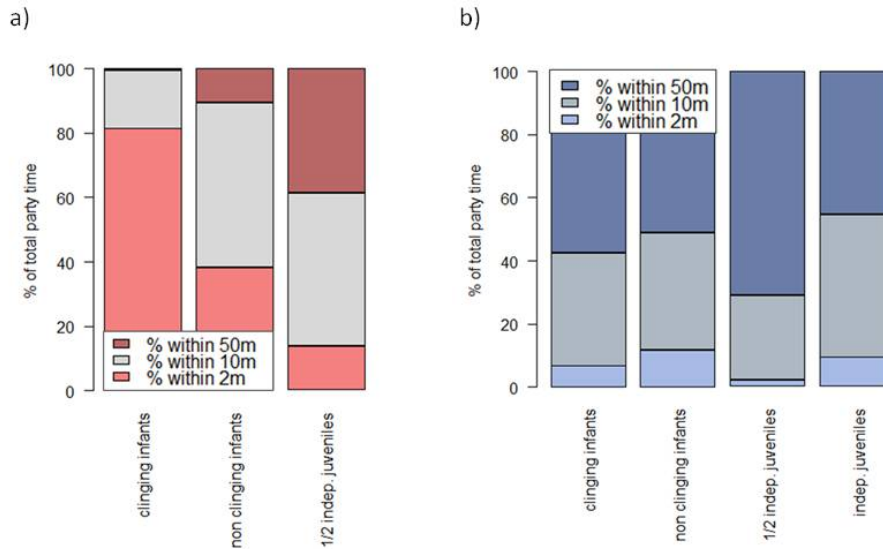


Figure 3.9: **a) Distances when in party with mother.** Time immature (clinging infant, non clinging infants and semi- independently ranging juveniles) spent within different distance classes (0-2 m, 2-10 m and 10-50 m) in percentage of total party time with the mother. **b) Distances when in party with individuals other than the mother.** Time immatures (clinging infant, non clinging infants, semi-independently ranging juveniles and independently ranging juveniles) spent in different within different distance classes (0-2 m, 2-10 m and 10-50 m) in percentage of total party time with individuals other than the mother.

within two meters of party members other than their mothers (figure3.9b). Semi-independently ranging juveniles seemed to spend less time in close distance to their non-mother party members compared to older juveniles or infants (figure3.9b).

The amount of time spent in feeding tolerance with individuals other than the mother varied across different age classes (figure3.10) and was in line with the distance pattern described above. For infants the proportion of feeding time spent in feeding tolerance with individuals other than the mother varied remarkably (between 3 and 25%). This is most likely attributable to the older sibling of some infants, representing a very tolerant party member. In the first study period Fredy (2-3 y) was around 75% of the total follow time in party with his juvenile sister Ellie. 15% of this time he spent within two meters of her. Ronaldo (1-2 y) was around 65% of the time in party with an adolescent female that might have been his sister, however genetic data is not available yet. Lois (0.5-1 y) on the other hand was seen only once and very briefly in association with his older sister Lilly. Semi-independently ranging juveniles spent only around three percentage of their feeding time in feeding tolerance. This is consistent with the observation that during the second study period, Chindy (9 y) seemed to actively avoid parties with individuals other than her mother; and (once in party with them) close distance to these individuals. This was especially pronounced when she was ranging independently from her mother. Independently ranging juveniles spent up to 26% of their total feeding time in feeding tolerance with other individuals. However, the oldest juvenile (Tina 14-15 y in the second study period) spent only around 5% of her feeding

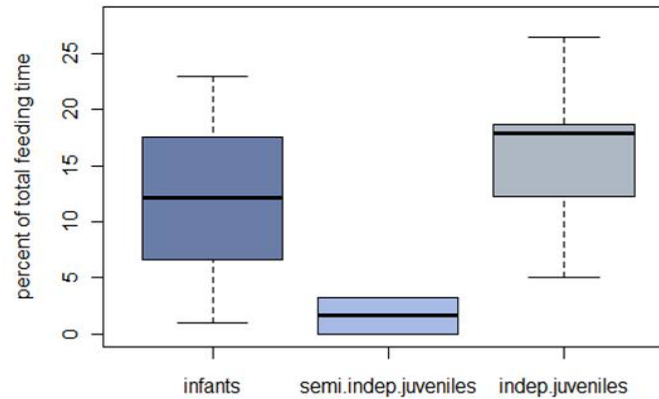


Figure 3.10: **Time spent in feeding tolerance with individuals other than the mother.** Percentage of total feeding time infants, semi-independently ranging juveniles and independently ranging juveniles spent in feeding tolerance with individuals other than the mother.

time with other individuals. She also seemed to actively avoid parties with any other individual: eventhough other juveniles and unflanged males regularly approached her she distanced herself as soon as she could.

The five ranging juvenile females of the second study period were often in party with each other. Several times they were observed to range in groups of two to four for several days in a row. These parties were always very peaceful and individuals spent a lot of their time in close distance to each other (figures3.9, 3.10). The association times varied remarkably between different dyads: Some dyads spent up to 19% of their total time with each other whereas others had never been observed o be in party with each other 3.2.

Table 3.2: **Association times and home range overlaps of the juveniles.** Below the grey bars: Percentage of total time spent in party with each other (averaged for the two perspectives of each dyad). Above the grey bars: Percentage home range overlap (averaged for the two perspectives of each dyad). All data comes from the second study period. Red and blue colored names represent different mtDNA lineages, for the black names the genetic data is not available yet.

	Chindy	Ellie	Lilly	Shera	Tina
Chindy		62.6	73.1	44.1	57.5
Ellie	1.7		46.9	67.8	62.0
Lilly	0.0	5.3		37.5	55.7
Shera	0.9	18.6	13.6		58.3
Tina	0.0	3.0	0.2	3.5	

To calculate home range overlaps I used minimum convex polygons (MCP). Not of every individual the same amount of ranging data was available. Furthermore, the analysis contained many follows of consecutive days. Hence, the calculated home ranges may not be too accurate. However, what can be said is that all their home ranges overlapped to a large extent (mean overlap was $56.55 \pm 10\%$ (SD); figure3.11)

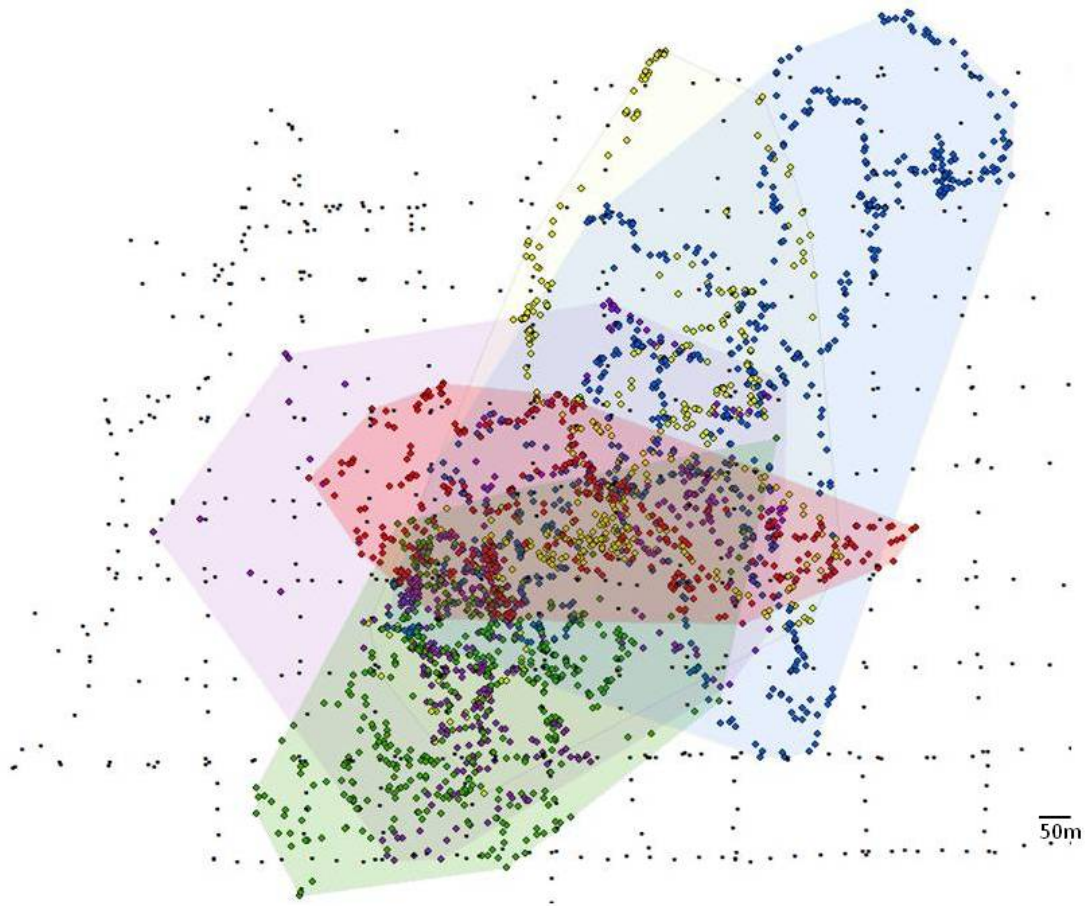


Figure 3.11: **Home ranges of the juveniles.** The Suaq Balimbing research area with all collected ranging data and calculated home ranges (MCP) of the four juveniles of the second study period (2007-2011): green: Shera, purple: Ellie, red: Tina, yellow: Chindy, blue: Lilly.

and that association times of the different dyads did not seem to be a simple measure of home range overlap (Spearman: $n = 5$, $r = -0.16$, $p = 0.663$).

In an earlier study on the same population Singleton and van Schaik (2002) suggested that adult females preferentially associate with relatives. Unfortunately, the genetic data of the Suaq individuals is not fully available yet (table 3.2). However, the current study provided some evidence that the juvenile females at Suaq associate irrespective of relatedness: Shera seemed to preferentially associate with Lilly and Ellie, which stem from two different mtDNA lineages. Lilly showed a high association tendency with Shera whilst she seemed to avoid Ellie (who is from a different mtDNA lineages). Lilly was also never seen in party with her aunt Chindy, even though in the first study period in which both of them were still ranging with their mothers, they spent a lot of time in party with each other (Forss, personal communication).

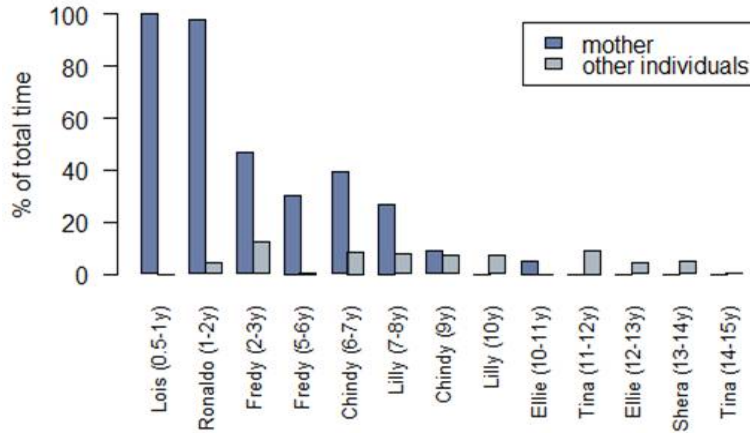


Figure 3.12: **Opportunities to peer: time spent within 2 m of others.** Percentage of total follow time the immatures spent within two meters of the mother and of other individuals.

3.2.2 Peering

By peering, orangutans might learn socially from each other. The definition of peering includes that the peering individual has to be at a close enough range that enables it to observe the details of the technique used by the other. For most foraging activities this range lies at less than two meters. The proportion of time the immatures spent within two meters to the mother, when being in association, decreased significantly with age (Spearman: $n = 13$, $r = -0.95$, $p < 0.001$, figure3.12). The proportion of time within two meter of individuals other than the mother, when in association, varied between the individuals and showed no clear age effect (Spearman: $n = 13$, $r = -0.11$, $p < 0.972$, figure3.12). Infants and juveniles spent between 0 and 12% of their time within two meters of party members other than their mothers what offered them different opportunities to learn socially from other individuals.

The number of peering events per follow hour decreased with age (Spearman: $n = 14$, $r = -0.89$, $p < 0.001$, figure3.13). Infants exhibited peering rates between 0.3 and 1.5 events per follow hour whereas juveniles showed rates between 0 and 0.3. To correct for opportunities to peer I looked at the number of peering events per time spent within 10 m of other individuals. I found that the average number of peering events per time decreased with growing age of the immatures (Spearman: $n = 14$, $r = -0.66$, $p = 0.014$, figure3.14).

In summary, the analyses of the peering data showed that the number of peering events per total time as well as the number of peering events per association time decreases with age.

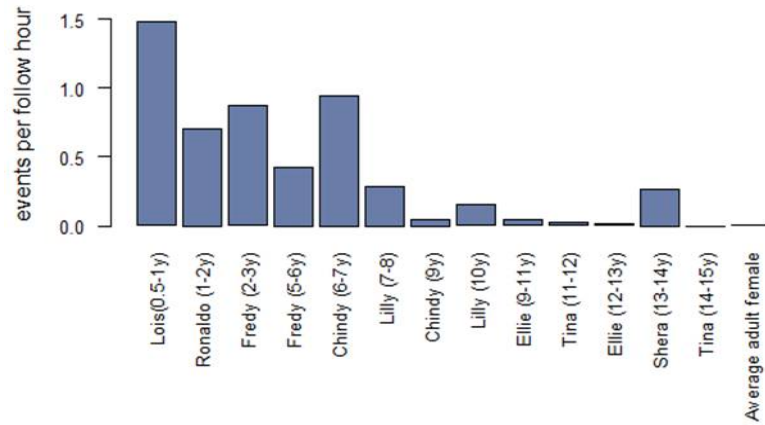


Figure 3.13: **Peering rates.** Mean number of peering events per follow hours for all immature and the average adult female.

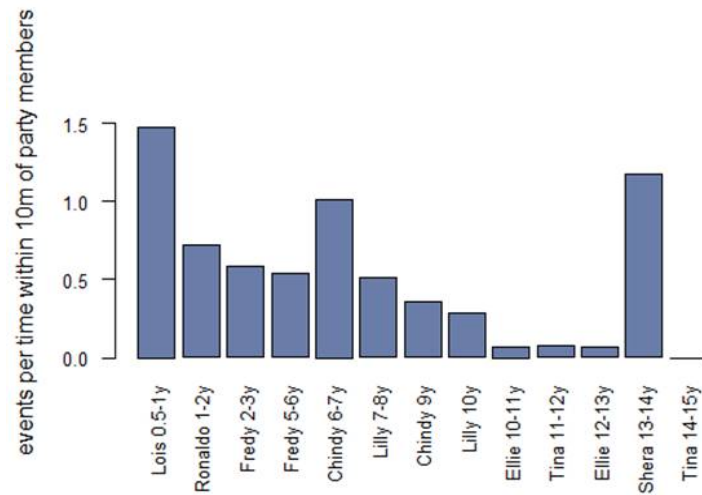


Figure 3.14: **Peering events per time spent within 10 m of party members.** Mean number of peering events per hour spent within 10 m of at least one party member (including the mother) for all immatures.

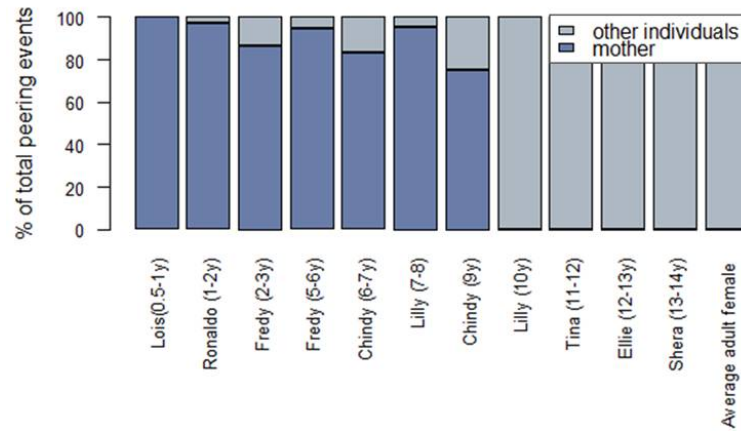


Figure 3.15: **Vertical versus horizontal peering.** Peering events at mother and at other individuals in percentage of the total peering events of each immature. Only immatures with a minimum of five recorded peering events are included.

Peering at whom: Horizontal versus vertical transmission

When looking at whom immature peer I found that the proportion of peering events towards the mother decreased with age (Spearman: $n = 11$, $r = -0.91$, $p < 0.001$, figure3.15) and consequently the proportion of peering events toward other individuals increased. From around the age of ten years on immatures only seemed to peer at individuals other than their mothers. For the juveniles all horizontal peering events were exclusively directed at either other juveniles or unflanged males.

In 35% of all peering events by juveniles they started feeding in the food patch (in which the other individual was feeding) right after peering. In most of these cases, juveniles slowly approached a feeding conspecific, peered at him and then started to eat next to him. In 52% of juveniles' peering events, the peerer had been eating in the food patch before whereas then peering was usually followed by a closer approach of the peerer towards the other individual. This suggests that peering might serve as a social tool, maybe to signal submission or simply to seek the permission to eat next to a conspecific. Of all recorded peering events in the second study period that involved juveniles (either as peering individual or individual which was subject of peering), 65% took place among two juveniles, whereas 35% involved a juvenile and an unflanged male (figure3.16). To investigate whether peering might have this social function I looked at the direction of peering whereby I assumed that if peering is a means to demonstrate submission, peering events in one dyad should always go in one direction most likely from the younger individual to the older one. Peering for learning on the other hand could go in both directions. For peering among juveniles no age effect was found: peering from younger to older individuals was equally frequent as peering from older to younger individuals (Chi-square: $df = 1$, $\chi^2 = 0.02$, $p = 0.889$, figure3.16). I also found no consistence of peering direction in the different dyads: in all dyads for which more than three peering events were recorded peering happened in both directions but was however biased in one direction 3.3. All in all, to find out

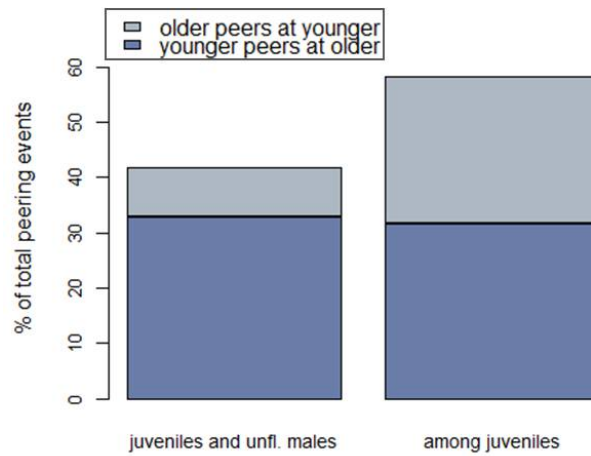


Figure 3.16: **Peering directionality.** Direction of peering events between juveniles and unflanged males and among juveniles only; in percentage of all horizontal peering events in which juveniles were involved.

whether peering follows a potential dominance hierarchy among the juvenile females, more peering events need to be recorded.

Table 3.3: **Peering directions within juvenile dyads.** Below the grey bars: Percentage of total peering events into one direction (from individual listed in column (peerer) to the one listed in row (peree)). Above the grey bars: total number of recorded peering events for the different dyads.

peerer/peree	Tina	Ellie	Shera	Lilly
Tina		2	3	0
Ellie	100%		22	0
Shera	100%	32%		19
Lilly	n.a.	n.a.	31%	

However, when peering events involved juveniles and unflanged males it was more likely that the juveniles peered at the unflanged males than the other way around (Chi-square: $df = 1$, $\chi^2 = 7.00$, $p = 0.008$, figure3.16). The latter could be explained not just by the fact that juveniles show submissive behavior but it may also be that unflanged males show lower peering rates than juveniles just for being adults who are more skillful and less curious. In sum, it can be concluded that it could well be that peering has a social function, what could go hand in hand with the one of information transfer.

For the infants I investigated whether they would peer more frequently at individuals other than their mother (choosing the less familiar role model) once they have the opportunity to do so. Hourly peering rates when being within two meters of the mother and of other individuals were tracked whereby I only included peering rates of days on which the mother infant pair was in party with another individual for at least two hours in the analysis. The youngest infant (Lois 0.5-1 y) could not be considered in

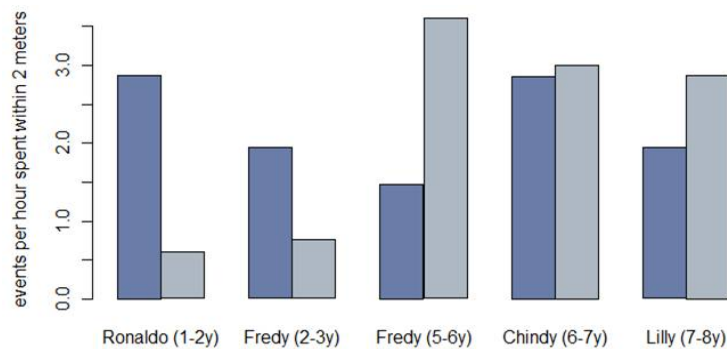


Figure 3.17: **Peering at mother versus peering at others.** Mean hourly peering rates of infants when being within two meters of the mother and when being within two meters of other individuals.

the analysis because of the small amount of time spent in party with individuals other than the mother. Using the overall peering rate of each infant (average peering events per hour spent within two meters of any other individual) I found evidence that the two clinging infants peered more frequently than expected when within two meters of the mother than when within two meters of other individuals: Ronaldo (1-2 y) showed a trend (Chi-square: $n = 40$ peering events, $df = 1$, $\chi^2 = 2.95$, $p = 0.089$) and for Fredy (2-3 y) I found significant effect (Chi-square: $n = 134$, $df = 1$, $\chi^2 = 13.24$, $p < 0.001$, figure3.17). For the non-clinging infants there might be a trend for peering more frequently at other party members than at the mother, but for none of the infants I found a significant difference (Fredy (5-6 y): $n = 24$, $df = 1$, $p = 0.125$, $\chi^2 = 2.35$; Chindy (6-7 y): $n = 84$, $df = 1$, $p = 0.848$, $\chi^2 = 0.34$; Lilly (8-9 y): $n = 45$, $df = 1$, $p = 0.260$, $\chi^2 = 1.66$; figure3.17). Ideally, to investigate whether infants truly have no preference for a certain role model one would have to look at situations where both mother and other party members are within two meters of the infant at the same time. Only then the infant has a true choice between the two types of role model. However, such situations are extremely rare and at the current state of research a too low number of such set-ups have been recorded to draw any conclusions.

To sum up, with increasing age immature orangutans in total peer more and more towards individuals other than their mothers, what basically reflects their association pattern. When looking at rates of peering events per time in association I found that younger infants might show a preference for peering at their mothers whereas older infants some evidence for a trend in the opposite direction for the older infants.

Peering at what: complexity and rarity

If peering is a mechanism of social learning one would expect that peering rates increase with an increasing processing complexity or rarity of the food item. I investigated the effects of rarity and complexity of the food item separately for juveniles and infants. The extent to what the two factors influence peering rates differed for the two age classes.

To investigate the effects of several factors on peering rates I used a multiple linear regression model with peering rate as a dependent variable and processing complexity of the food item, frequency of the food item and age of the immature as independent variables. I used data of both study periods whereby I included only immatures with more than five recorded peering events. This created a sample including six infants and four juveniles:

i) For the infants (Lilly (7-8 y), Chindy (6-7 y), Fredy (5-6 y), Fredy (2-3 y), Ronaldo (1-2 y) and Lois (0.5-1 y)) I calculated peering rates by dividing the number of peering events for a given item by the number of bouts the mother was feeding on this item (in order to correct for the opportunities to peer). As a measure of rarity I took the frequency in the mothers' diet (in percentage of total diet). In order to reach normal distribution, both of these variables had to be log transformed. Factors and interactions between the factors were stepwise included in the model. The model with the highest power was highly significant ($n = 97$, $R^2 = 0.72$, $p < 0.001$, AIC = 56.32, figure 3.18 a+b) and included the factors frequency in mothers diet ($p < 0.001$, slope = -0.63), complexity ($p = 0.001$, slope = 0.0079), age of the infant ($p < 0.001$, slope = -0.04) as well as interaction between age of the infants and rarity ($p < 0.001$, slope = -0.06).

ii) For the juveniles (Shera (13-14 y), Ellie (12-13 y), Lilly (10 y) and Chindy (9 y)) I calculated peering rates by dividing the number of peering events for a given food item by the number of bouts their party members were observed feeding on this item when in party with the focal. As the party members were not always simultaneously followed with the focal, I further approximated the frequency with which the party was observed to be feeding on a certain item by using the feeding tolerance data of the focal animal. The frequency in the own diet served as measure of rarity. In order to reach normal distribution peering frequency had to be log transformed whereby for the frequency in own diet a Box Cox transformation was used. Factors and interactions were again stepwise included in the model. In none of the models the factor complexity reached significance. The most powerful model ($n = 25$, $R^2 = 0.77$, $p < 0.001$, AIC = 28.82, figure 3.18 c+d) included two factors: frequency in own diet ($p < 0.001$, slope = -0.18) and age, whereby age was not fully significant but showed a strong trend ($p = 0.051$, slope = -0.09).

All in all the regression models produced convincing evidence that infants peer more frequently with increasing processing complexity of the item and with decreasing frequency of the item in their mothers' diet. Younger infants peer more frequently than older ones and the negative effect of frequency on peering rates is more pronounced with increasing age of the infant. Juveniles peering rates increase with decreasing frequency of the item as part in their own diet whereas processing complexity does not seem to influence their peering rates. Like for infants, peering rates of the juveniles decreased with age.

In order to assure that the peering rates reflect no sampling bias in the way that observers might pay more attention when the eaten item is more complex, I analyzed

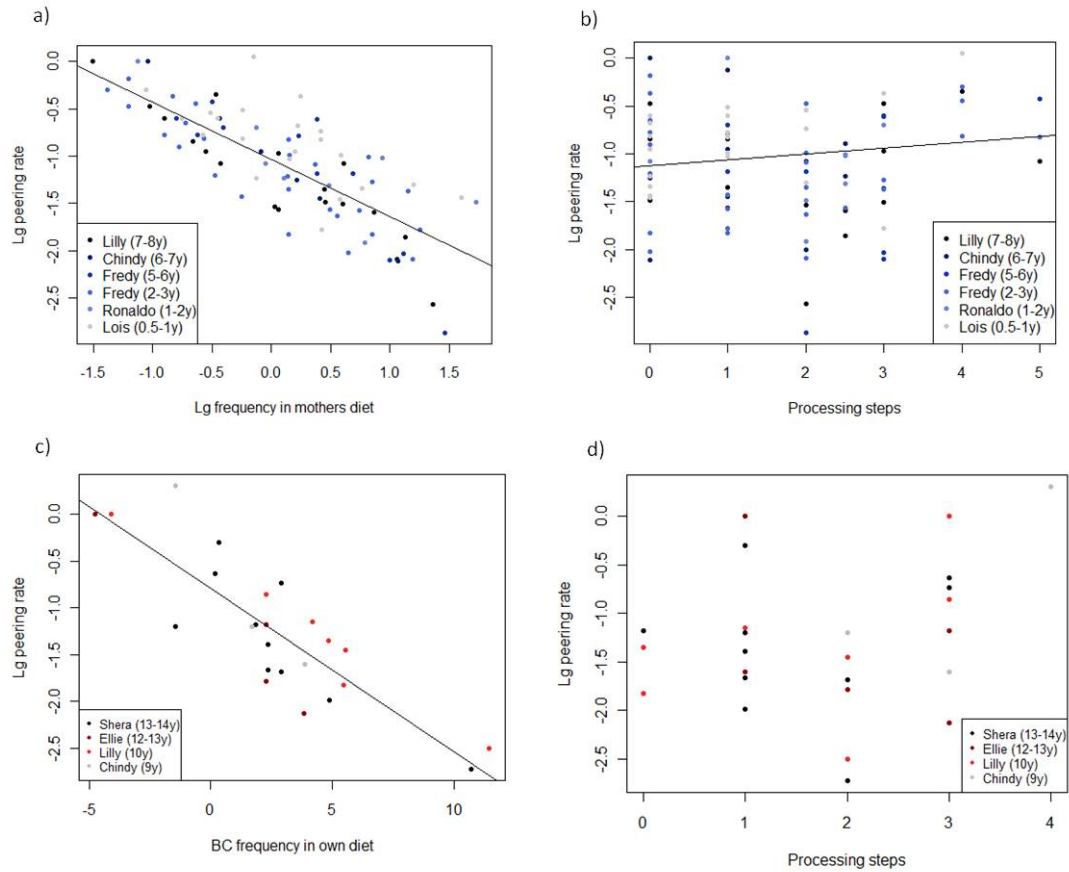


Figure 3.18: **a) Peering and rarity: infants.** Peering rates of infants (peering events per bout mother was feeding on the item) against frequency in mothers diet (%), both variables are log transformed. **b) Peering and complexity: infants.** Peering rates of infants (peering events per bout mother was feeding on the item) against complexity of the food item (processing steps). **c) Peering and rarity: juveniles.** Peering rates of juveniles (peering events per bout their party members were feeding on the item, log transformed) against frequency in their own diet (%), Box-Cox transformed). **d) Peering and complexity: juveniles.** Peering rates of juveniles (peering events per bout their party members were feeding on the item, log transformed) against complexity of the food item (processing steps).

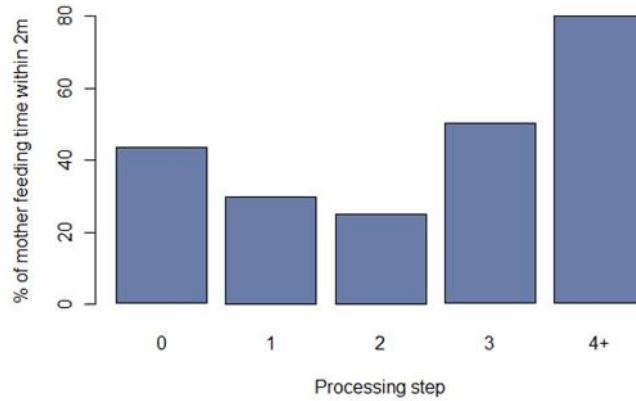


Figure 3.19: **Distance to mother and processing complexity of the food item.** Mean percentage of time spent within two meters of the mother of the total time the mother was feeding on items of each processing complexity for Fredy (5-6y).

the recorded distances between mother and infant for items of different complexity. If an infant selectively pays more attention when its mother is feeding on more complex or rarer items, it is expected that the infant spends more time within two meters of the mother when she is feeding on those items compared to other items. I did this analysis on Fredy (5-6 y) in the second study period. He showed still very high peering rates but was old enough to travel almost completely without assistance from his mother and could therefore freely determine the distance to his mother. When looking at the mean percentage of time Fredy spent within two meters of his mother for each item processing complexity class the following pattern emerged: for complex food items Fredy seemed to spend a higher percentage of time within two meters (figure3.19). For many items of processing step zero Fredy likewise spent a comparably high amount of time within two meters of his mother. This might be for the rarity of many of those items (mainly leaves) in his mothers' diet. To underpin this result I calculated for each item the percentage of feeding time spent within two meters and within more than two meters of the mother. I only considered items in the analysis for which the sample was large enough that both distance classes were recorded. A linear regression model showed a pattern very similar to that for peering rates: with increasing processing complexity and with decreasing frequency in mothers' diet, the share of time spent within two meters increased for a given food item (whole model: $n = 27$, $R^2 = 0.25$, $p = 0.034$, $AIC = 251.10$; processing step: $p = 0.034$, slope = 11.84; frequency in mothers diet: $p = 0.019$, slope = -18.51; figure3.20 a+b). In sum, both peering rates and physical distances between infant and mother showed that infants pay attention to their mothers in a selective manner, depending on the complexity and rarity of the food item in their mothers' diet. Juveniles on the other hand only show increased peering rates for items that are rare in their own diet.

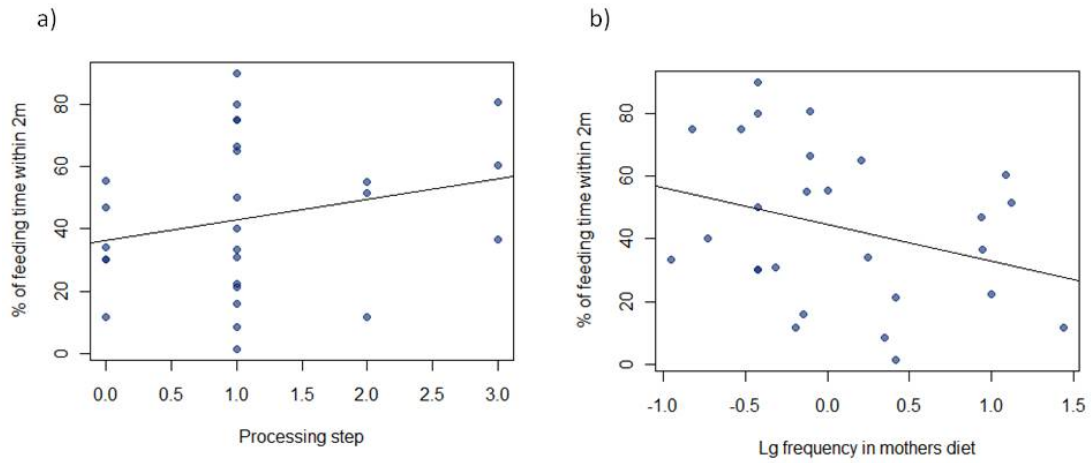


Figure 3.20: **a) Percentage of time within two meters of the mother and complexity of the food item.** Percentage of mothers feeding time on a given item Fredy (5-6 y) spent within 2 meters of the mother against processing complexity of the item. **b) Percentage of time within two meters of the mother and rarity of the food item.** Percentage of mothers feeding time on a given item Fredy (5-6 y) spent within 2 meters of his mother against frequency in mothers diet (in percent of total diet, log transformed).

3.2.3 Independent exploration

Try feeding, exploration and object play are thought to represent potential mechanisms of independent exploration. Both object play rates and rates of explorative behavior (which includes try feeding and exploration: these two behaviors were not separated in the first study period) decreased significantly with age (Spearman: $n = 14/14$, $R^2 = -0.93/ -0.98$, $p < 0.001/ < 0.001$; figures 3.21 and 3.22).

In the second study period (2010-2011) explorative behavior was subdivided into try feeding and exploration (see definitions above). I looked at how the composition of explorative behavior changed with age: the relative proportion of try feeding decreased with age and consequently, the proportion of exploration increased (Spearman: $n = 8$, $R^2 = -0.91$, $p < 0.001$; figure 2.23). This means that with increasing age, explorative behavior is less frequently carried out by taking objects into the mouth but rather carried out by exploring them with hand and eyes.

For studying try feeding behavior in more detail I made a differentiation by creating three classes depending on whether the item involved was edible (other orangutans had been observed to eat it before), inedible or potentially edible. Try feeding on edible food items might represent a lack of food processing competence whereas try feeding on inedible food items might mean a lack of food detection competence. Whenever the item looked edible but no orangutan had been seen feeding on it, it was scored as potentially edible. Every time an orangutan was observed feeding or trying to feed on such an item it was collected, photographed and carefully identified. However, this was not possible in all cases, as those items were not always found after the orangutan

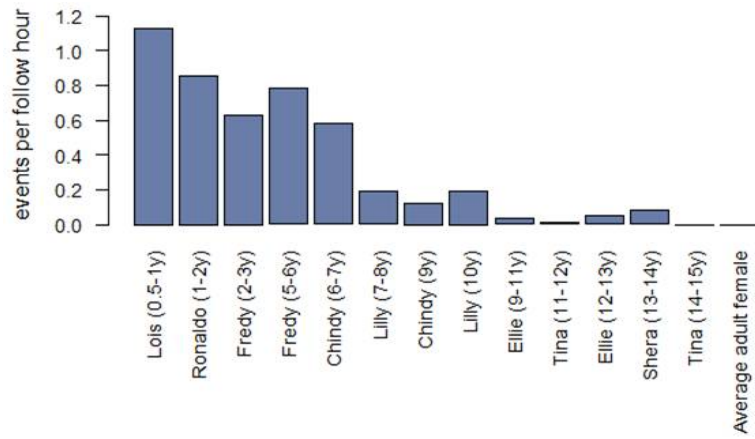


Figure 3.21: **Object play.** Hourly rates of object play for all immatures and for the average adult female.

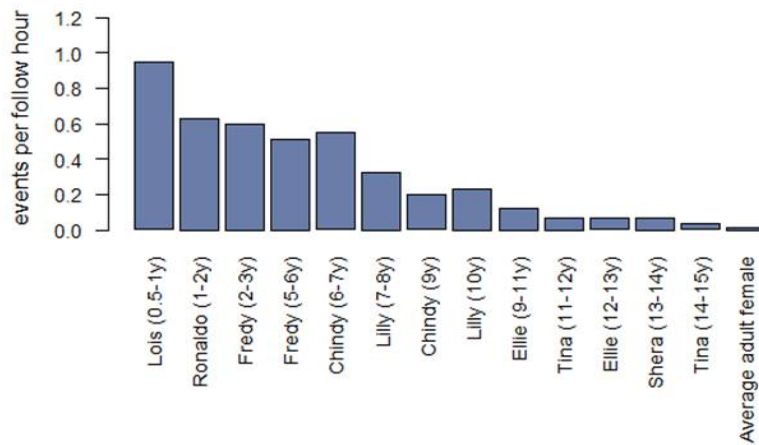


Figure 3.22: **Explorative behavior.** Hourly rates of explorative behavior (try feeding and exploration) for all immatures and for the average adult female.

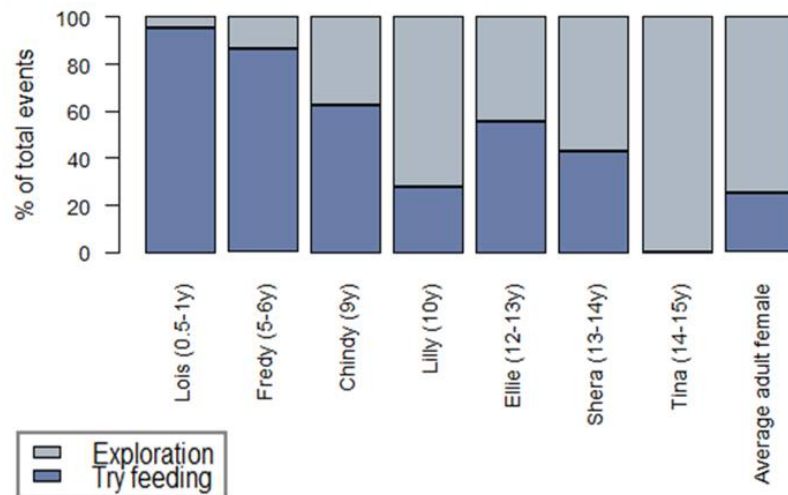


Figure 3.23: **Composition of explorative behavior.** Try feeding and exploration in percentage of total events of explorative behavior.

had released them. The category of potentially edible items might therefore include items that were indeed known food items but simply were not recognized by the observer. However, it may still be a measure for sampling. To investigate a potential age effect on the frequencies of the different try feeding categories I calculated hourly rates of each category. For the juveniles, I pooled data of the two semi-independently ranging juveniles and all data of the independently ranging juveniles, so that each individual or age class contained at least 13 try feeding events. The hourly rate of try feeding on inedible and edible items decreased with age (Spearman: $n = 8/8$, $R^2 = -0.89/-0.77$, $p = 0.03/0.026$, figure3.24), whereby the decrease of try feeding on edible items seemed to happen at an older age. For try feeding on potentially edible items I found no such age effect (Spearman: $n = 8$, $R^2 = -0.59$, $p = 0.128$, figure3.24).

In general this suggests that both food detection and food processing competence increase with age, whereby food processing competence may lag behind (figure3.24). Try feeding on inedible and potentially edible items also shows, that try feeding not simply follows the mothers feeding pattern and is therefore not a simple outcome of social learning: young orangutans also explore items in their environment that they have never seen eaten by their mothers.

Furthermore, I investigated whether try feeding rates on edible food items increased with growing complexity and rarity of the food item. Because of the age effect of try feeding on edible items (see above), I analyzed clinging infants, non-clinging infants and juveniles separately.

In a first step, I calculated mean hourly try feeding rates on edible items for each of the processing step class of food items for all immatures. Furthermore, for each infant I calculated the mother's mean feeding rate for each processing step class. For juvenile animals I used their own mean feeding rate. When plotting the try feeding

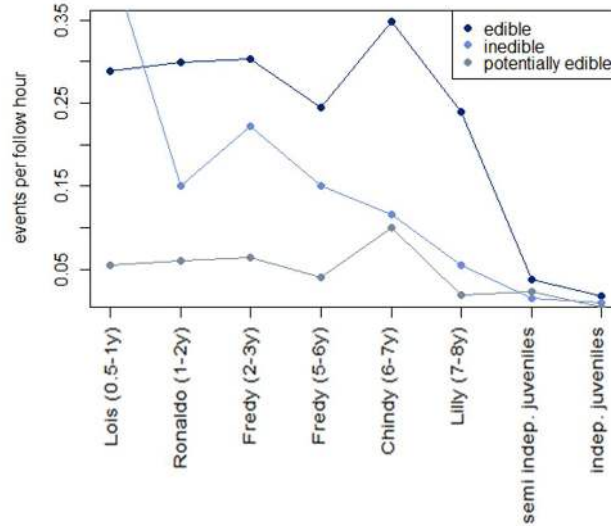


Figure 3.24: **Rates of try feeding on different classes of items.** Hourly rates of try feeding on edible food items (measure of lack of food processing competence), inedible food items (measure of lack of food detection competence) and potentially edible food items.

rate and feeding rates against the processing steps one can easily see that the three age classes showed different patterns (figure3.25). In clinging infants the try feeding rate seemed to mainly follow the mothers feeding rate (figure3.25a), whereas in non-clinging infants the try feeding rate seemed to increase with the number of processing steps (figure3.25b). For juveniles try feeding only seemed to happen on items of high processing complexity (figure3.25c). Interestingly, the diet of mothers of clinging infants seemed to differ from the diet of mothers of non-clinging infants and from the ones of juveniles (figure3.25a-c): adult females with younger infants showed a lower percentage of food items with high complexity in their diets. However, to properly test this and disentangle it from environmental effects, a much bigger sample would be needed. To look at the patterns in more detail, I calculated an hourly try feeding rate as well as the mothers feeding frequency (in percentage of the total diet) for each item on which try feeding has been observed. For the two infant age classes I computed multiple linear regression models, whereas the small sample size for the juveniles did not allow any statistical testing. Variables had to be log and Box Cox transformed in order to reach normal distribution. The three factors frequency in mothers diet, processing steps and age of the infant were stepwise included in the model:

i) For the clinging infants I found that try feeding rates increased with the mothers' feeding frequency whereby the number of processing steps had no effect. A model including the factors age and frequency in mothers diet was the most powerful predictor of the try feeding rate ($n = 38$, $R^2 = 0.51$, $p < 0.001$, $AIC = -257.17$), whereby frequency in mothers' diet had a significant positive effect ($p = 0.002$, slope = 0.01) and age a significant negative effect ($p < 0.001$, slope = -0.01, figure3.26 a+c). The

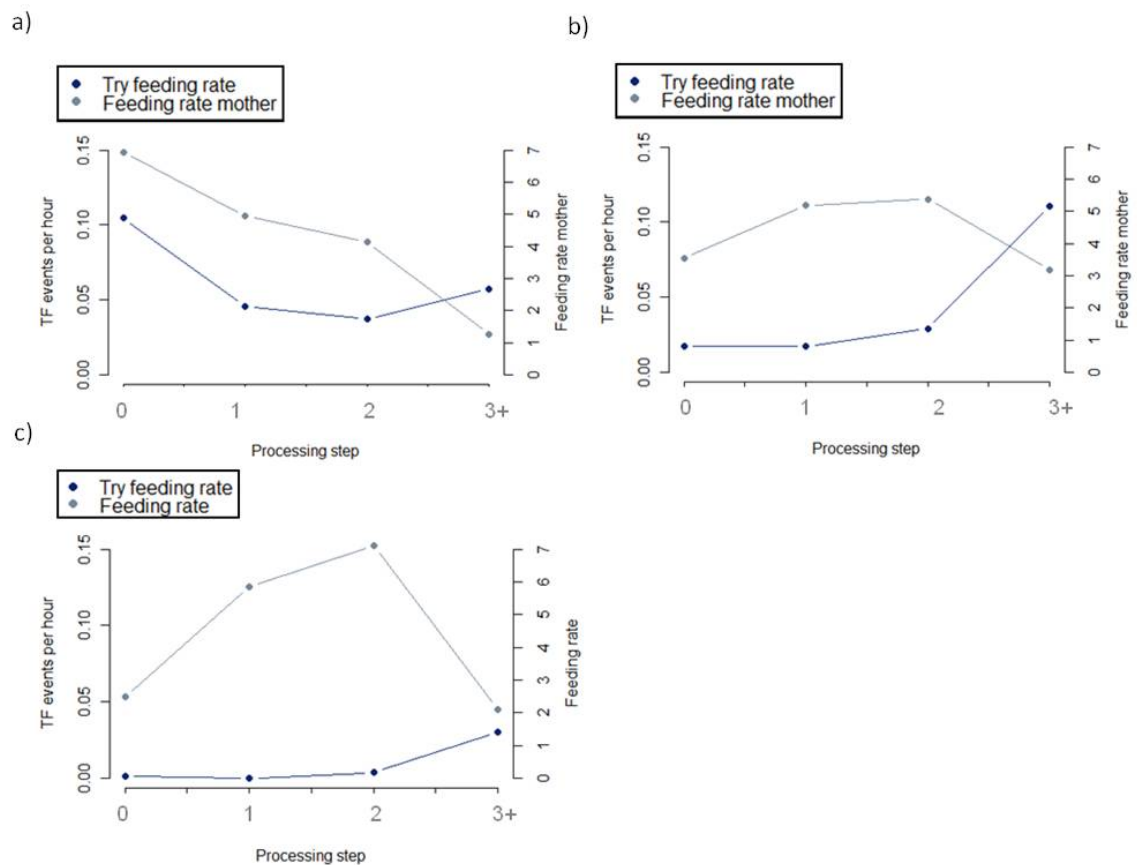


Figure 3.25: **a) Try feeding (TF) and complexity: clinging infants.** Mean hourly rates of try feeding on edible items and mean hourly feeding rates of the mother for items requiring different steps of processing. **b) Try feeding (TF) and complexity: non clinging infants.** Mean hourly rates of try feeding on edible items and mean hourly feeding rates of the mother for items requiring different steps of processing. **c) Try feeding (TF) and complexity: juveniles.** Mean hourly rates of try feeding on edible items and mean hourly feeding rates for items requiring different steps of processing.

factor processing step was not significant in any of the models.

ii) For the non-clinging infants I found that try feeding rates increased with increasing processing complexity of the food item whereby frequency in mother's diet had no effect. The most powerful model ($n = 21$, $R^2 = 0.43$, $p < 0.006$, $AIC = -127.282$) included the factors age, which displayed a strong trend ($p = 0.061$, slope = -0.01) and processing steps, which had a significant positive effect ($p = 0.014$, slope = 0.01 , figure 3.26 b+d). The factor frequency in mother's diet never reached significance in any of the models.

In summary, it seems that in younger infants the try feeding pattern mainly follows the mothers feeding pattern whereas older infants selectively try feed on more complex items. This obviously is consistent with the expectation that with increasing age infants become more skilled and show less and less try feeding on items that are easy to process.

3.2.4 Does peering lead to explorative behavior?

If orangutans learn socially from each other by peering, try feeding and exploration rates should to some extent follow their peering patterns, especially in unskilled foragers (younger infants). In order to investigate the effect of peering on explorative behavior, I determined the number of try feeding events, exploration and object play with the food item in the food patch before and after each peering event. I found that infants showed significantly higher rates of explorative behavior after peering than before peering (Wilcoxon: $n = 6$, $p = 0.028$, figure 3.27a). For juveniles, I found no such effect (Wilcoxon: $n = 5$, $p = 0.273$, figure 3.27b), whereby the sample size was very small in this case. For juveniles try feeding rates on edible items were extremely low (see above), therefore we might expect that their feeding patterns rather than their try feeding follows their peering pattern. In 35% of all peering events of the juveniles they started eating in a food patch after peering at a party member (feeding in this patch). In 53% of all peering events juveniles had already been eating in the food patch before. Twice it was observed that juveniles peered at a party member eating something that they had never been observed eating before. On one of these occasions the juvenile was then (right after the peering event) observed feeding on the same food item for the first time.

Based on Jaeggi et al.'s work on infant Bornean orangutans (2010), I also investigated whether practice like try feeding on dead wood (which includes biting open dead wood) is more frequent after the mother has fed on insects in dead wood herself. I only included data of the second study period, taken by Sofia Forss and me in this analysis to assure that only goal directed, practice like try feeding cases as described in Jaeggi et al. (2010) were included in the analysis. Consequently, I could only include data of one infant (Fredy 5-6 y) in the analysis, as the other infant in this study period (Lois 0.5-1 y) did not show this behavior yet. In total 58 insect feeding bouts by the mother were

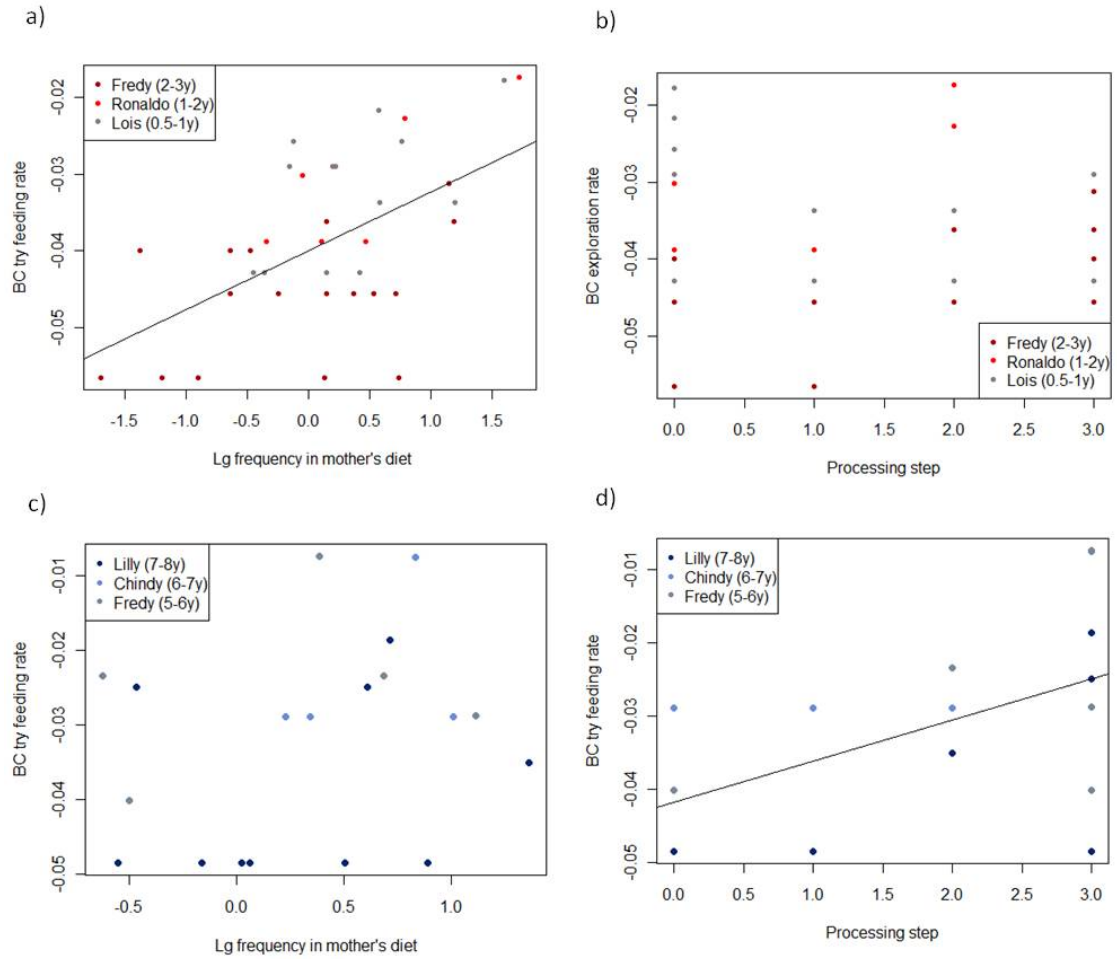


Figure 3.26: **a) Try feeding rates on edible food items and rarity: clinging infants.** Hourly try feeding rates (Box Cox transformed) against frequency in mothers diet (in percentage of total diet, log transformed) for all clinging infants. **b) Try feeding rates on edible food items and complexity: clinging infants.** Hourly try feeding rates (Box Cox transformed) against processing step of the food item for all clinging infants. **c) Try feeding rates on edible food items and rarity: non-clinging infants.** Hourly try feeding rates (Box Cox transformed) against frequency in mothers diet (in percentage of total diet, log transformed) for all non clinging infants. **d) Try feeding rates on edible food items and complexity: non-clinging infants.** Hourly try feeding rates (Box Cox transformed) against processing step of the food item for all non clinging infants.

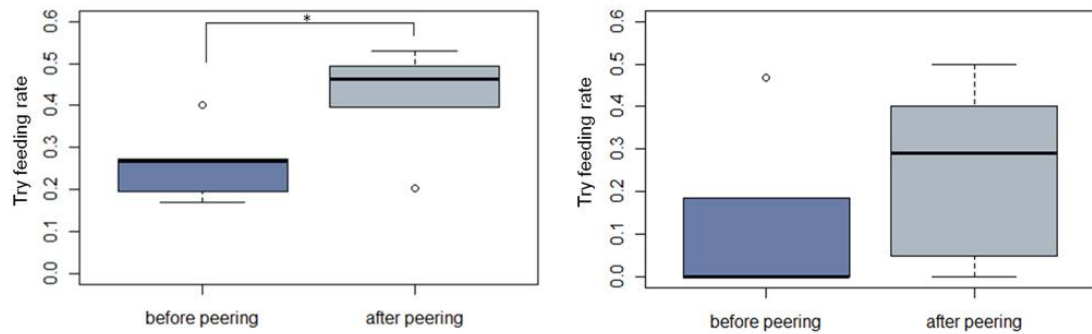


Figure 3.27: **a) Try feeding and exploration before and after peering: infants.** Mean number of exploration and try feeding events before and after peering in a given food patch. **b) Try feeding and exploration before and after peering: juveniles.** Mean number of exploration and try feeding events before and after peering in a given food patch. $*p < 0.05$.

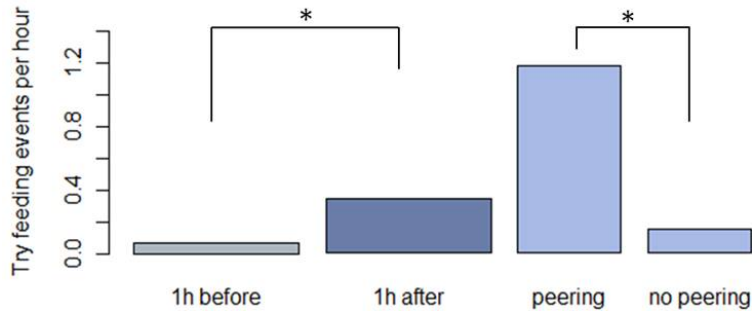


Figure 3.28: **Try feeding on dead wood before and after the mother was feeding on insects: Fredy (5-6 y).** Mean try feeding events of Fredy (5-6 y) on dead wood per hour in the periods one hour before and one hour after the start of the mothers feeding bout on insects. The time after the peering event was additionally divided into two classes depending on whether Fredy had been peering during the mothers feeding bout. $*p < 0.001$.

recorded while the above described practice-like try feeding was observed 27 times. Four of the latter observations occurred in the one hour period before the feeding bout was started, 20 in the one hour period after the start of the mothers feeding bout and three fell outside both of these periods. The number of those try feeding events was significantly higher in the one hour period after the start of the mothers feeding bout than in the preceding one hour period (Chi-square: $n = 24$, $df = 1$, $\chi^2 = 10.67$, $p = 0.001$, figure3.28). I further looked at whether the occurrence of infant's peering at the mother during the mothers feeding bout influenced the occurrence of these try feeding events. In 11 out of the 58 feeding bouts the infant had been observed to peer at least once, which resulted in a mean peering rate of 0.19 times per bout. In 13 out of the 20 try feeding events that occurred in the subsequent one hour period, Fredy had been observed peering before. This differed significantly from expected using the calculated peering rate of 0.19 (Chi-square: $n = 20$, $df = 1$, $\chi^2 = 27.50$, $p < 0.001$, figure3.28).

In summary, I found that in infants explorative behavior follows their peering pattern to a certain extent. The feeding pattern of the mother seems to strongly influence the try feeding pattern of the infants.

4 Discussion

The aim of this study was to investigate at what age immature Sumatran orangutans reach adult levels of skill competence and what sort of learning mechanisms are involved in the process of skill acquisition. Adult orangutans range widely solitarily and rely completely on their own skills: unlike other more social species, orangutans cannot simply follow group members to food sources or nesting sites but are fully dependent on their own knowledge.

The skills immature orangutans need to acquire in order for them to become successful adults can be divided into the following categories: non-food related technological skills, loco-motor skills, social skills and ecological competence, social skills and. The most important non-food related technological skill of orangutans is nest building. Former studies have shown that Sumatran and Bornean infants are able to build their own nests around the age of three but share night nests with their mothers for another couple of years before they finally stop sleeping in their mother's nest around the age of final weaning (7-9 years of age at Sumatran sites and 6-7 years of age at the Bornean sites) (van Noordwijk and van Schaik, 2005; van Noordwijk et al., 2009).

For the loco-motor development it is known that in Bornean orangutans the amount of maternal travel assistance is close to zero around the age of weaning (Phillips et al. in preparation). For Bornean as well as for Sumatran orangutans it seems as if complete loco-motor independence is reached before weaning (Phillips et al. in preparation, van Noordwijk et al., 2009).

Very little is known about the development of social competence in orangutans. To date, no study has found evidence for a lack of social skills in immature orangutans. The probably most important skills of female orangutans namely mothering skills, are most likely acquired on the job rather than through any other learning mechanism.

Several projects have been conducted on the development of ecological competence in Bornean orangutans (Jaeggi et al., 2010; Dunkel, 2006; Latscha, 2008). The aim of my study was to investigate the development of ecological competence in immature Sumatran orangutans. I looked at various measures of foraging skills as well as at indicators for social learning and independent exploration in wild immature Sumatran orangutans aged from approximately six months till 15 years. In the following section I will discuss my results and compare them with data on Bornean orangutans.

4.1 Ecological competence

To assess ecological competence, according to Galef and Giraldeau (2001) I looked at diet composition and *food selection competence* (what to eat), *processing competence: processing techniques and foraging efficiency* (how to eat) and *range use competence*

(when and where to eat).

4.1.1 Food selection competence: What to eat?

In terms of diet composition I found that with increasing age immature Sumatran orangutans eat a growing proportion of their mothers' diet. However, around the age of weaning the offspring eats approximately 80% of the mother's food items, much less than I had predicted (prediction 1a). Studies on Bornean orangutans at Tuanan show a different pattern: Dunkel (2006) and Jaeggi et al. (2010) found that around the age of weaning immatures eat more than 95% of the mother's food items.

Furthermore, my findings show that shortly before the age of weaning immatures at Suaq Balimbing start to include food items into their diets that their mothers have never been observed eating. The proportion of these items increases with age and reaches around 12% of the immatures' diet around the age of weaning and up to 20% in late juvenility. The fact that most of these items are known components of other adult females' diet shows that this not simply reflects differences in food preferences between adult and immature animals. In Tuanan on the other hand, infants were observed to have only a minor share of food items in their diets that their mothers did not eat: at about the age of weaning this proportion reached only around 3%.

This result confirms my initial prediction (2f) that after the age of weaning the overlap between mother's and offspring's diet decreases. Consequently, immatures must either discover new food items through independent exploration or learn them socially from individuals other than their mothers. Former studies suggested that when they have the possibility to do so, immature animals should rely on social information for diet choice in order to avoid the risk of independent exploration (in the form of starvation, intoxication or injury) (Galef and Giraldeau, 2001). However, opportunities for social learning vary across taxa, depending on sociality and resource distribution (van der Post and Hogeweg, 2006). Consistent with studies on other primates (Krakauer, 2005) I found evidence, that both mechanisms (independent exploration and social learning) might play an important role during the development of Sumatran orangutans (further discussed below).

Diet spectra sizes of the adult females were similar at the two study sites: in Suaq Balimbing diets of the three adult females that were followed in both study periods comprised 52-71 different food items whereas the adult females in Tuanan showed spectra sizes of 55 to 71 different food items at the time of the Jaeggi et al.'s (2010) and Dunkel's (2006) studies. The amount of follow hours for the different studies were also comparable: at the stage of these studies between 350 and 480 follow hours of the Tuanan females had been collected, whereas in Suaq Balimbing we had 160 to 570 hours per adult female. I found that immatures at Suaq Balimbing reach adult diet spectra size around the age of twelve and some evidence could be gained that older juveniles have bigger diet spectra than adult females. This suggests that juvenile Sumatran orangutans expand their diets gradually during development, to a certain extent independent of their mothers' diets, and then at adult age abandon some of the

food items of their diets. Bornean immatures at Tuanan though show diet spectra of the same size as their mothers around the age of weaning.

Furthermore, consistent with prediction 1b I found that at around the age of weaning, Sumatran orangutan infants discover about 50% of all patches they feed in independently (they either start feeding before their mothers do or they feed while their mother is engaged in another activity). This is very similar to what has been found for Bornean immatures: Latscha (2008) found that at around the age of weaning Bornean immature orangutans only spend about 9% of their total feeding time in feeding tolerance with their mother and when in feeding tolerance they enter around 45% of the food patches before their mothers do.

The development of diet repertoires and independent feeding patch discoveries showed that Sumatran and Bornean immatures reach food selection competence around the age of weaning or shortly thereafter. However, to fully confirm these results one would have to redo the analysis once a more complete record of the diet repertoires of the Suaq Balimbing individuals has been achieved: whereas the record of diet repertoires in Borneo seem to be more or less complete (shown in a big overlap between the adult females ($77.6\% \pm 7.4SD$, (Jaeggi et al. 2010)) the record of the repertoires of the Suaq Balimbing animals might still be incomplete at the current state of research (diet spectra of all females increased drastically between the two study periods). However, the comparison of the two populations provided preliminary evidence that Sumatran immatures acquire diets that are only to a certain extent similar to the ones of their mothers whereas Bornean immatures seem to fully adopt diets of their mothers. This suggests that Sumatran immatures acquire additional knowledge about food items either by independent exploration or by learning socially from individuals other than their mothers.

4.1.2 Food processing competence: How to eat?

I found that feeding rates for items of all processing complexity classes increase with growing age whereby the trajectories differ for the different complexity classes. Consistent with prediction 1c I could show that feeding rates reach adult like rates between the age of weaning and first reproduction: For items that need only one or two steps of processing, adult-like feeding speed seems to be reached around the age of weaning. For items with three processing steps adult level seems to be reached at around the age of 12. Interestingly, older juveniles showed slightly higher feeding rates than adult females. This might indicate their high energetic needs to reach full adult body size before they start reproducing. Consistent with my result, a study on immature Bornean orangutans Dunkel (2006) found that at around the age of 8-10 years immature have reached adult-like feeding speed.

Like Dunkel (2006) in her study on Bornean immatures I couldn't find any systematic difference in the feeding techniques between adult and immature animals. When looking at tool use, I found some evidence that competence in insect tool use is reached between the age of 10 and 12 years. In a former study on the same population van

Noordwijk and van Schaik (2005) found that seven year olds are competent Neesia tool users, even though efficiency could not be quantified. To confirm that juvenile animals are as efficient tool users as adults in a quantitative way, one would have to look at processing times and success rates when. However, this can only be done in the future once a bigger sample, including more tool use incidents is available.

Studies on other primate species report varying patterns for the development of food processing competence: Low-land gorillas (*Gorilla gorilla*) and Mountain gorillas (*Gorilla Beringei*) reach adult-like processing skills in late infancy, around three to four years of age (Watts, 1985; Nowell and Fletcher, 2007). Squirrel monkeys (*Saimiri Sciureus*) show adult-like feeding rates around the age of weaning (Stone, 2006). In Brown capuchins (*Cebus apella*) on the other hand it seems that adult-like feeding speed for certain food items coincides with age of first reproduction (Gunst et al., 2008, 2010). In humans as well as in many social carnivores (e.g. wolves (*Canis lupus*)) hunting return rates reach peak values long after age of first reproduction (Gurven et al., 2006; MacNulty et al., 2009).

The comparison of feeding rates and feeding techniques of immatures with the ones of adult animals provides strong evidence that immature Sumatran orangutans reach adult competence in food processing skills latest around the age of twelve. Bornean immature might reach competence slightly earlier, however with the current data sets the exact timing of events is very hard to evaluate.

4.1.3 Range use competence: Where and when to eat?

To investigate range use competence (the competence to find food in correct proportions and time intervals) I looked at sinuosity values of the travel routes (ramble ratios, for definitions see Material and Methods). In general it is very difficult to assess range use competence through ramble ratios as many other factors can influence travel routes of individuals: Former studies could show that females with dependent offspring adjust their travel routes after they have heard long calls of flanged males (Mitra Setia and van Schaik, 2007; Spillmann et al., 2010) and van Noordwijk et al.'s (2012, submitted) work suggests that adult females avoid encounters with unrelated females.

My findings suggest that daily ramble ratios of independently ranging Sumatran juveniles do not differ from the ones of adult females. For the feeding ramble ratios I found some evidence that the youngest juvenile (Chindy) showed higher feeding ramble ratios than adult females when ranging independently of her mother. Therefore, it might be that individuals that have just started to range independently of their mothers still encounter problems locating food patches in the forest at a wide range. However, other factors, such as social factors may have influenced Chindy's travel routes: she was often observed climbing up tall trees, looking around and then moving on, as if she was looking out for something or somebody. She seemed to avoid the company individuals other than her mother and was several times observed to try to distance

herself from her association partners as soon as she could. It might also be that she tried to follow her mother (who was almost constantly in consort ship with males) from a long distance. Both could of course result in higher ramble ratios. However, Lilly, who was estimated to be only about a year older than Chindy, as well as all other juveniles showed consistently adult-like daily ramble ratios and feeding ramble ratios.

In a study on Bornean juvenile orangutans Latscha (2008) found that a newly weaned female (aged 7 years) showed significantly higher ramble ratios than her mother. However, this juvenile female was still constantly at least in auditory contact with her mother and followed her from a long distance for most of the time: several times she was observed to actively move away from her mother but then, after climbing a tall tree, go straight back to her from distances of more than 100 meters. Therefore her ranging behavior is well comparable to the one of Chindy. In a study on Hamadryas baboons (*Papio hamadryas*) Sigg and Stolba (1981) conclude that the exploratory tendency might have a positive effect on sinuosity of the travel route. The explanation of the higher ramble ratios of semi independently ranging juveniles might be explained by the fact that they start to explore their environment on their own but still want to stay close to their mother rather than that they lack home range use competence.

In general, the analysis of the ramble ratios produced no evidence that juveniles have a lower range use competence than adult females. Consistent with prediction 1d this suggests that the competence to locate food patches in the forest at a wide range emerges around or shortly after the age at which immature orangutans start to range independently.

4.2 Learning mechanisms: Social learning or independent exploration?

Commonly, learning is divided into social learning and asocial learning (independent exploration) (Heyes, 2011). Whereas for a long time these two learning mechanisms had been strictly separated, recent studies suggest that they both rely on the same basic processes, often act simultaneously and are therefore often difficult to tell apart (Heyes, 2011; van der Post and Hogeweg, 2006). Basically both, independent exploration and social learning could form part of the skill acquisition of immature orangutans. Former studies could show that infant Bornean orangutans learn many of the above presented foraging skills socially from their mothers (Jaeggi et al. 2010). Forss (2009) found evidence that infant Sumatran orangutans not just learn socially from their mother but also demonstrate a certain degree of explorative behavior that is not a direct outcome of social learning but is rather based on independent exploration.

To what extent immature orangutans learn socially from their mothers or by independent exploration and whether there is a difference between Bornean and Sumatran orangutans has not yet been fully resolved. Likewise it has remained unclear so far to what extent immature orangutans learn from individuals other than their mothers and how much social learning takes place after weaning. With my study I tried to fill these

gaps. For social learning I investigated time spent in association and peering rates. For independent exploration I looked at object play, try feeding and exploration.

4.2.1 Time in association with others

To investigate opportunities for social learning I looked at the time immature orangutans at Suaq Balimbing spend in association with their mother and with other individuals.

Consistent with other studies on the same as well as on other orangutan populations I found that the time immatures spent in association with the mother decreased steeply from the age of weaning onwards (van Noordwijk and van Schaik 2005; van Noordwijk et al. 2009). As other studies have already shown, during infancy the time spent within close distance to the mother decreased with increasing age of the infant: younger infants spent most of their time within 2 meters of their mothers and were carried whenever the mother traveled (van Noordwijk et al. 2009). This provided the infants with plenty of opportunity to learn socially from their mothers. With increasing loco-motor skills from the age of two years on, the distance between mother and infant gradually increased. However, up to the age of six to eight years immature orangutans of all populations spent more than 50% of their time within ten meters of their mothers (van Noordwijk et al. 2009). The distance at which an individual can observe the details of the actions of an association partner lies within two meters for most activities (e.g. feeding with a certain technique). I found that the time immatures at Suaq Balimbing spent within two meters of the mother decreases with age but was still around 30% of the total time for immature around the age of weaning. These findings show that at least until the age of weaning immature orangutans have plenty of opportunities to learn socially from their mothers.

For associations with individuals other than the mother I found no clear age effect. Immatures spent between 5 and 70% of their time in association with individuals other than their mothers. In the comparative part of her study Forss (2009) found that immature Bornean orangutans at Tuanan spent on average less time in association with individuals other than their mothers than the Sumatran ones. Furthermore, the time spent in feeding tolerance with individuals other than the mother was significantly lower for Borenan immatures than for Sumatran ones (Forss 2009).

The five juvenile females in my study period spent on average 40% of their time in party with other juveniles or unflanged males. Interestingly, none of the male association partners tried to copulate with any of the juvenile females. This shows that all juvenile females of my study period were still before the age of sexual maturity and that the associations were not consort-ships. On average the juvenile females spent 15% of their feeding time in feeding tolerance with individuals other than their mothers. This was least pronounced for the youngest and the oldest juvenile female: As described above, the youngest juvenile, Chindy (9y) seemed to actively avoid parties with individuals other than her mother. The oldest juvenile Tina (14-15y) seemed to avoid any association with other individuals: she only spent about 14% of her time in association with others. She was frequently approached by unflanged males and

sometimes by other juveniles. However, most of the time she tried to distance herself as soon as she could. Once I observed an unflanged male inspecting Tina's genitals with his hands. However, he then moved on without an attempt to copulate with her. A pregnancy test confirmed that Tina was not pregnant at the end of the second study period. These observations, as well as her age suggest that Tina is probably not far away from the onset of sexual maturity.

The three medium aged juvenile females of the second study period (aged 10 to 13) spent on average 62% of their time in association and up to 26% of their total feeding time in feeding tolerance with other juveniles or unflanged males. These associations often lasted for several days and were very peaceful: the party members spent lots of time in close proximity, and some incidents of food transfer (non-resisted tolerated theft, often in both directions in a given dyad) and brief grooming (twice an unflanged male briefly groomed a juvenile female) were observed. Antagonistic interactions were observed only twice. The association times of the juvenile females varied remarkably between different dyads: some dyads spent up to 19% of their total time with each other whereas others had never been observed to be in party with each other. Preliminary home range overlap data provided evidence that the associations are selective and not simply a function of home range overlap. In an earlier study on the same population Singleton and van Schaik (2002) showed that adult females have selective associations, which they suggest could be based on relatedness. A recent study on Bornean orangutans based on genetic data on the relatedness of individuals has confirmed that adult females associate more often than one would expect from the observed home range overlaps with their relatives than with unrelated animals (van Noordwijk 2012 et al. submitted).

Regrettably, the genetic data of the Suaq individuals is not fully available yet. However, the current study provides some evidence that the juvenile females in Suaq might differ in their association patterns from what is expected from relatedness: Shera seemed to preferentially associate with Lilly and Ellie who stem from two different maternal lineages (mtDNA lineages). Lilly showed a high association tendency with Shera whilst she seemed to avoid Ellie (who is from a different maternal lineage). Lilly was also never seen in party with her aunt Chindy, even though in the first study period in which both of them were still ranging with their mothers, they spent a lot of time in party with each other (Forss, personal communication).

Data collected in the nineties at Suaq Balimbing also showed that juveniles often range in peer groups: at this time several independently ranging juvenile males were often observed to be together in small groups (van Schaik personal communication). Contrarily, in the first study period at Suaq Balimbing (2007-2009), no such juvenile parties had been observed. Results from Tuanan, where data is extensively collected since 2004, neither provide evidence for such juvenile associations. However, Galdikas (1995) reported that at Tanjung Puting, another Bornean site, independently ranging juvenile ("adolescent") females were the most social of all age sex classes: they spent 41% of their total observation time in association with other individuals, something

strikingly similar to my findings. Like seen with the independently ranging juveniles of my observation period, the most frequent association partners of these adolescent females were peers and adult as well as subadult males. Galdikas (1995) further describes that the associations between adolescent females were extremely social and often lasted for several days. Furthermore, she observed that adolescent females sometimes groomed one another or the male they were in party with. All in all, the pattern described by Galdikas (1995) is very similar to what I observed during my field study and shows that such associations between independently ranging juveniles are not exclusive of Sumatran individuals. Furthermore, this can be seen as evidence that the formation of those juvenile parties strongly depends on demography and probably also on the current orangutan density of a given population.

Association times show that in the six to eight years until weaning both Sumatran and Bornean orangutans are provided with plenty of opportunities to learn socially from their mothers. Association times with individuals other than the mother suggest that opportunities to learn from individuals other than the mother are highly dependent on demography and therefore variable over the years. Even though there seems to be no general difference between Sumatran and Bornean orangutans, it is likely that the probability of juvenile associations are lower for the Tuanan than for the Suaq Balimbing population when considering the difference in the local orangutan density. In general the high tolerance levels of these juvenile parties suggest that if juveniles can form such associations, there is a high potential for social learning.

4.2.2 Peering: At whom and at what?

Numerous lab experiments have shown that observing other individuals when they perform a task is a common form of skill transmission in primates (Dindo et al., 2008; Whiten et al., 2004, 1996). Learning through detailed observation of the close by conspecifics' actions is commonly called observational learning (Zentall, 2011). Field studies on the development of tool use in immature chimpanzees (*Pan troglodytes*) and capuchins (*Cebus apella*) confirmed this finding in that they showed that selective observation of skilled individuals is an important aspect of the learning process (Biro et al., 2003; Ottoni et al., 2005). Peering rates might therefore be a reliable measure of observational learning in orangutans.

Consistent with hypothesis 2b I found that with increasing age peering rates of Sumatran immature orangutans decrease. This is true for absolute peering rates (peering events per observation time) as well as for peering rates corrected for the time spent in association with other individuals. Furthermore, my findings showed that with increasing age, the proportion of total peering events immatures dedicate to their mother decreases and consequently the proportion of peering events directed at other individuals increases. Consistent with their association patterns juveniles only seem to peer towards peers or unflanged males. I couldn't resolve whether peering of juvenile animals primarily has a social function or the one of information transfer. In general it is very difficult to separate the two potential functions of peering and one does most likely not rule out the other. Whatever the main purpose of peering is, the fact that it

occurs regularly between juveniles and their association partners indicated that there is a high potential for horizontal transmission.

Especially for older infants who have already acquired most of their mother's skills I expected that once they have the opportunity to peer at an individual other than their mother (once they are within two meters of another individual) peering rates would be increased. In other words, I anticipated higher peering rates towards individuals other than the mother compared to peering rates towards the mother because these 'foreign' role models might show skills that are new to the infant (prediction 2c). Even though I found some evidence that this might be true for older (non-clinging) infants the result did not reach significance. For the younger infants I found the opposite pattern: they showed significantly higher peering rates towards their mothers than towards other party members. What has to be taken into account for these infants is that they are not able to regulate distances to their party members: for the lack of loco-motor skills, they are totally dependent on their mothers. However, the fact that they peer less frequently at foreign role models when within two meters of them than they do at their mothers shows that these infants are very focused on their mothers.

Ideally, to investigate whether infants in fact have a preference for a certain role model one would have to look at situations where the infant has a true choice between both role models for example when both role models are within two meters of the infant. Regrettably, this was not possible with the current data set. However, even though I could not fully confirm hypothesis 2b these results can be seen as evidence that younger, less knowledgeable infants are very focused on their mothers whereas older infants show interest in all potential close by role models.

Consistent with hypothesis 2a I found that for infants, both processing complexity of the food item as well as rarity of the food item have a positive effect on peering rates: peering rates increased with growing number of processing steps of the food item as well as with increasing rarity of the item in their mothers' diet. With a distance analysis done for one of the infants these results were verified: with increasing complexity and rarity of the item in his mother's diet Fredy (5-6y) spent a higher proportion of the mothers feeding time within two meters of her. This shows that selective attention also manifests itself in how the distance is regulated between infant and mother.

Furthermore, my findings confirmed that with increasing age of the infants, peering rates decrease and that the impact of item rarity on peering rates is more pronounced with increasing age of the infant. The latter is most likely due to the fact that with increasing age, the infants are familiar with a growing proportion of their mothers' diets. Consistent with my results, in a study on Bornean immature orangutans Jaeggi et al. (2010) found that infants peer more frequently when their mother eats difficult to process food items rather than easy ones. These results are comparable to watching rates reported for nut-cracking of Tai chimpanzees (Boesch and Boesch-Acherman 2000). Interestingly, Jaeggi (2006) found no correlation between peering rate and total feeding time of the mother or infant age.

For the juveniles I found no effect of processing complexity of the item on their peering rates, suggesting that they know how to process all food items. However, I could show that peering rates increase with decreasing frequency of the item as part in their own diet. It therefore seems that juveniles selectively pay attention when their association partners feed on items that are rare in their own diet. Twice it was observed that juveniles peered at a party member who was eating something that they had never been observed eating before. On one of these occasions, the juvenile was then (right after the peering event) observed feeding on the same food item for the first time.

In sum, my findings show that infants and juveniles peer selectively at their party members. Infants mostly peer at their mothers and their peering rates increase with increasing complexity and rarity of the food item. I found no preference for foreign role model; however, some evidence was gained that smaller infants prefer their mother as role model whereas older infants show no such fixation. Juveniles peer with increased frequency at their party members if those are feeding on items that are rare in their own diet. All in all this suggests that before the age of weaning infants learn socially by observing their mothers (observational learning) whereas after weaning horizontal transmission (again in the form of observational learning) seems to be common.

4.2.3 Independent exploration: How and with what?

For young human children it is very well known that from the age they have gained the motor capacity to do so they try to seize every object in their environment, take it into to their mouth or examine it with their hands (Power, 2000; Piaget, 1952). This behavior is thought to "reflect the active attempt of infants to learn about the physical world around them through their actions and their senses" (Power, 2000). This exploratory tendency in humans is especially pronounced in the second half year of life, following which it decreases with age (Power 2000).

In agreement with prediction 2c, I found that rates of explorative behavior and object play of immature Sumatran orangutans decrease with age and reach adult levels before the age of first reproduction. In the comparative part of her study, Forss (2009) could demonstrate that Sumatran immatures perform try feeding significantly more frequently than the Borneans. For object play she found no such difference. This is in agreement with the above described development of the diet repertoires: immatures at Tuanan adopt diets that are extremely close to the one of their mother whereas my data suggests that Suaq immatures acquire diets that are less alike. The latter finding has to be treated with caution as we cannot rule out a sampling bias at the current state of research (see above). However, this provides preliminary evidence that Sumatran immatures might have a higher tendency to independently explore objects (potential food items) in their environment. This difference can be explained by the cultural intelligence hypothesis (discussed below).

Furthermore, my results show that with increasing age, explorative behavior manifests itself less frequently in taking objects into the mouth but rather in exploring them with

hand and eyes. This is consistent with explorative behavior in human infants (Power 2000). Try feeding might occur for different reasons. Try feeding on items that are edible most likely represents a lack of food processing competence while try feeding on inedible items may be the result of a lack of food detection competence but also of the genuine interest in items that are not part of the mother's diet. Try feeding on items that look potentially edible (such as green leaves or ripe fruits) but do not form part of orangutan diet may be a measure of more goal directed attempts to explore novel (potentially edible) food items. The last two categories are very hard to separate but both are most likely based on the inherent urge to explore items that would not give account of observational learning but rather true independent exploration.

My findings show that both, feeding rates on edible items as well try feeding rates on inedible items decrease with age. Interestingly, try feeding on edible items decreases at a later time than try feeding on inedible items. This suggests that both, food detection and food processing competence increase with age whereas food processing competence may lag behind. This differs from what I expected after looking at the peering rates: rarity seemed to have a stronger effect on peering rates than complexity, implying that food detection competence is harder to acquire than food processing competence. Rates of try feeding on potentially edible items did not change with age. This can be seen as evidence that the inherent curiosity in items that look edible stays constant during immaturity. The occurrence of try feeding on inedible and potentially edible items in general shows that try feeding not simply follows the mothers feeding pattern and is therefore not simply the outcome of social learning: in agreement with prediction 2e, young orangutans explore items in their environment that they have never seen eaten by their mothers.

When looking at whether try feeding on edible items increases with growing complexity or rarity of the food item (prediction 2d) I found that with increasing age the pattern changes. It seems that in younger infants the try feeding pattern mainly follows the mothers feeding pattern. This shows that younger infants' try feeding is rather unselective, they just try feed on what they are exposed to. Contrarily, older infants selectively try feed on more complex items, regardless of the frequency in mother's diet. Juveniles only try feed on items of high processing complexity. This pattern is consistent with the expectation that with increasing age immatures become more skilled and show diminishing try feeding on items that are easy to process.

The analysis also produced some evidence that the diet of mothers of clinging infants might differ from the diet of mothers who have non-clinging infants and from the ones of juveniles: mothers with younger infants seem to feed more on low complexity items and less on high complexity items compared to mothers with older infants. However, to properly test this and disentangle it from environmental effects, a much bigger sample would be needed.

In sum, I found that rates of explorative behavior and object play in immature Sumatran orangutans decrease with age. Younger infants frequently take objects into their

mouths to try them whereas older infant in a similar situation tend to make more use of their hands. The development of try feeding rates shows that food detection and food processing competence increases with age. In younger infants try feeding on edible items mainly follows the feeding pattern of their mothers whereas older infants only try feeding on high complexity items. Infants of all age classes explore items that are not part of their mother's diet suggests that immatures have an inherent urge to explore items in their environment that is independent of social enhancement.

4.2.4 Does peering lead to explorative behavior?

If orangutans learn socially from conspecifics by peering, their try feeding and exploration rates should to some extent follow their peering patterns, especially for unskilled foragers (younger infants). In order to find out to what extent immature orangutans put the knowledge they gained from observing their role models into practice I looked at the correlation between peering and exploration.

I found that in infants, explorative behavior in a given food patch is more frequent after a peering event compared to before it took place. For juveniles, however, exploration rates were not significantly higher after peering but showed a weak trend. For juveniles try feeding rates on edible items were extremely low (see above) which suggests that juveniles can probably process all food items.

Consequently, their feeding patterns rather than their try feeding is expected to follow their peering pattern. In 35% of all peering events of the juveniles they started eating in a food patch after peering at a party member (feeding in this patch) and once a juvenile was observed feeding on a food item for the first time right after it had been peering at a conspecific feeding on the item. However, those observations remain anecdotal and we cannot be sure whether we truly observed the first feeding event of an individual on a given item.

In his study on immature Bornean orangutans Jaeggi et al. (2010) found that practice-like try feeding on dead wood by infants is more frequent after the mother herself had fed on insects hidden in dead wood. I could confirm this result by redoing the same analysis on one of the infants (Fredy 5-6y) during my study period. Fredy not just showed more of the practice-like try feeding after his mother was observed feeding on insects but the try feeding rates were even higher if he had been peering during the mothers feeding bout.

In summary, consistent with prediction 2f my results showed that in infants try feeding and exploration behavior mainly follows their peering pattern. For juveniles I found only limited evidence that their try feeding and their feeding pattern follow their peering pattern. These results strongly suggest that immature orangutans' explorative behavior is an outcome of observational learning.

4.3 Is there a difference between the two orangutan populations and can the cultural intelligence hypothesis explain it?

Several of the above presented findings provide evidence for differences between the Bornean orangutan population at Tuanan and the Sumatran one at Suaq Balimbing. At the current state of study, conclusions have to be drawn very prudently: sample sizes are still small and the infants used for the comparative study are not exactly of the same age. Furthermore, as the data was collected by different observers at the two sites, I cannot rule out that to some degree differences between observers are the root of the reported variation. Future research including more immatures of different ages and observers who will have collected data at both sites will show how big the difference between the two populations truly is. Keeping all this in mind I nevertheless now attempt to evaluate whether these preliminary results can be explained by the cultural intelligence hypothesis.

The cultural intelligence hypothesis suggests that the more opportunities for social learning an individual has during ontogeny, the larger its set of learned skills should be as an adult. Furthermore, at a certain point these differences become evolutionarily fixed and consequently individuals of species with more opportunities for social learning also show an innate predisposition to be more exploratory and have enhanced capacities in problem solving (van Schaik and Burkart, 2011). Consistent with this prediction it has already been shown that among primates, the ability for social learning correlates positively with the innovation tendency (Reader and Laland, 2002).

The two orangutan populations of Suaq Balimbing and Tuanan provide an ideal natural setup to test the cultural intelligence hypothesis. At Suaq Balimbing individuals spend more time in association with other individuals than at Tuanan (van Noordwijk et al., 2009; Forss, 2009). This provides them with more opportunities for social learning. Consequently, one would expect that Sumatran individuals show a bigger set of learned skills and maybe even a higher exploratory tendency.

The comparison of my findings with results from Tuanan showed that the general skill acquisition trajectories are very similar for the two populations. Due to environmental differences one has to be very careful when comparing the set of learned skills of the two populations. However, consistent with the predictions of the cultural intelligence hypothesis the reported number of simple as well of complex cultural variations is bigger at Suaq than at Tuanan (Whiten and van Schaik, 2007). So far the comparison of the two populations provided some evidence that at Suaq immatures show more explorative behavior than the ones at Tuanan. It also seems that at Suaq the diet overlap between mother and infant is smaller than at Tuanan. Consequently, Suaq individuals must acquire a bigger part of their diet independently of their mother, which can be viewed as an evidence for higher exploratory tendencies of the Suaq Balimbing individuals.

4.4 Do orangutans fit into the General Developmental Constraint Model?

According to the General Developmental Constraint Model (GDCM), the energy that species which live in energetically limiting habitats need, to grow and differentiate brain tissue, is the main constraint on the length of the developmental period. The bigger the brain the more pronounced these energetic constraints will be. Other factors such as amount of skills to learn may influence developmental pace in species that have additional energy subsidies to the mother and the developing young.

Because of their relatively big brains (on average 388 cc for Sumatran orangutans (Taylor and van Schaik, 2007)) and their poor habitats the GDCM predicts that the developmental pace in orangutans is determined energetically rather than by time constraints: the energy to reach adult constitution and not the time to acquire skills sets the pace of development in orangutans.

Former studies could already demonstrate that immature orangutans reach competence in non -food related technological skills as well in loco-motor and social skills long before the age of first reproduction. Regrettably, no data on the physical development of wild orangutans has been collected to date. Under the GDCM one would expect that adult-like body size of females is only reached shortly before age of first reproduction. However, during my observation period even the oldest of our juvenile females (Tina 14-15y) was estimated to be smaller in size than adult females.

With my project I could show that immature Sumatran orangutans reach adult-like levels of all domains of the ecological competence (food selection competence, food processing competence and range use competence) long before the age of sexual maturity. Food selection competence seems to be reached around weaning, food processing competence around the age of 12 and range use competence around or shortly after weaning. The comparison with data from Tuanan suggests a very similar picture. Consequently, it is very unlikely that the acquisition of foraging skills has a limiting effect on the developmental pace in either of the two populations.

The question why individuals at Tuanan develop faster than the ones at Suaq (shown in earlier weaning, earlier age of first reproduction and shorter inter birth intervals (Wich et al., 2009; Knott et al., 2009, van Noordwijk personal communication) remains unresolved. Van Noordwijk and van Schaik (2005) point out that long inter birth intervals most likely mean that for older infants the mother still has a high contribution to survival (either because the infant still lacks ecological skills or because the presence of the mother reduces other risks such as the one of predation) and therefore she better delays the birth of the next offspring. My findings showed that it is unlikely that the need to learn ecological skills have an effect on the developmental pace. For the age of weaning it might however be that if Suaq individuals acquire bigger diets than their Bornean relatives (what might well be as the number of different items eaten per individual is the currently the approximately the same for both populations but likely

to increase for the Suaq individuals due to the smaller amount of follow hours) infants need longer to acquire adult like diets. Therefore, infants at Suaq Balimbing might profit more from staying longer with their mothers as they then have expanded opportunities for social learning. Earlier age of first reproduction and shorter inter birth intervals on the other hand might be explained by differences in the food availability between the two populations: Bornean forests are less productive than Sumatran ones, and thus availability of edible food is lower in the Bornean habitats (reviewed by (Russon et al., 2009)). It known that in humans, women start reproducing earlier and have more children if they were exposed to famine during gestation (Roseboom et al., 2011).

All in all, these results are consistent with studies on other primate species including gorillas (*Gorilla gorilla* and *Gorilla beringei*), squirrel monkeys (*Saimiri sciureus*) and golden lion tamarins (*Leontopithecus rosalia*) which also showed that foraging skills are reached long before age of first reproduction (Watts, 1985; Nowell and Fletcher, 2007; Stone, 2006; Rapaport and Brown, 2008).

In summary I found that the predictions of the GDCM fully apply for the development of immature orangutans. It seems that like in many other primate species, energetic constraints set the pace of development in orangutans rather than the time to acquire adult-like skills.

5 Conclusions

With my study I could show that immature Sumatran orangutans reach adult-like levels of ecological competence long before the age of first reproduction. Former studies on orangutans produced similar results for skill development in other domains. It is therefore very likely that rather than skill acquisition, energetic constraints act as limiting factor for orangutans' development.

In terms of learning mechanisms, my results suggest that both, social learning (in the form of observational learning) as well as independent exploration play an important role for the development of foraging skills in immature Sumatran orangutans. Consistent with previous studies I found that immature orangutans learn most foraging skills socially from their mothers. I also found evidence that social learning continues after the age of weaning, mainly in the form of horizontal transmission between immatures and unflanged males as well as among peers. When comparing my data to data collected on Bornean orangutans at Tuanan I found that skill learning trajectories are very similar for the two populations, despite differences in the timing of several life history parameters related to reproduction. However, immatures at Suaq Balimbing seem to have more frequent opportunities for social learning and I found some preliminary evidence that this might have resulted in distinct exploratory tendencies among the two populations. Consequently, my findings have provided evidence that opportunities for social learning might determine the intelligence of a species. Social transmission of knowledge and skills or in other words culture might have been an important ingredient that made us humans smart.

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