Social Learning and Independent Exploration in immature Sumatran Orangutans, *Pongo abelii*

Master's Thesis

Sofia Forss

Supervisor: Prof. Dr. Carel P. van Schaik
Anthropological Institute and Museum
University of Zurich

Social Learning and Independent Exploration in immature Sumatran Orangutans, *Pongo abelii*

Additional comparative study between two populations; Suaq Balimbing, Sumatra and Tuanan, Borneo

Master Thesis by

Sofia Forss
University of Zurich
April 2009

Supervised by:

Prof. Dr. Carel van Schaik
Anthropological Institute and Museum
University of Zurich
Switzerland

Sponsored by following Institutions:

State Ministry of Research and Technology
Republic of Indonesia, RISTEK

Indonesian Institute of Science
LIPI

University of Zurich

Universitas Nasional, Jakarta, UNAS

SUMMARY

Orangutan populations at different sites show cultural variation. The orangutans, *Pongo abelii* around the swamps of Suaq Balimbing, Sumatra exhibit the largest cultural repertoire of all orangutan population and are the only ones using tools while foraging in the wild. This field study focused on the underlying mechanisms producing traditional differences among geographically separated orangutan inhabitants. Social learning is the key process to transmit culture. Orangutan infants are suggested to acquire most foraging skills through vertical social learning during the long, intense years following mother throughout their habitat before the reach of independence. This study support these implications, but also highlights the possibilities and importance of horizontal/ oblique learning in order to promote culture. Our intentions for this study were to examine which processes during foraging promote infants to pay attention to their mothers or others, and so what mechanisms drive the course of social learning among immature orangutans. Orangutans at Suaq Balimbing display great social tolerance. Hence offspring raised here are exposed to opportunities to learn socially from others, beyond own mother, already at an early age. One part of this study was a comparison between the study population at Suaq Balimbing and a population of *Pongo pygmeus wurmbii* from the Bornean site Tuanan. This comparative approach enables us to explore the reasons for cultural differences and contribute to our understanding for how social learning is abundant for a successful life of orangutans and further and how “culture makes you smart” (*van Schaik 2004*).

Table of contents

Table of contents for graphics and pictures

INTRODUCTION

METHODS

RESULTS

1. GENERAL INTRODUCTION

Human social units such as individual societies and individual families produce different expressions in various behavioral domains. In other words, the social environment in which we are raised strongly influences our behavioral traditions. But humans are not the only ones with this uniqueness; social input affects behavior in a broad range of animal species. These diverse traditions in the animal kingdom have so far mostly been described in the foraging context. Human infants rely on social inputs for dietary knowledge*,* and the same is true throughout nearly the whole primate order: infants rely on socially learned mechanisms when acquiring their foraging behavior *(Rapaport & Brown 2008)*. The present study was designed to examine social learning and independent exploration in one of humans' closest relatives, the Sumatran orangutan, *Pongo abelii*. We focused on how immature wild orangutans acquire and develop their foraging skills. Foraging behavior is probably one of the most challenging problems great apes face, and hence where we expect their cognitive skills to be apparent (*Hermann, E. 2007*).

1.1 Social Learning as Evolutionary Adaptation

Learning can be defined as: "A set of complex ontogenetic processes that allows animals to acquire, store, and subsequently use information about the environment" *(Galef and Laland 2005)*. If the information obtained derives at least in part from other individuals rather than the environment alone, we classify it as social learning. The broad topic of social learning includes various phenomena and has been described in a number of different animal species, from insects to primates. What connects them all is how a behavior becomes modified as a result of social interaction with other individuals of its species.

When foraging with other conspecifics threespine stickleback fish have been shown to prioritize social conformity using social cues rather than private information (*Webster & Hart 2006).* This is just one example of studies reporting simple forms of socially learned behavior. Moving closer to humans, through mammals, primates and the great apes studied here, we see that social learning in the form of local enhancement not only plays a role where to find a food source, but can affect the learning of an entire diet, as well as other behavior patterns. The more sophisticated forms of social learning are mostly studied from a psychological point of view to address whether animals are capable of acquiring skills by observing and imitating behaviors of others.

From an ecological and evolutionary standpoint, social learning is expected to be found in wild animals whose fitness are enhanced by imitating and copying behaviors of others (*Galef 1996*). It is most likely that social learning has become an adaptation driven by natural selection in species where having an information-acquiring system is more profitable than being preprogrammed by genes that can not adjust to environmental changes during a lifetime *(Galef and Laland 2005)*. Furthermore, we expect social learning as an adaptation in species where learning, by observing and imitating other more experienced individuals, serves as a shortcut to crucial information that would take far too long to obtain by individually error and trial concept. We expect this in great apes, where for example diet has achieved such a complexity that it would be fairly disadvantageous for each generation to develop their feeding niche individually. Apart from being time consuming, individual learning can also be very costly. Compared to a young naïve animal, an older more experienced conspecific is already adapted to a habitat, having assembled previous experience with non-edible maybe even poisonous food items, and is thus able to serve as a potential model. With these assumptions in mind, and the fact that the potential role model and its naïve observer share an environment, it is more likely that such animals rely on social learning (*Galef and Laland 2005).* Adding time to the assumption the longer a naive, young individual spends around a beneficial demonstrator, the more social learning we expect to find. And as for this study, we further predict that the more role models are around, the smarter an animal may become.

1.1.1 Mechanisms of Social Learning

Table 1: A list of the various forms social learning can take (*Rapaport and Brown 2008*)

Mechanism	Definition
Social 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.
Local Enhancement	An individual may learn to orient its acts to a food item or location as a result 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 food; for example, by observing another individual eat a novel food, a naïve animal may learn to recognize the item as food.
Imitation	A naïve individual learns a new behavior, such as a foraging technique, by matching the detailed sequence of actions performed by another.
Teaching	Individual A modifies its behavior only in the presence of a naïve observer B at some cost or at least no direct benefit, thereby encouraging or punishing B´s behavior and providing B with experience, or setting an example for B; as a result, B acquires knowledge or learns a skill faster or efficiently than it would otherwise do.
Opportunity Teaching	A way of teaching in which individual A puts B in a situation conductive to learning a new skill or acquiring knowledge.
Coaching	A way of teaching in which individual A directly alters the behavior of B by encouragement or punishment.

1.2 Independent Exploration

To decide that an animal engages in social learning one must be able to exclude that the animal discovered the skill on its own. To complete a process of social learning, in form of imitation found among primates, an individual has to discover and learn a behavior, has to perform certain evaluation or practice of the behavior, and finally must make a decision whether it is going to integrate the respective behavior in its behavioral repertoire (*Castro and Toro 2004*). The evaluation and practicing as a consequence of observational learning might then lead to an independent discovery of a behavior; hence independent exploration is possible as a preceding mechanism of social learning. Even in humans practicing is an important mechanism before any behavior is fully learned. Observing other individuals handling objects for example, is the first step of a learning process then completed only by the individual experience with the same activity.

1.3 Social Learning in Primates

Among the primate order all infant and juvenile animals pay attention to feeding adults (*Rapaport and Brown 2008*). Primatologists have suggested that social learning should be prominent in this order. First, if set in relation to other animals, primates show a relative long juvenile period, which increases the time before a young animal reaches independence. Second, many primate species possess a very diverse diet. On average a primate diet consists of hundred of species of plants and animals (*Rapaport and Brown 2008*). A juvenile may encounter some a few times a year at best, depending on the seasonality of the habitat. As a third argument, most primates are gregarious, which puts them in position to interact with other individuals in many different ways. The large brain size found among the great apes is further thought to facilitate the more cognitively demanding social learning processes.

As the number of studies showing social learning in other mammalian orders grows, the assumption of social learning playing a greater role in primates than in other animals, has lately encountered challenges as well as conflicts. Results from experimental studies on rodents show that they are more likely to rely on social information when choosing between two unfamiliar food types suggesting that uncertainty in decision making of food preferences promotes social learning (*Dewar 2004; Galef B.G. 2007*). Likewise, meerkats have been reported to use socially learned mechanisms such as teaching by gradually providing their novice pups with difficult-to-handle-prey (*Thornton and McAuliffe 2006*). Findings from these studies require that we consider social learning in a broader perspective and allow us to question to what extent brain size and complex cognitive behavior, found in primates for example, have an influence on social learning per se. Different animal species face different kinds of environmental challenges. Thus if social learning is seen as an evolutionary adaptation evolved to solve environmental problems an animal may encounter, we should expect to find social learning abilities among multiple orders (*Lefebvre and Giraldeau 1996*). For this study our interest lies in the outcome of such adaptation and how it expresses itself onto higher levels such as animal cultures. In the wild it is much harder to recognize social learning, since no experiments presenting new skills and models can be performed. One way is to search for geographically variation in behaviors, where ecological and genetic reasons can be ruled out, hence the behavior is most likely to be socially transmitted. Further young, novice animals can be followed in order to detect how they attribute attention to others while foraging on skills, where they are still incompetent. In this study we concentrated on detecting how young animals pay attention to feeding adults, referred to as peering (see Methods). If the purpose of such close range watching, from the infants perspective, is to obtain knowledge and information on skills, such as feeding techniques and ability to find food sources, we would expect peering to occur more frequent by items that are complex to process or hard to find. We would also expect that target skills of peering would change with infant age, as an infant gets more familiar with different food items.

1.4 Social Learning as precondition for Culture

Captive experimental studies of great apes have shown that chimpanzees and orangutans are capable of imitative social learning. One example to illustrate this is the study by *Whiten et al (2005)* using two groups of captive chimpanzees. For each group a role model was trained with one foraging technique, “lift door” versus “slide door”, in order to obtain food from a device. The outcome of the experiment showed that in each chain, individuals would strictly copy the technique they observed by the model *(Horner, Whiten et al. 2006).* This study confirms that chimpanzees indeed are able to maintain a learned skill across simulated generations. Similar experiments have also examined social transmission of information in captive orangutans. Those subjects provided the opportunity to observe a model opening an artificial fruit showed higher success in the task than control subjects that did not watch the model (*Stoinski and Whiten 2003*), suggesting horizontal social transmission of knowledge.

Experimental studies like these are of great importance in the understanding of what is the actual cognitive potential in these great apes although they contribute less to our understanding of how cognition evolves in the wild. Like Chimpanzees also captive orangutans perform tool use tasks and other cognitively challenging experiments with no problem due to enculturation by humans. Yet their brain size is the same as their wild relatives, so how is that potential intelligence used by the free-living animals of these species?

Great ape infants raised in a human environment are cognitively more productive in experimental performances (*Gardner and Gardner 1989; Tomasello and Call 2004*). If enculturation has this effect on ape infants it clearly shows us the biological cognitive potential hiding in these species; but how does this intelligence express itself in the wild? So far it has been difficult to assess how far experimental studies capture the wild conditions an animal faces, and which learning mechanisms are actually found in free-living animals. *This study aimed to examine social learning in situ in a wild population of Sumatran orangutans, Pongo abelii. What are the consequences of social transmission in the wild?*

In both chimpanzees and orangutans behavior repertoires have been shown to show geographic variation and were classified as cultural differences *(van Schaik, Ancrenaz et al. 2003).* Culture defined as "*the possession of multiple traditions*, *spanning different domains of behaviors*" (*Whiten 2005*) is no longer treated as a human-specific phenomenon but existing also in those species showing the cognitive demands of maintaining it. For any cultural traits to emerge in the first place, innovations, new solutions to challenges in the environment, have to arise. The processes then responsible for spreading and maintaining innovations, hence creating traditions, are social learning and transmission throughout a population, which were of focus in this study. As referred to previously, many animal species have evolved to use some sorts of social learning, but most of them lack the establishing of real traditions continuously over generations. So far, for other mammals and monkeys there are few reports of traditions, however in Capuchin monkeys of Costa Rica it has been established some cases of site specific food-processing techniques, where particularly the youngsters seem to coordinate their dietary pattern according to the adults in their groups (*Perry 2008*). Furthermore great apes seem to show preferences to establish especially the most complex foraging techniques as community traditions.

Nut cracking behavior and cooperative hunting in chimpanzees as well as tool-use distribution in orangutans are just a few examples of the contexts in which these species have become cultural. These findings push back the origin of what we call culture per se to our last common ancestor 14 million years ago *(van Schaik, Ancrenaz et al. 2003)*. Still the dimension of culture we find in modern human societies is a major evolved step from great ape culture. It has been argued that early hominids equipped with the capacity of a theory of mind could predict behaviors of members of their social groups and take that into consideration in their own actions (*Tomasello 1999*). Furthermore, our early ancestors possessed the capacity to approve or disapprove their offspring's learned behavior, this would promote for cooperation as well as making learning less costly and more efficient creating a cultural inheritance system (*Castro and Toro 2004*). Finally humans have evolved mechanisms such as language, mathematical abilities and social norms, to which a human infant has to be trained for a successful life in its cultural environment. All these phenomena enable us to increase the complexity of cultural variants (so-called cumulative culture) over the generations. Abilities like these have not been reported from any great ape.

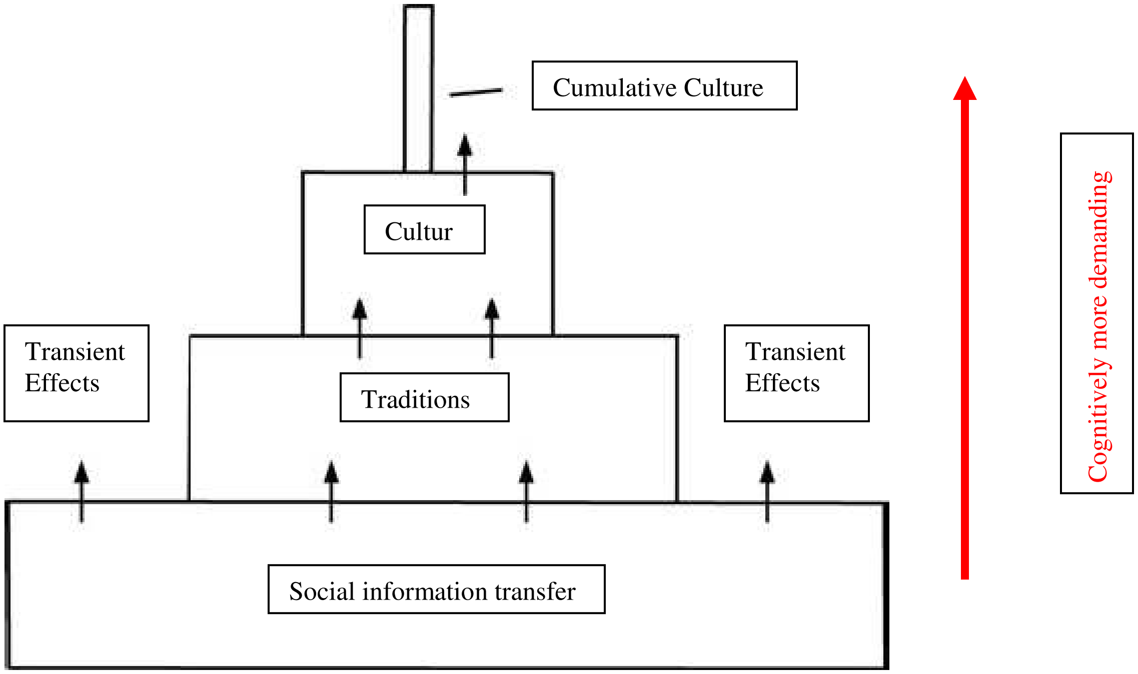

Figure 1: (Whiten and van Schaik 2007): Culture pyramid. Social learning in form of simply using public information to trace food patches is wide spread among animals. Second level of this pyramid illustrates the ability to sustain such information over generations. Only a few species such as the great apes, whose social learning mechanisms is of other characteristics than in other orders, show a repertoire of traditions classified as culture. Cumulative culture, evidenced only in humans allows cultural traditions to build upon each other due to complex cognitive skills.

There are a few hypotheses addressing the driving forces for natural selection on intelligence. The Machiavellian intelligence hypothesis (MIH) or the Social intelligence hypothesis (SIH) are often used in same context, implying that intelligence as we see it among monkeys and great apes were emerged to adapt these animals to face the demanding form of socially complex lives. Further it has been argued that this social complexity may select for particular domains of intelligence (*Whiten and van Schaik 2007*). The Ecological intelligence hypothesis (EIH) traces the origins of intelligence to the need for an animal to be smart in an environment where it has to improve foraging techniques and skillfully solve habitual problems to its feeding niche (*Byrne, Whiten et al. 1988*).

2. BACKGROUND AND PURPOSE OF THIS STUDY

2.1 Orangutan cultures and sociality

Throughout the years of orangutan research in the wild on the islands of Borneo and Sumatra, evidence for cultural differences has accumulated. Long-term studies continuously provide us with a growing number of behavioral traits that differ between sites, which raises the question regarding how all these differences came about. Our target community of orangutans for this study, found at Suaq Balimbing, provides us with many characteristics that we were looking for to address such differences and the social learning mechanisms behind them. Orangutans as a semi solitary primate have a social organization of a individual based fission-fusion model (*van Schaik 1999*). Suaq orangutans show a greater tendency towards the fusion part of the expression in relation to other studied populations. This variation in gregariousness among orangutans provides us with an excellent opportunity to study how sociality influences social transmission. The second contributing fact to our interest in particularly the Suaq population for this study is the broad and complex foraging repertoire present there (see appendix). Suaq orangutans have mainly made themselves famous due to for their species-unique, prevalence of tool-use behavior. Orangutans there use tools in form of twigs and sticks to poke into tree holes to extract honey, ants or termites hiding inside such hollow tree trunks. They also process tools when foraging on the fruits from the *Neesia* tree, whose fruits are large five-angled capsules filled with nutritious seeds inside a wooden shell and a layer of sharp hairy needles (*van Schaik 2006*). When unripe, the capsule is still closed and orangutans need to use great strength to be able to open up such a stone-hard husk by biting in it. As the fruit ripens, its shell opens up a bit (“dehisces”) but the seeds are still concentrated in the deep core area in the middle of the fruit, but at this point they become popular in the orangutan feeding repertoire. Orangutans can extract the seeds from the middle of the fruit with help of tools in form of short twigs, which are manipulated and processed by peeled off bark and occasionally bitten in the end of the tool creating a brush like structure (Figure 2.1 and 2.2).

Figure 2: Tool used for *Neesia* seed extraction, by a female juvenile.

Figure 3: Three tools used for termite fishing

The reason for this detailed explanation of processing of this particular fruit lies in the underlying cognitive demands this kind of tool- use requires and has an influence on the social learning mechanisms we found at Suaq (see Results). Tool use on *Neesia* is only observed in orangutan populations along the North western Sumatran coast line in the Kluet Swamp area; Suaq Balimbing, Singkil, Tripa and Batang Toru (*van Schaik 2009*). At Batu- Batu a Sumatran site located on the other side of the wide impassable Alas river, orangutans do feed on *Neesia* but use the "bite them open" technique. This is also the same way the seeds of *Neesia* are fed on at the site of Gunung Palung on Borneo. The solution to obtain *Neesia* seeds out of its complicated package with the help of tools has only been recorded on the same side of the Alas river in swamps proximately close to Suaq, suggesting a case of a clear cultural spread innovation (*van Schaik 2006*). This patterns suggests that intelligence is not a completely innate quality, neither in humans nor great apes. Suaq orangutans are therefore not thought to be having a higher level of innate intelligence, but to behave smarter because they have the profit of many learning opportunities.

2.2 Mother's role for Vertical transmission

The nature of orangutan life history already provides each and every offspring years of learning opportunities from their own mother. Great apes show an extended interbirth interval compared to other primates and mammals. Among gorillas, chimpanzees and orangutans, orangutans have the longest interbirth intervals of 6.1- 9.3 year. Gorillas show 3.9- 4.6 years and chimpanzee interbirth periods lies is 4.6- 6.2 years (*Wich, de Vries et al. 2009*). Interestingly the birth distances between the two sub species, *Pongo pygmeus* and *Pongo abelii* on Borneo and Sumatra differ as well. Bornean orangutans seem to be weaned earlier than their Sumatran relatives and also tend to range independently at an earlier stage. Sumatran immatures on the other hand tend to associate with and visit their mothers on a more regular basis (*Marshall et al. 2009*). Whether these differences have a root in developmental variation between the two sites is still to be answered. It is still unclear whether this stage of a young orangutan's life is essential to horizontal and oblique learning opportunities, which we assume to exist in a higher frequency at denser populations such as Suaq Balimbing. In this study we argue that Sumatran immatures have much more skills to learn from their mothers, hence extending time with her might be highly profitable.

Previous research on immature orangutans at Tuanan, Borneo have demonstrated that by the age of weaning young orangutans closely match the diets of their mothers, whereas diets display variation among mothers *(Dunkel 2006),* suggesting a vertical socially learned acquisition of dietary choice in orangutans *(Jaeggi, Dunkel et al. 2007)*. On the same population, social learning involving mechanisms such as food solicitation was studied, which reported a negative correlation between an infant's ecological competence and the frequency of food solicitation, illustrating begging for food is, despite its nutritious value also an attempt for obtaining knowledge about edible food sources (*Jaeggi, van Noordwijk et al. 2008*). With these background data we conducted this project with the intentions to address the hypothesized relationship between the higher sociality and larger cultural repertoire found in our study population at Suaq Balimbing.

2. 3 Study Aims and Predictions

1. Sociality encourages social learning and generates culture. As supported from the MIH and SIH we predict the repertoire of Suaq orangutans to have emerged from a series of mechanisms mutually influencing each other; “multiple traditions select for enhanced social learning, multiple traditions generate smarter individuals, smarter individuals innovate and learn better” (*Whiten and van Schaik 2007*). For this explanation to be valid we first aim to establish whether:

    - **Suaq immatures spend more time in association and co-foraging** (see Methods) **situations than their conspecifics of Tuanan.**

    - **Suaq orangutans possess a more complex diet, so infants there have more skills to learn.**

2. Due to the intense and long time an infant spent with its mother, we would predict that if any social learning is taking place among orangutan infants, the mother is most likely to be the main role model. Indications for social learning were measured in terms of peering, begging as well as try-feeding events. Further if young orangutans observe adult individuals selectively in order to gain information about food sources we would suspect the frequencies of these measured behaviors to vary with infant age and characteristics of the food item.

    - **Infants peer most toward their own mother, since they are provided with most learning opportunities by her.**

- **Peering and begging are to be more frequent for food types that are hard to acquire:**
  - increasing processing level
  - embedded
  - rare

3. For innovations to develop into traditions and establish themselves as cultural repertoires in a population, horizontal and oblique learning are also needed. Ape social learning has been argued to be almost exclusively bound to the ontogeny of infants (*Rapaport and Brown 2008*). We investigated whether this holds for orangutans and at which stage an individual starts paying attention to potential role models.

   - **Do immature orangutans at Suaq Balimbing pay attention to role models beyond their own mother in the form of peering and begging?**

4. Independent exploration, estimated as try- feeding and object manipulation, can be expressed as a result of observational learning or stimulus enhancement or as independent exploration of novel objects.

   - **Infant try- feeding pattern is expected to follow the peering pattern if it is an outcome of observational learning.**

5. Lastly, our comparison of the two populations, predicts that all cognitive mechanisms previously mentioned are likely to be more abundant at Suaq than at Tuanan, if sociality actually constructs cultural richness. We predict more feeding skills among Suaq orangutans to promote more peering in this population compared to Tuanan.

   - **Peering, begging and try- feeding is likely to be more frequent among Suaq immatures than at Tuanan.**

6. Differences in feeding repertoires between Suaq Balimbing and Tuanan can be due to:

- **More observational learning at Suaq from different role models leads to more skills**
- **More exploration at Suaq leads to more skills**
- **Combination of both mechanisms**

3. METHODS

3.1 Study site and time period

This field study was conducted at Suaq Balimbing research station (03º 02´87´´N; 97º 25´01´´E) in the Kluet region of Gunung Leuser national park, Indonesia. The peat swamp forest here can still be classified as primary forest (*van Schaik 2004*) and has remained unlogged except for a strip along the Leumbang river. Within the study site the habitat can change quite dramatically, for example from a very wet, regularly flooded swamp area closer to the river, to a drier and slightly higher forest closer to the hill side of the site. These wet habitats nourish a low diversity of plant species, resulting in a highly productive habitat with a lot of food for the orangutans ranging here. Due to these ecological factors, Suaq Balimbing is the site with the highest density of wild orangutans (7 individuals/ km^2) (*van Schaik and Singleton 2001*) and the high density was one of the reasons this study site was considered the most appropriate for the questions we address in this thesis.

The field study took place between September 2007 and June 2008. Data has been collected at this study site since 1994, although in 1999 all research work had to end due to civil war. In May 2007, Suaq Balimbing was re- established as a research station and the data collection resumed. All individuals found from the new study period, 2007 on, were re-identified and habituated.

3.2 Data collection and definitions

Observations and data collection were performed using focal animal sampling methods (*Altmann 1974*). A focal animal was followed from time of encounter until its night nest and during subsequent days continuously from morning nest to night nest, for a maximum of ten days in a row. Focal sampling was based on standard protocols, which are used at all orangutan study sites for direct comparability *(http://www.aim.uzh.ch/orangutannetwork.htm)*. At every second minute the activity of the focal animal was recorded, and every five minutes its distance to other individuals. Priority was given to all social interactions and these behaviors were strictly defined. A complete record was kept of all social interactions, feeding techniques and other interesting behaviors using special data sheets. Because the project focused on behavior of immature individuals, every time a mother-offspring pair was followed, one observer was exclusively taking data on the infant and the other on the mother, ensuring adequate recording of the behavior of the smaller, sometimes less exposed infant.

Since we used certain activities as measurement for behaviors and expression of social and independent learning mechanisms, it is crucial that these are correctly defined and understood. By any social association, with own mother as well as with other individuals, the distance, time as well as the individual responsible for the approach and leave, was recorded.

3.2.1 Social association and distances

Distances between individuals were used to asses certain behavior patterns.

Party: When any individual other than the mother was within a 50m radius from the focal animal. A party can include more individuals and thus differ in size. Mothers with dependent offspring were counted as one party member. Thus, party size 1 includes only the focal animal alone or with its mother, party size 2 is the focal animal, alone or with mother, plus an additional individual (within 50m), party size 3 contains additional two other individuals and so on.

10- 50 m: More than 10 meter but less than 50 meter. Individuals within a 50 meter distance are empirically determined to travel in a coordinated fashion.

2- 10 m More than two meter but less than ten meter. A distance less than ten meter may indicate social tolerance between the individuals in association.

0- 2 m: Less than two meter, but without body contact. This close distance may be indicative of a high social tolerance and even favorable opportunities for social learning of feeding skills and techniques.

0 meter: Two individuals having body contact.

3.2.2 Behavior elements

Co- Foraging: Whenever two individuals are feeding, in the same food patch or on the same food item, within ten meter distance from each other.

Co- Feeding: Two individuals feeding from the same food item.

Independent Feeding: Whenever an infant was feeding on its own in a separate food patch from its mother.

Social Play: Non-aggressive interactions between individuals including poking, wrestling, slapping, chasing, biting or boxing each other, often accompanied by a so-called relaxed open mouth (or play) face.

APO: Solitary object play: seemingly non-functional manipulation of objects.

Try- Feeding: Any attempt to feed on an item without properly ingesting it.
Peer: Close range watching (< 2 meter) for at least five seconds at another individual and clearly paying attention to the other individual's activity.

Begging: Any attempt by an individual to obtain food from another individual, often involving stretching out a hand

Tolerant theft: A successful begging attempt, where the owner let's the beggar take the food item without any active transfer or refusal.

3.2.3 Food

(http://www.aim.uzh.ch/orangutannetwork.htm, Jaeggi et al 2008)

Embedded Food items: Items that are closed up or visually hidden; for example pith, inner bark (phloem and cambium), social insects (ants, bees, termites) in nests and seeds of those fruits whose pulp is inedible.

Non- Embedded Food items: Items that are easy accessible and not hidden, for example, most fruits, flowers and leaves.

Processing step 0: No processing required before ingestion, food item can be ingested as it is found and picked. (Example see appendix)

Processing step 1: One step of process: food item has to be broken up/bitten apart or certain parts spit out or peeled off. (Example see appendix)

Processing step 2: Two steps of process: a food item has to be broken/ bitten apart and further processed by spitting out, sucking, peeling off item parts. Combination of two mechanisms of process step 1. (Example see appendix)

Processing step 3: Three mechanisms from description of process step 1 are required before complete ingestion: (Example see appendix)

Processing step 4: All foraging involving tool use.

Tree Hole Tool-use: Using tools (e.g. twigs) to poke into tree holes to obtain social insects or their products.

Seed Extraction Tool-use: Using tools to extract seeds from the protected fruits of *Neesia* sp. These seeds are embedded in irritating hairs, hidden within the very tough outer casing of the fruit and exposed only through slowly opening fissures in the fruit’s valves. (Video sequence viewable at www.aim.uzh.ch/orangutannetwork.htm)

Extractive Foraging: Foraging on food types which are invisible to the forager. This often requires processing by multiple steps involving splitting up, ripping apart for example termite feeding, ants from nests, inner layer of plant parts, cambium and bark feeding as well as sap hidden behind bark.

3.3 Focal animals

This study exclusively concentrated on immature individuals, from young infants to adolescents. During the study period, 14 Mother- infant pairs and eight adolescent animals were identified in the area. For the analyses three to six mother- infant pairs were used, as well as two adolescent females. One of the adolescent females was already ranging independently whereas the second one was still ranging with mother and younger sibling for 62 % of the time followed. The focal animals are listed in table 2 and pictured in figures 5- 11. All focal animals were found and habituated in 2007 to 2008, and thus unfortunately no exact ages could be established. We therefore ranked the infants according to developmental age, for which we measured how much of the total time an offspring would spend in body contact with its mother. Also the relative size of the immature could be settled and we often used this to create an idea of age effects playing a role in the different questions we were interested in. According to locomotion skills infants were divided into two age related groups: dependent travelers and independent travelers. This was measured by how often an infant would cling onto mother’s body while traveling between trees throughout the canopy (Figure 4).

Table 2: Focal animals used for the analysis. Since the animals have not been habituated since time of birth, all ages are estimates

Focal Animal	Mother	Focal Minutes	Age Estimate	Sex

Ronaldo	Raffi	3930	1- 2 years	Male
Fredy	Friska	13 608	2- 3 years	Male
Ian	Intai	1954	3- 5 years	Male
Chindy	Cissy	3888	4- 5 years	Female
Lilly	Lisa	9916	6- 7 years	Female
Ellie	Friska	9776	> 8 years	Female
Tina	Unknown	6934	> 10 years	Female

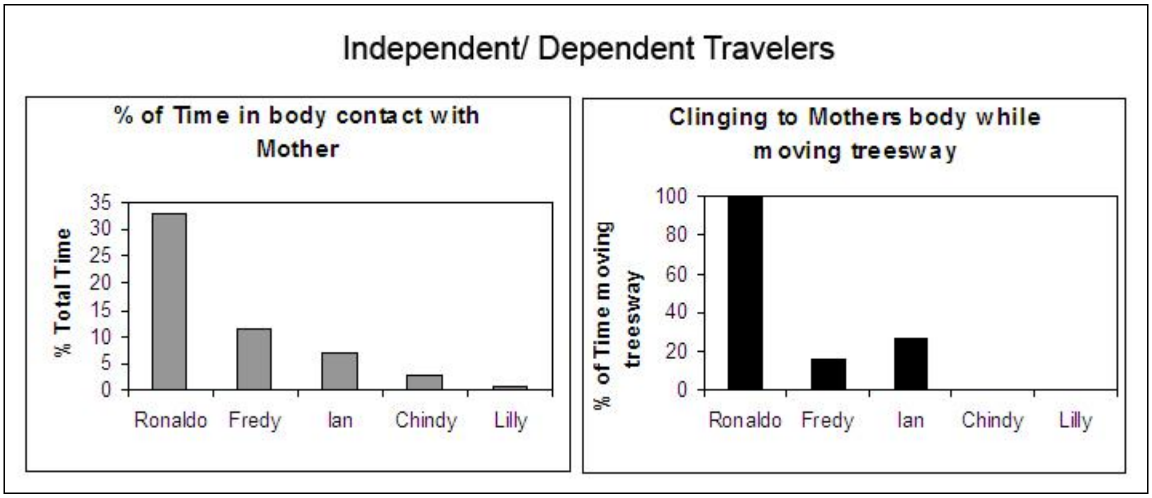

Figure 4: Ronaldo, Fredy and Ian are classified as independent travelers, since they still cling to their mother's body over 10% of the time while moving between trees. Chindy and Lilly are classified as dependent travelers because they do not cling to their Mother's body anymore while moving through the canopy.

3.3.1 Mothers with offspring

Figure 5: Raffi & Ronaldo

Figure 6: Friska & Fredy

Figure 7: Intai & Ian

Figure 8: Cissy & Chindy

Figure 9: Lisa & Lilly

3.3.2 Adolescent individuals

Figure 10: Tina

Figure 11: Ellie

3.4 Comparison to Tuanan

For some of our study aims comparisons to another site, Tuanan (2º09´06.1´´S, 114º26´26.3´´E), central Kalimantan, Indonesia were made. Data of orangutans has been collected at Tuanan field station since 2003. The study area of Tuanan lies in the Mawas Reserve and consists mostly of selectively logged peat swamp forest. The orangutan density of Tuanan is around 4.25 individuls/ km² *(van Schaik et al., 2005)*. For the comparison to this study four mother/offspring pairs were used; Jinak/ Jerry, Sumi/ Susi, Mindy/ Milo and Kerry/ Kondor, from the period of 2003- 2006. All the behavioral definitions were based on the same criteria used in previous projects regarding cultural questions and social mechanisms. Using identical methods from previous studies we can assure comparability between these two sites. For the main questions, of this project, regarding peering, begging and try- feeding, only data from year 2005 from Tuanan was used for analysis. In 2005 Adrian Jaeggi and Lynda Dunkel concentrated on cultural questions and hence established the study methods in Tuanan we now build on further in Suaq Balimbing. For more general data questions we used a more complete long term data set from Tuanan. Data from both Tuanan and Suaq Balimbing are kept in similar access data bases, making comparisons between the sites easier.

3.5 Inter- observer reliability

To assure the comparisons between two study sites inter- observer reliability was calculated between Adrian Jaeggi, who conducted the social data at Tuanan and Sofia Forss, who recorded the data at Suaq Balimbing. Both observers scored two video clips, containing a high frequence of the behaviors compared between the sites in this study: Peering, begging and try- feeding. The video clips were conducted with the ad libitum method, to focus especially on the behaviors in question. We then calculated the frequency of agreed scores and scores made by only one of the observers. As an index for inter- observer reliability we then calculated Cohen's Kappa coefficient. This index range from 0- 1.00 and for our results we established a Kappa value of 0.79. A Kappa index > 0.70 is considered satisfactory and an improvement from the general % of agreements, and so we can assure inter- reliability between the data set of the both sites (*Martin and Bateson 2007*). Data between the two observers sampling data from Suaq Balimbing: Ellen Meulman and Sofia Forss days were compared when the both observers would follow the same focal animal. Pearson correlation between the two observers delivered a correlation coefficient of 0.905 used as an inter- observer reliability index (Pearson $r = 0.905$, $N_{behavior} = 12$, $p = 0.000$).

3.6 Statistical Analyses

All data were entered in a Microsoft Office Access 2003 data base. All statistical tests were run in SPSS 16.0. Only a few analyses, regarding comparison between the sites consisted of normally distributed data and could be performed using t- tests. All other analyses were of data, not normally distributed, and so assessed using non- parametric tests such as; Mann- Whitney U, Wilcoxon signed rank, Friedman ANOVA, ANCOVA, Kruskal- Wallis, Jonckheere- Terpstra test, Kendalls taub and Spearman correlations. A few presented results were unfortunately not statistically assessed due to small sample sizes. As in many other great ape studies our statistical power is low because of few focal individuals.

4. RESULTS

4.1 Social Associations

A behavior can be socially transmitted only when individuals encounter role models to imitate, copy and hence learn socially from. Due to a considerably long interbirth interval, Sumatran orangutan infants are provided with their mothers presence and care for up to nine years (*van Schaik 2004*) (*van Noordwijk 2009*). These conditions may well favor the vertical transmission of behavior and this is indeed supported by previous studies regarding food choice and diet overlap between mother and offspring *(Jaeggi 2005; Dunkel 2006)*. As a semi-solitary species, orangutans are not often surrounded by neighbors, and therefore seldom exposed to horizontally/ oblique potential role models. To address the primary questions of our study, we investigated the sociality and association patterns of the Suaq immature orangutans. This chapter will concentrate on establishing the underlying facts upon which our hypothesis is built: sociality in a population promotes social learning.

4.1.1 Time in association

Compared to other wild populations the Suaq orangutans show a higher tendency to form parties. On average immature orangutans at Suaq Balimbing spent significantly more time in association with other individuals than their Bornean relatives (Suaq Balimbing, N_{indiv} = 6, Mean = 73.883, SE = 7.99, Tuanan: N_{indiv} = 6, Mean = 7.417, SE = 2.15, Dependent t test: p = 0.000 see Figure: 12).

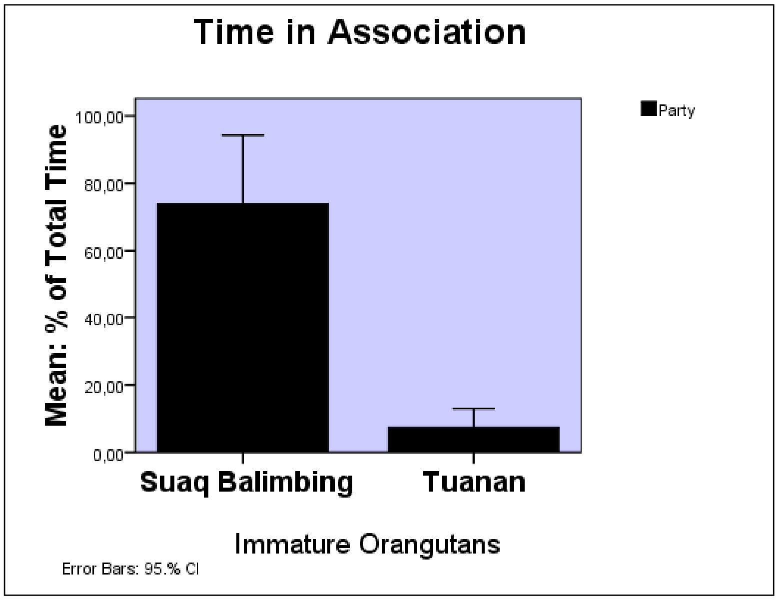

Figure 12: Suaq orangutans far more often stay associated < 50 m to any other individual, than the compared population in Tuanan.

4.1.2 Association distances

Associations with other individuals, than the mother were divided into different distances and compared between individuals from both studied populations (Figure 13).

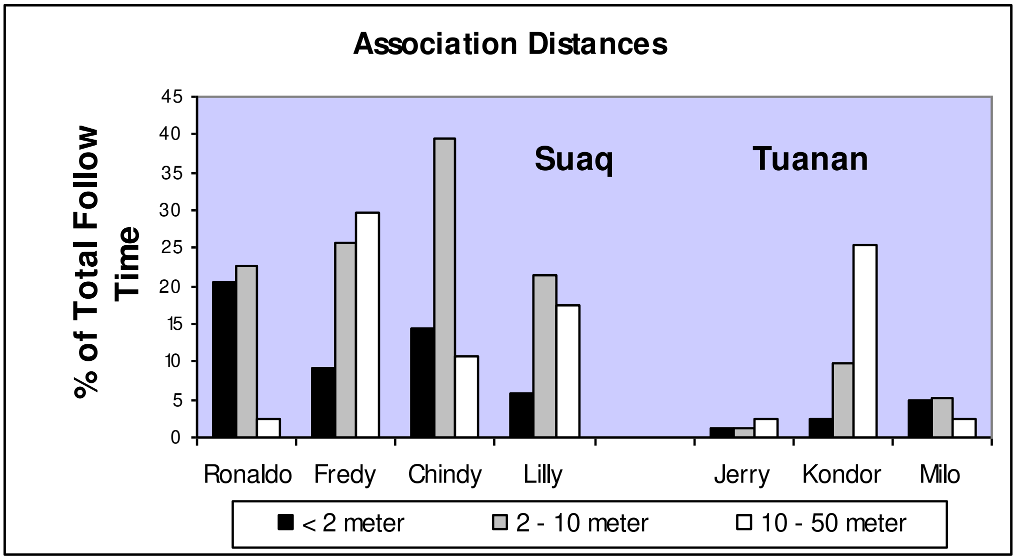

Figure 13: Those individuals we had enough association data on (minimum 1000 min in party), were plotted according to distances to party member. All distances within 10 m are considered highly relevant for social transmission.

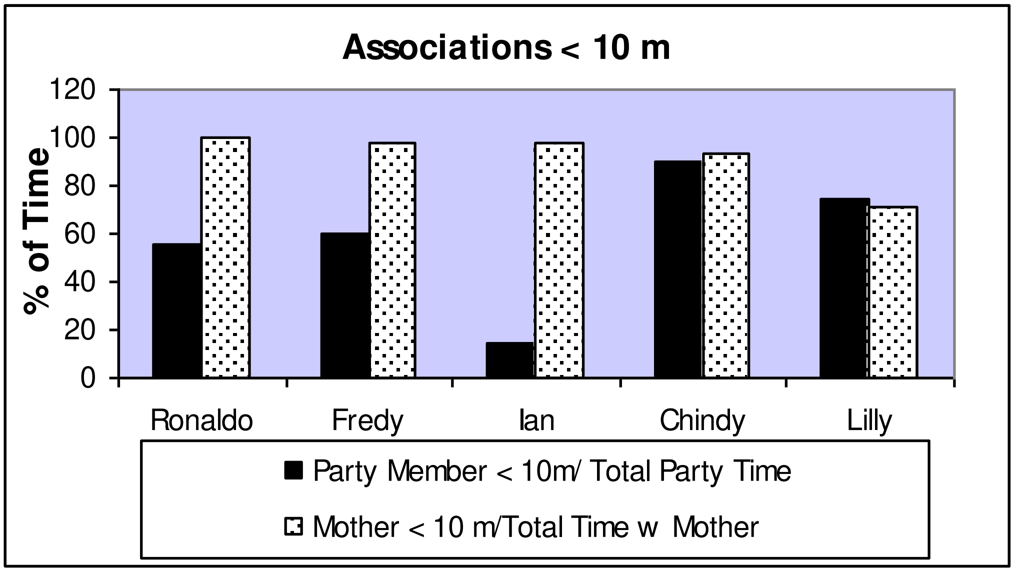

Figure 14: Suaq; Time with mother compared to time spent with party member within 10 m, calculated from total time with those categories. There was a trend found that the older the infant grows the more time it spent with another individual whenever an association took place.

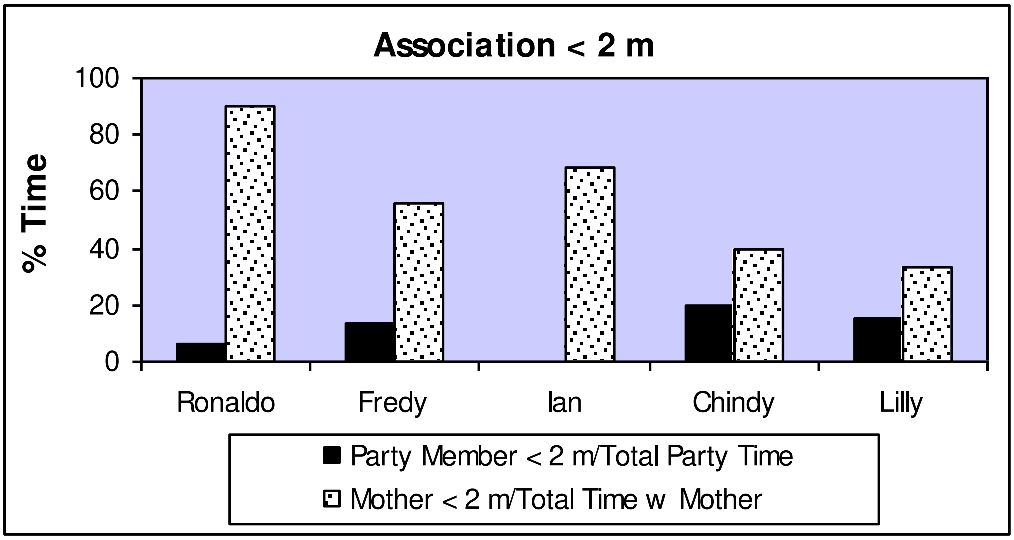

Figure 15 Suaq; Time with mother compared to time spent with party member within 2 m, calculated from total time with those categories. The older the infant gets, the less it keeps a close distance to its mother, whereas the closer distance to other individuals seem to slightly increase with infant age.

4.1.3 Opportunities for horizontal/ oblique learning

For any oblique or horizontal social learning to occur there need to be enough opportunities for it. We determined co- foraging behavior of mothers as providing another role model for the infant. Mothers of Suaq spent on average more time co- foraging with other individuals, than mothers of Tuanan (Suaq Balimbing; N_{indiv} = 5, X = 20.78, SE = 4.244, Tuanan; N_{indiv} = 5, X = 3.32, SE = 1.231, Dependent t test: p = 0.026, t = 3.440, see Figure 16). One mother at Tuanan showed an exceptionally high co- foraging level compared to her conspecifics, due to frequent association with her previous offspring, however this did not influence the significance level of the difference between the two sites.

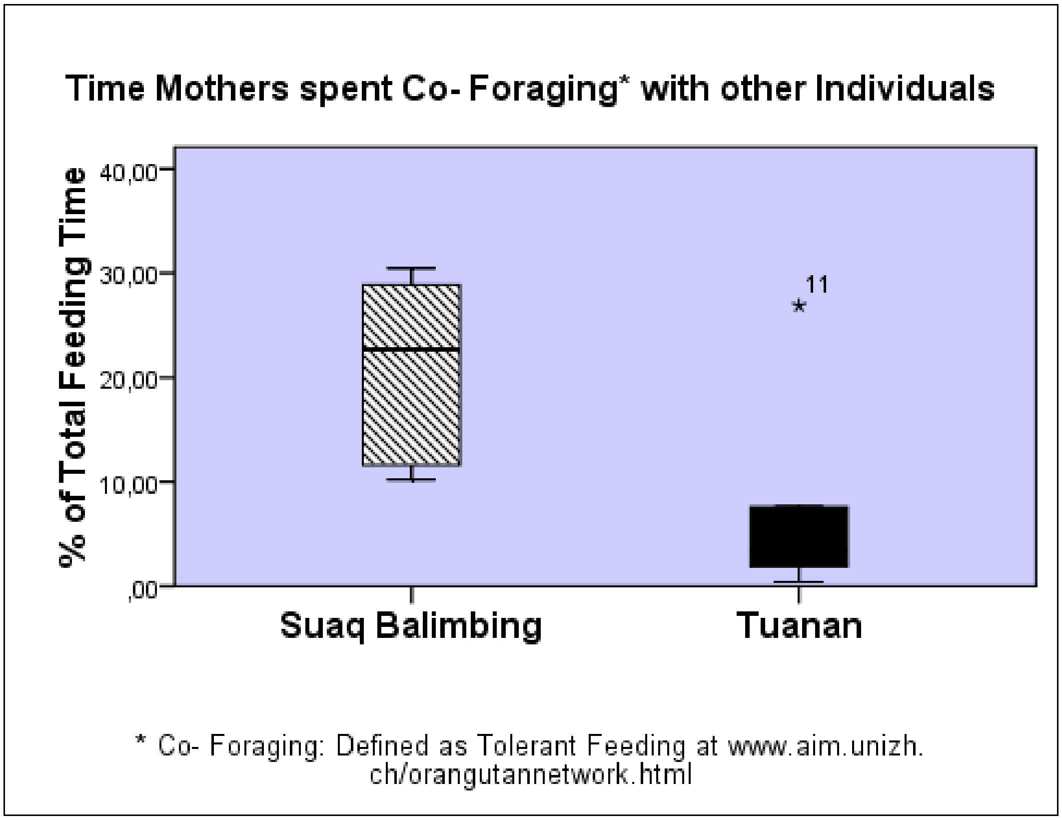

Figure 16: This graph present the % of total feeding time of the mothers between the two sites, when another individual was present within 10m

.

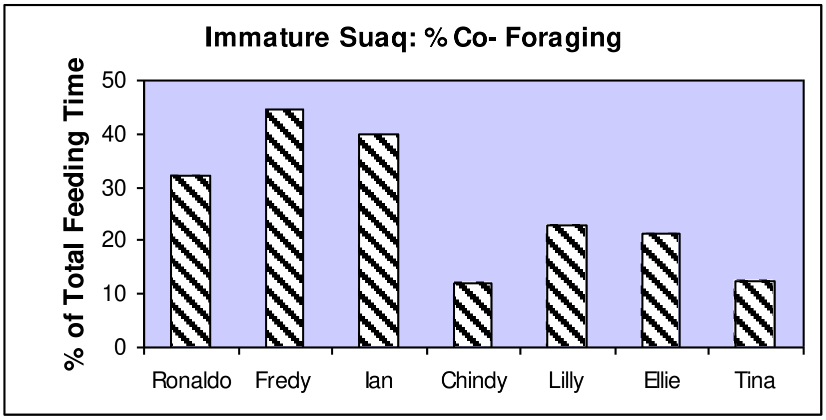

Figure 17: % of total feeding time of the Suaq immatures they spent feeding within 10m to another individual.

4.1.4 Party members and sizes

Whit whom an association is formed could play an important role in social transmission mechanisms. We examined how much time an immature on average spent with different categories of party members, and also compared this between the two sites. Since we lack genetic data from Suaq we concluded potential older siblings to the category of adolescent individuals. Own mother was not counted as a party member. Whenever two or more party members were simultaneously present, the time (recorded with 5 minutes scan), was counted twice. Hence in figure 18, we can conclude that on average 25 % of total time the infants at Suaq would be in association with an unflanged male, 10 % with a flanged male and up to 45 % with an adolescent individual. Same treatment of the data was used for Tuanan. At Suaq both unflanged and flanged males were often seen to form parties with mother-infant pairs and tolerated in close distance. Associations mainly consisted of the focal animal and one partner, however at Suaq, the more gregarious population, there were often multiple partners present at the same time. Whenever the party size is larger, more potential role models are present. In Tuanan parties larger than size one were rarely observed. Party size 2 and 3 at Suaq were more frequent than at Tuanan. (Figure 19). (Partysize > 1 Suaq Balimbing; N = 6, X = 23.100, SE = 5.829, Partysize > 1 Tuanan; N = 6, X = 4.583, SE = 1.773, Dependent t-test, p = 0.031, t=2.988).

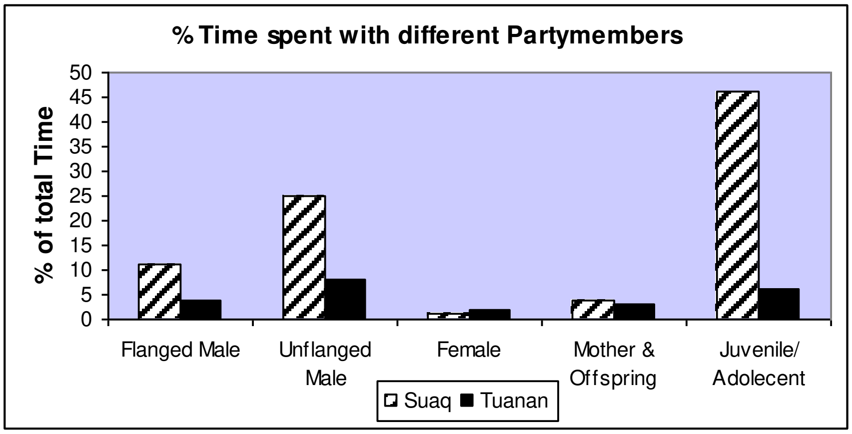

Figure 18: % of time infants spent with different categories of party members.

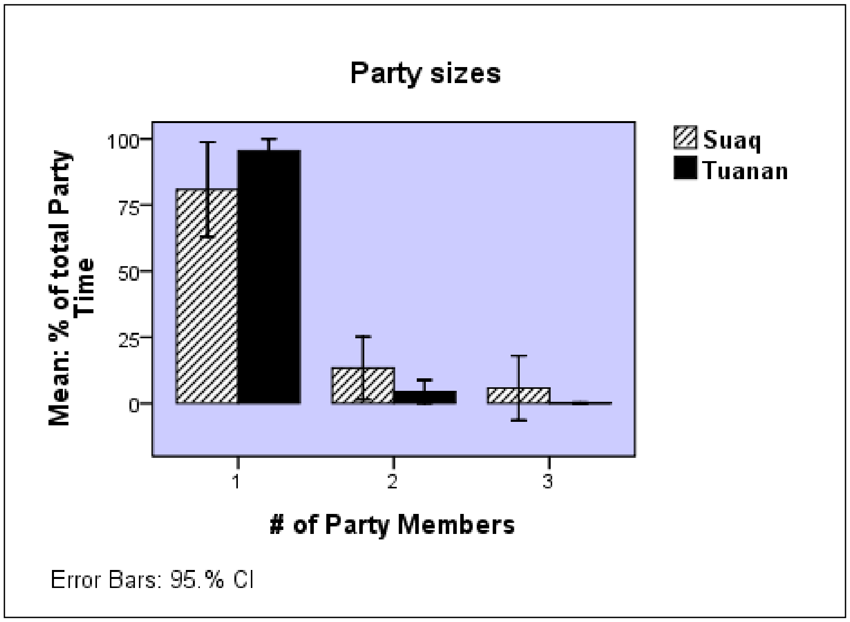

Figure 19: % of total party time there was one, two or three party members in association

4.2 Visual Attention

To address whether there are opportunities for observational learning, we measured peering events (see definition section in Methods), where the infant was intentionally observing either its own mother or other individuals. We use this measurement to examine whether observational learning is likely to take place vertically and horizontally and to show which activity preferences infants tend to pay attention to.

Orangutan habitats consist of various edible and non-edible leaves, hidden insect nests and numerous amounts of flowering and fruiting tree species to distinguish between. To learn how to find and extract all these food sources is a lot more profitable if a role model, such as the mother is constantly present. Therefore we predict that most peering should occur toward an individual's own mother.

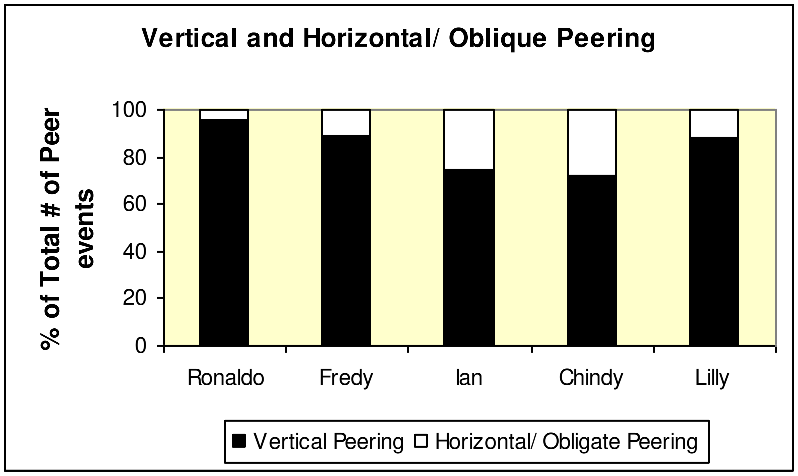

Figure 20: % of vertical and horizontal/oblique peering by Suaq infants.

We predict that social learning mechanisms are used by orangutan infants in order to accomplish ecological competence for their habitat. If this is true we expect more complex, cognitive demanding behavior to be the domains were learning socially would be more profitable than individual learning. We compared how much visual attention infants paid to adults during different behaviors, such as nest building, social activities, foraging, moving and resting (figure 21). (Peering at different activities in relation to time the role model spent on them: N = 25, Nest Building, Mean rank = 21.20, Social Activity, Mean Rank = 17.00, Foraging, Mean Rank = 14.20, Moving, Mean Rank = 5.60, Resting, Mean Rank = 7.00, Kruskal- Wallis test: p = 0.003)

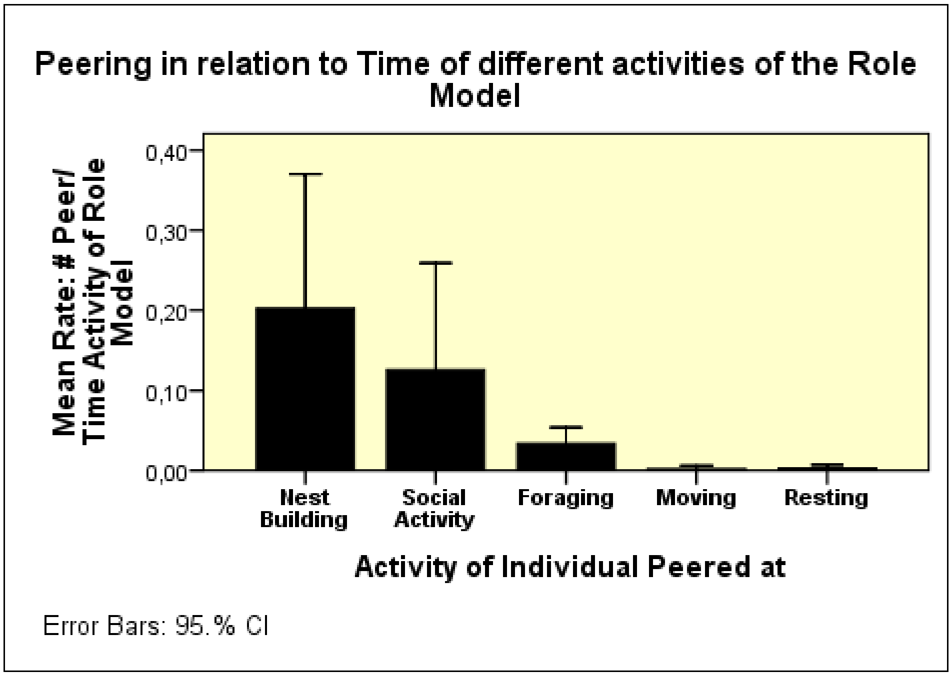

Figure 21: Peering at different behaviors by the role model, corrected for the time the model spent performing the different activities

We also classified the infants into two age- related groups; dependent and independent travelers, and discovered that indeed the older more competent infants would peer less than the younger ones. Tested on seven different activity categories of mother it turned out that younger infants peered at their mothers more than older offspring (Dependent travelers; X = 5.877, $N_{act.mother}$ = 7, Independent travelers; X = 3.318, $N_{act.mother}$ = 7, Wilcoxon signed rank test; Z = -2.2028, p = 0.043, figure 22). In this analysis, additional to foraging categories, nesting behavior of mother was also included, which showed that younger inexperienced infants paid more attention when their mother is building a nest.

Since foraging and food processing is believed to be socially transmitted among primates, we focused on foraging behavior for further analyses. Within feeding activities infant paid unequal amount of visual attention depending on the food type of the mother, presented in figure 23.

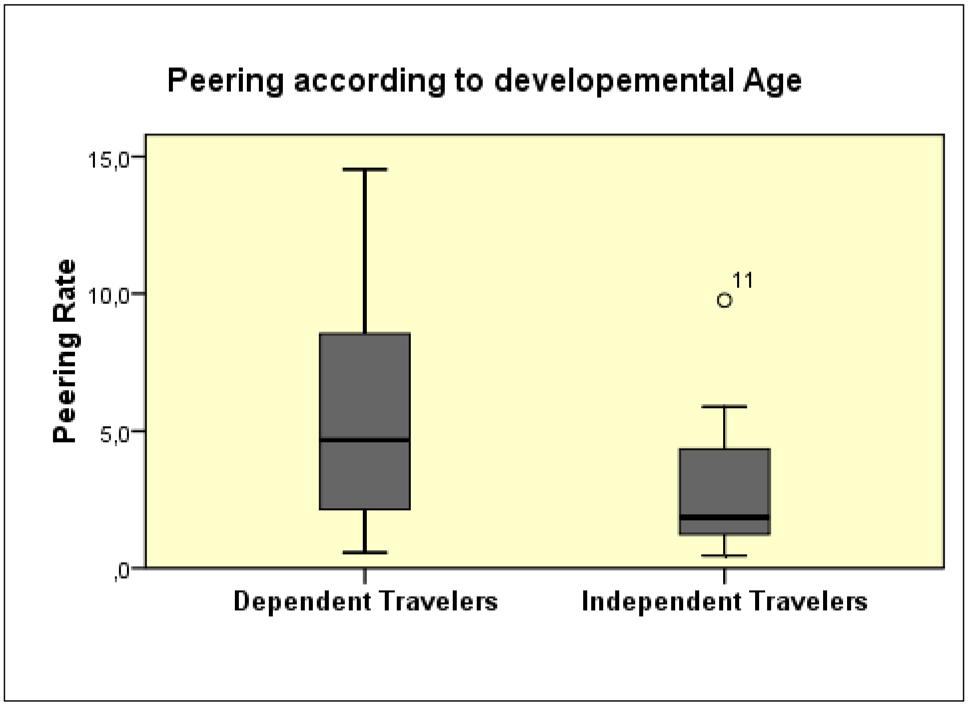

Figure 22: Peering rates according to age related groups; Dependent and independent travelers.

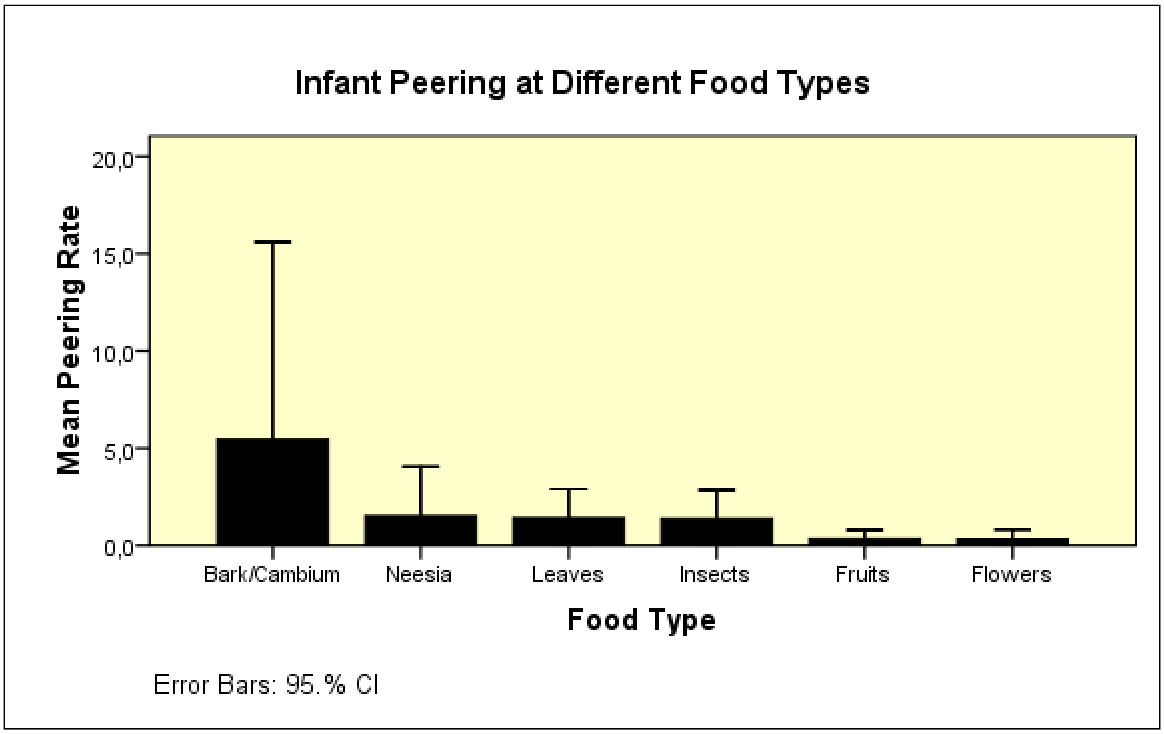

Figure 23: Infant peering rates for six different food types fed by the mother.

What makes infants show unequal interest in different food types? To discover which factors might affect peering rates we ranked food items according to complexity, visibility and rarity. Then peering rates were tested in relation to these categories. This approach has also been used with Capuchin monkeys in Costa Rica, and consequently showed that they pay attention to adults processing food items according to processing steps, rarity as well as fruit size (*Perry 2008*). First we tested whether visibility (i.e. embedded- and non embedded ness) has an impact on peering-, begging and try- feeding rates. Peering and begging occurred significantly more for embedded food items than for non embedded (Peering for embedded items: Mean rank = 66.23, N = 24, Peering for non-embedded items: Mean rank = 44.07, N = 74, Mann- Whitney U: Z = - 3.342, p = 0.001) (Begging for embedded items: Mean rank = 61.33, N = 24, Begging for non embedded items: Mean rank = 45.66, N = 74, Mann-Whitney U: Z = - 2.571, p = 0.010). For try- feeding there seems to be a trend towards the same result but we could not establish any significance (see Figure 24). These results are consistent with a social-learning function of these three infant activities.

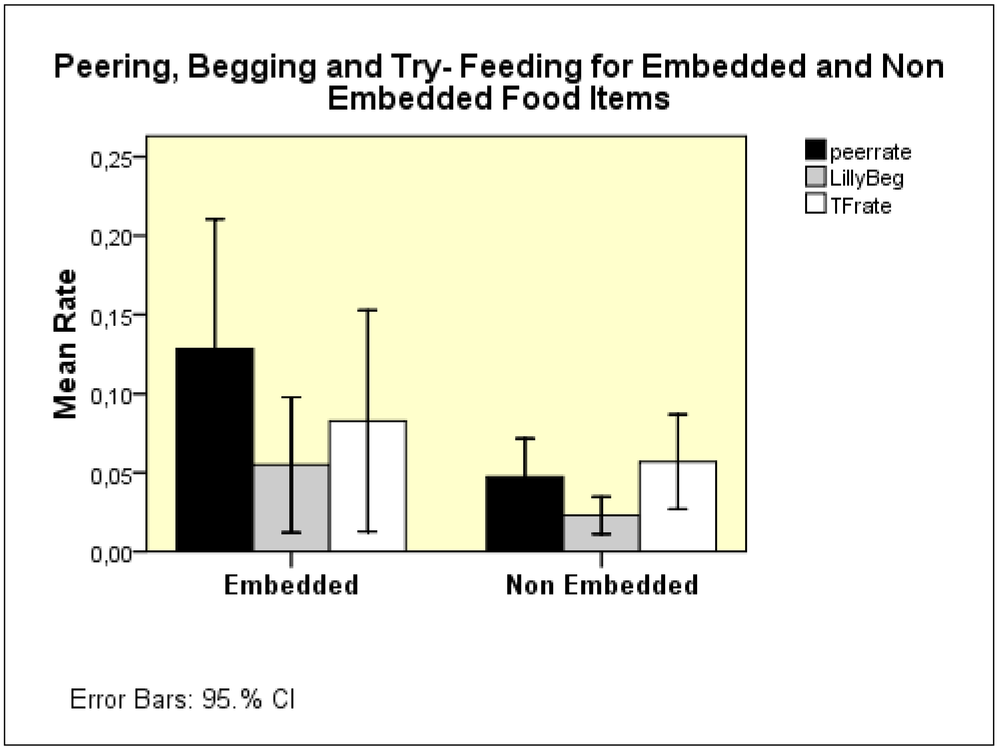

Figure 24: Peering-, Begging- and try- feeding rates for embedded and non embedded food items. .

The

complexity of foraging technique was divided into five classes according to how many processing steps are needed before a food item is completely ingested, from processing step zero being the least complex and four the most demanding (see methods section for definitions).Peering rates differed between food items of different complexity (Peering according to processing step of the food item: N = 98, Proc. Step 0, Mean rank = 49.98 Proc. Step 1, Mean rank = 46.83, proc. Step 2 = 37.96, proc. Step 3 = 68.85, proc. Step 4 = 77.33, Kruskal- Wallis test: p = 0.024, figure 25). Processing step zero would be mainly leaves, which we will later argue that requires learning due to other facts than complexity. Moreover, a significant positive trend between peering rate and processing complexity was apparent when we excluded processing step 0 from the analyses (Jonckheere-Terpstra test: N = 56, J = 2.675, p = 0.007).

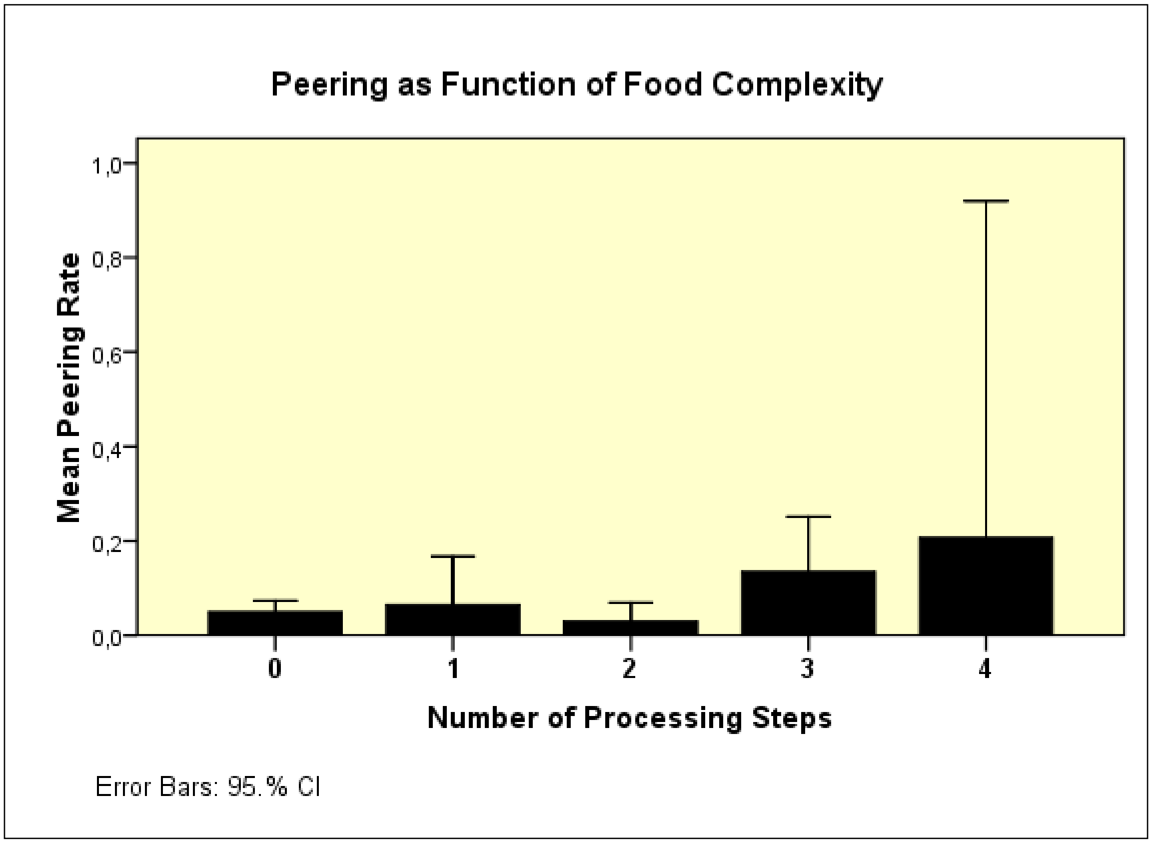

Figure 25: Peering rates according to number of processing step a food item requires

To establish any effect of fruit size on peering rates we categorized fruits into four size classes and tested for any correlation. Figure 26 might suggest a tendency for more peering at larger fruits, but no significant correlation was found

(Spearman's rho; r = 0.259, p = 0.232, N = 23, figure 26). Class four only included fruits of *Neesia* sp., hence the only fruit orangutans use tools when foraging, further arguing against a possible effect of fruit size. Different from capuchin monkeys, therefore, fruit size does not seem to matter in observational learning processes of orangutans.

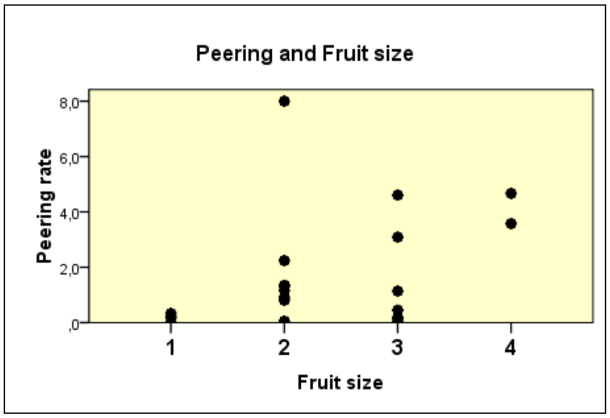

Figure 26: No clear correlation was found between peering rate and fruit size

Items that are rare in mother's diet are more likely to be unfamiliar to the infant, thus if infants pay attention in order to obtain knowledge of unknown food sources, we expect rarity to affect peering rates as well. We correlated peering rates for different food items to rarity in the diet of the mother for each mother-infant pair. There was a significant negative correlation between peering rate and how large part of mother's diet a food item exhibit by the two youngest infants Ronaldo and Fredy (Peering according to rarity: Kendall's tau_b: r = - 0.467, N = 44, p = 0.000, figure 27). The older infants showed no significant relationship between peering and rarity.

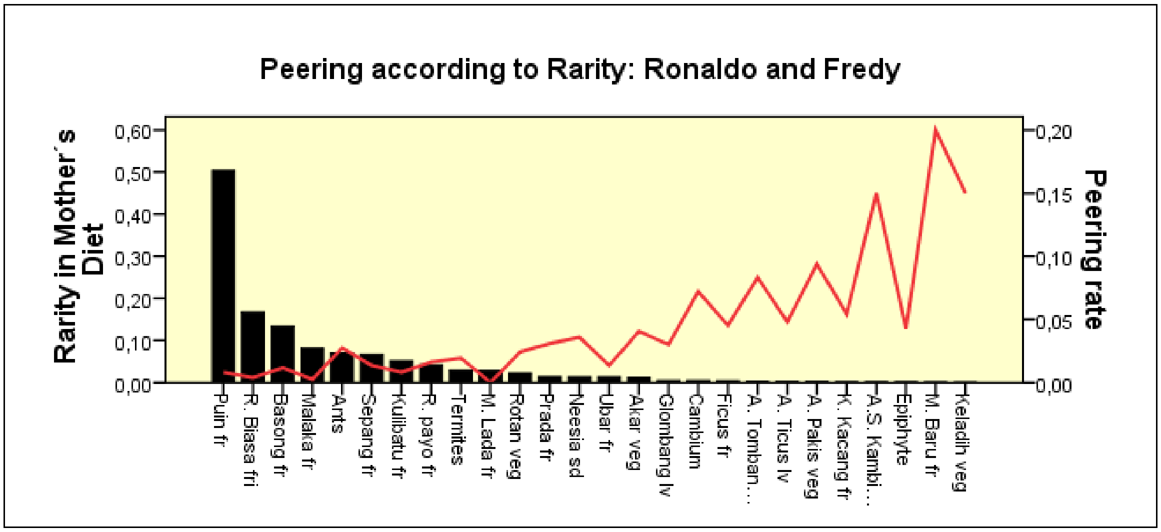

Figure 27: Peering according to rarity for the two youngest infants Ronaldo and Fredy. Black bars representing how large part of mother's diet a food item hold and the red line represent peering rate.

To also control for food complexity, we did the same analysis for food types with only zero and one processing step. We ranked these easy to process food items according to rarity and correlated this with peering rate for the two youngest infants (Figure 28). Even by easy processed fruits, infants peered more at rare species than on common eaten ones (Peering according to rarity for easy processed items only: Kendall´s tau b: r = - 0.324, N = 23, p = 0.032). Thus, rarity affected the rate of peering by the two youngest infants independent of other confounding factors, such as processing complexity or food type.

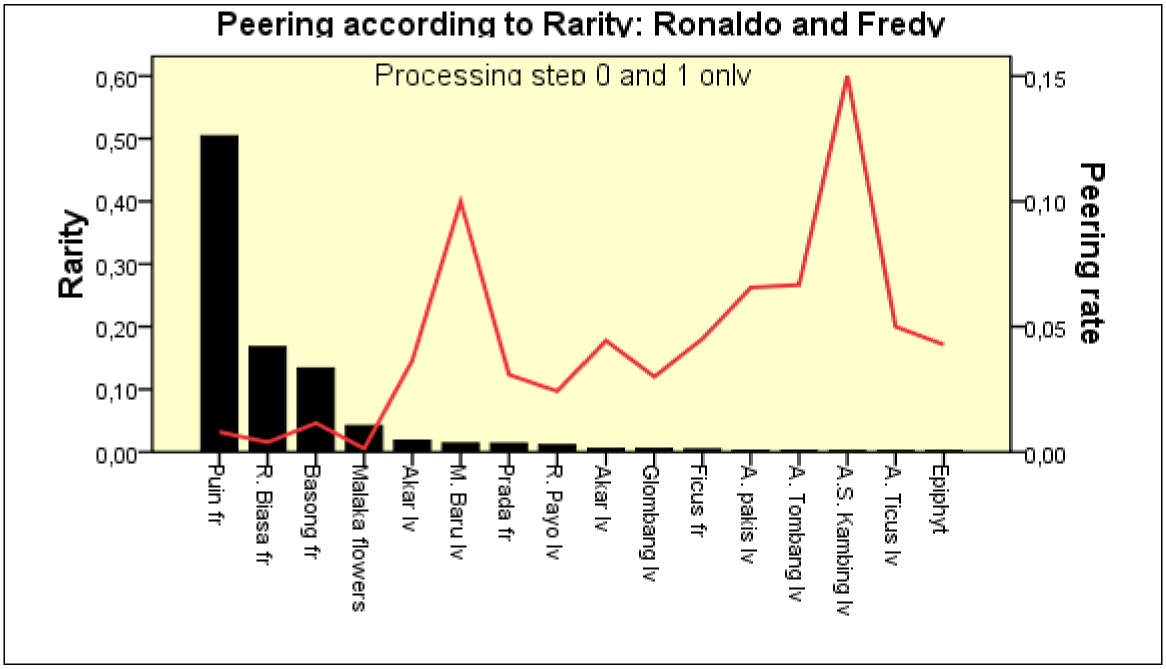

Figure 28: Peering rate in relation to rarity of food items in the category of zero or one processing step only

4.2.1 Horizontal/ Oblique transmission

For this section we wanted to investigate whether non-vertical social transmission pattern also has a rather early start. Thus, do Suaq orangutans already at an infant age show interest in individuals other than their own mother?

From each day an infant was followed we looked at how many of its peering events were at his/her mother and how many at a party member. Then we compared this number of events to how much time the infant spent within two meters of the respective individual; hence how many opportunities the infant got to perform such close watching. We found no significant difference between peering rates for mothers and party members. Only days with this data for both party member and mother was included. (Peer at mother; N_{days} = 19, Mean rank = 11.44, Peer at party member; N_{days} = 19, Mean rank = 8.70, Wilcoxon signed rank test; Z = - 0.322, p = 0.748, figure 29).

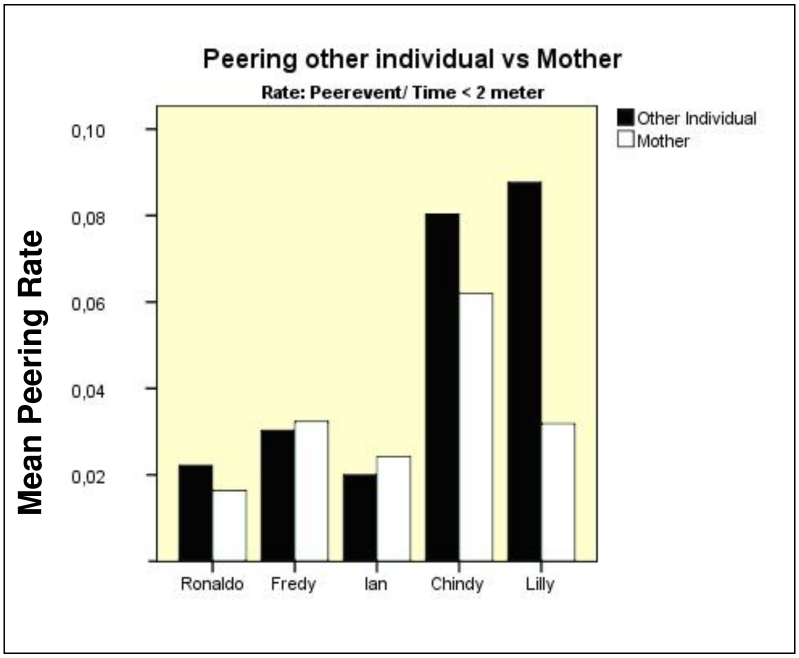

Figure 29: Peering rates compared between mother and party member on days were both were present around a focal infant.

Before any peer event would occur it was mainly the infants making the approach towards the other individual (Figure 30). Only infants with a minimum of 10 peering events by party members were used.

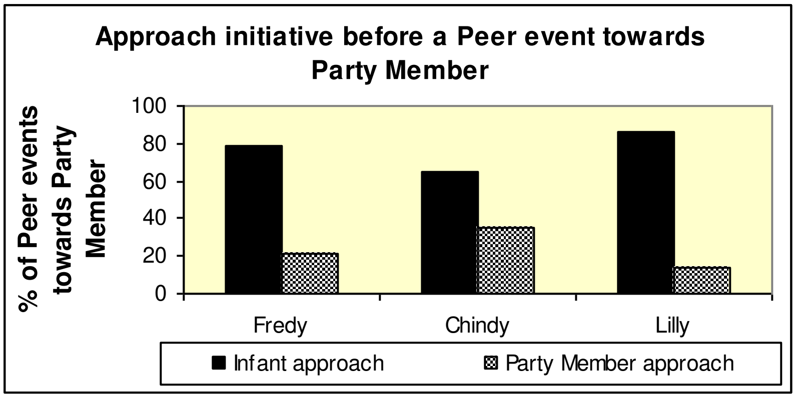

Figure 30: % of infant respective party member approach, before an event of peering.

4.2.2 Comparison between Suaq Balimbing and Tuanan

Finally we compared peering behavior for different food types between the two study sites and found that infants at Suaq, in general, pay more attention to adult individuals feeding than their conspecifics at Tuanan (Suaq Balimbing: Mean rank = 11.12, $N_{foodtype}$ = 8, Tuanan: Mean rank = 5.88, $N_{foodtype}$ = 8, Mann-Whitney: U = - 2.212, p = 0.027, Figure 31). For this comparison we only used data from observers from Zürich University, who were involved in projects with related questions (see inter observer test values in method section). Data of this kind should be easier to observe at Tuanan field site, since the forest is lower and observers can often watch the focal animals from quite close distance, whereas the higher primary forest at Suaq probably sometimes made those behaviors difficult to identify.

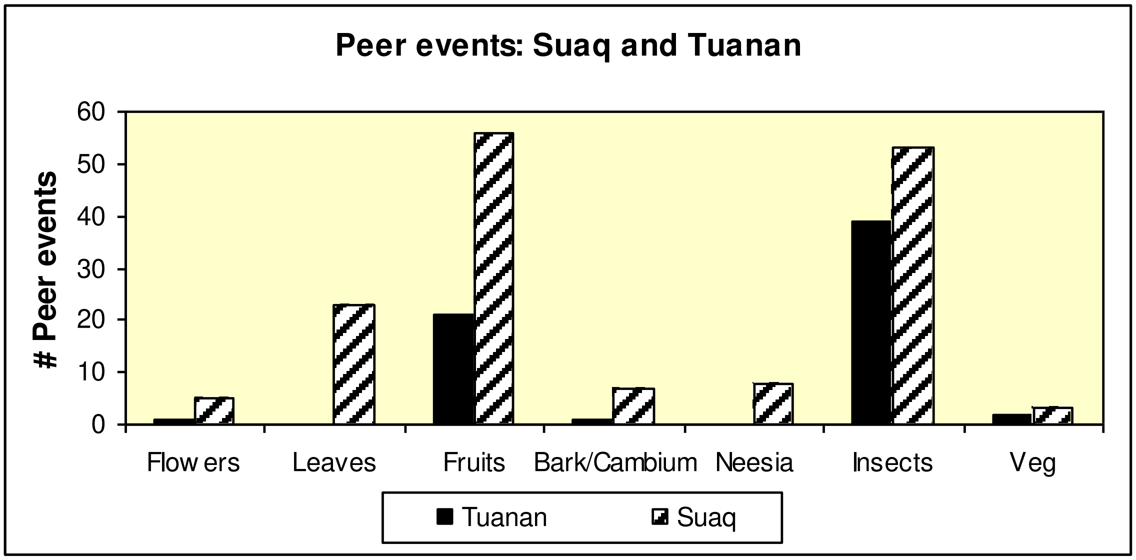

Figure 21: Peering for different food types compared between the two study sites

Also for Tuanan we classified food items in embedded and non-embedded to investigate whether the same pattern was found as for Suaq. For both sites there were significantly more peering at embedded items (Wilcoxon signed-rank, Z = -2.934, p = 0.003) than at items that are easy accessible (Figure 32).

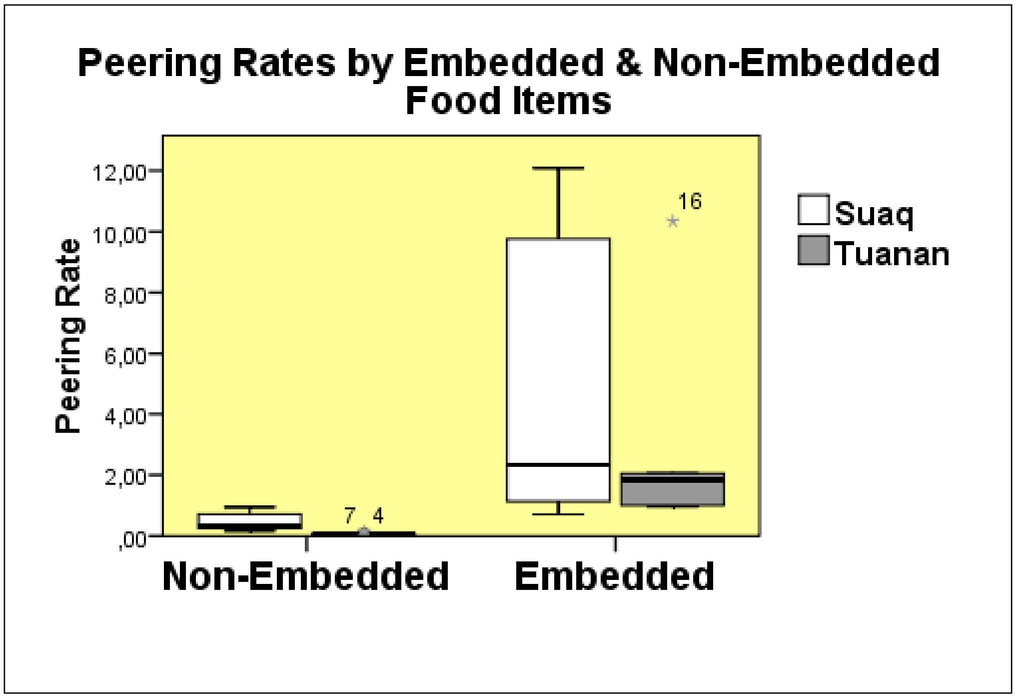

Figure 32: Peering rates from Suaq Balimbing and Tuanan as a function of embedded and non embedded food types

4.3 Diet Complexity

During the study time we found that 172 different food items were eaten by the Suaq orangutans. This number is likely to rise rapidly as data collection is continued at the site. However it already reveals a lot about how diverse the diet of an orangutan is. We looked at how the diets of our different focal animals were composed in order to get an insight into infant skill level and comparison between individuals (Figure 33).

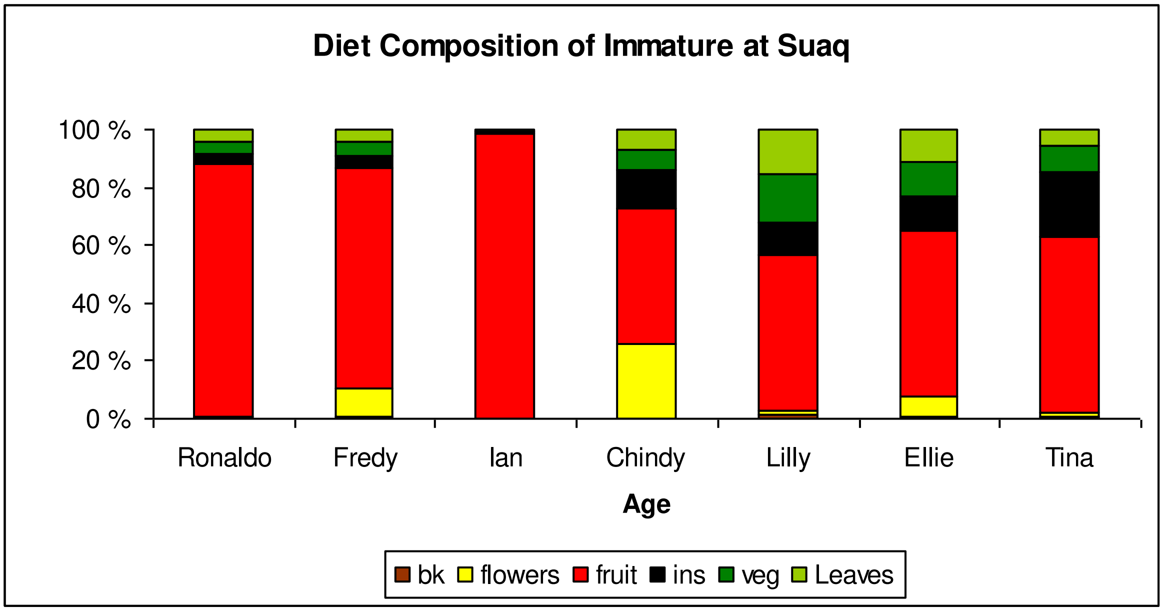

Figure 33: Diet constitution of the Suaq immatures

We also calculated diet overlap between mother and offspring and compared these data to previous data from Tuanan (*Dunkel 2006*). This was performed with an univariate analysis of variance (ANCOVA) were, time spent cling to mother while moving, was included as an age related covariate to percentage of overlap between infant's and mother's diet. The covariate, time spent clinging while moving, was not significantly related to the percentage of overlap with mother's diet F = 2.746, p = 0.149, however there was a significant difference in overlap between the two sites $N_{Suaq} = 5$, $N_{Tuanan} = 4$, F = 11.783, p = 0.014, figure 34). This data from Tuanan was collected in 2005 by Lynda Dunkel and the ages of the infants at that time were; Jerry: 2 years, Susi: 2,5 years, Milo: 3,5 years and Kondor: 5,5 years. For the Suaq infants age estimates are listed in table 1, but we can assume Ronaldo and Fredy were quite similar in age to Jerry and Susi in 2005, Ian and Chindy are approximately slightly older than Milo and slightly younger than Kondor in 2005. Lilly and Ellie were both older than any of these data points of the Tuanan infants. At the time of data collection Tuanan immatures overlapped a larger part of their mother´s diet than Suaq immatures. During sampling time Ellie was already a weaned offspring at Suaq and still she only overlapped her mother, Friska´s diet by 84 %. At Tuanan in contrast, Jerry already reached this level at the age of 2 years.

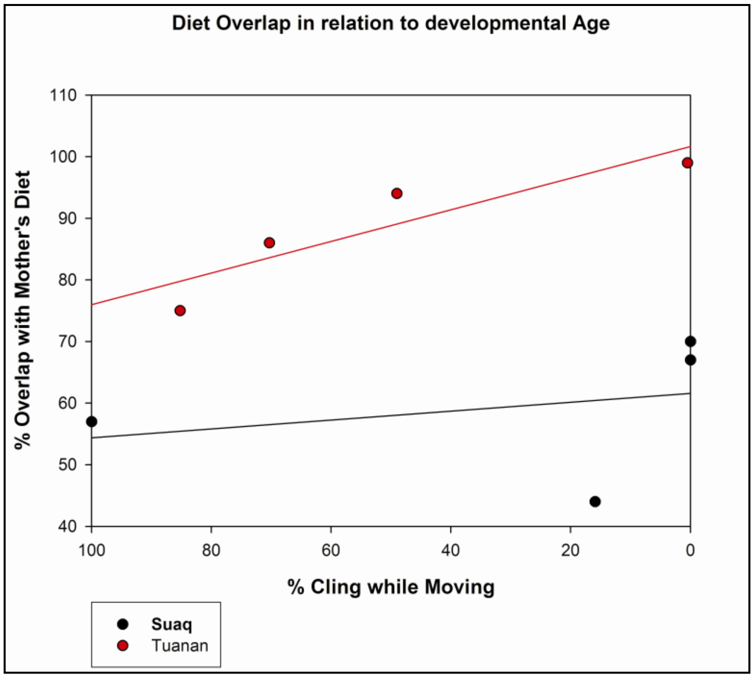

Figure 34: Diet overlap in relation to an age estimated covariate. Red line: Suaq Balimbing, black line: Tuanan.

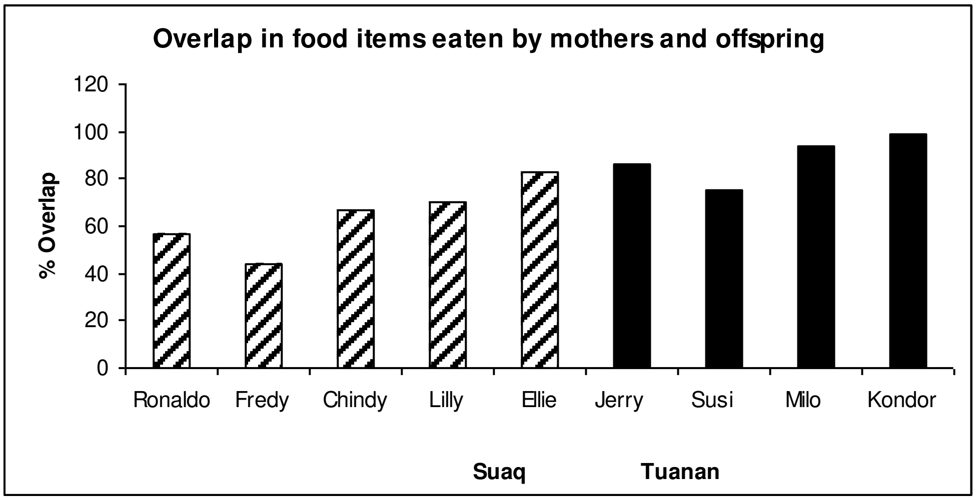

Figure 35: % of food items from mother's diet that offspring seen feeding on.

For further analysis we compared the diet composition and number of species in diet of Suaq and Tuanan mothers (Figure 36 and 37). Data from Suaq was collected only over one year whereas Tuanan data derives from six years of data collection. Furthermore as data collection continues at Suaq we can expect larger differences between these sites regarding diet questions. When feeding on leaves we could already see some interesting differences: Tuanan mothers were in general feeding more on leaves than Suaq mothers, although Suaq mothers would feed on a wider variety of leaf species (Figure 37). Fruit and flower species showed a larger diversity at Tuanan whereas at Suaq, mothers would extract more food out of different vegetation.

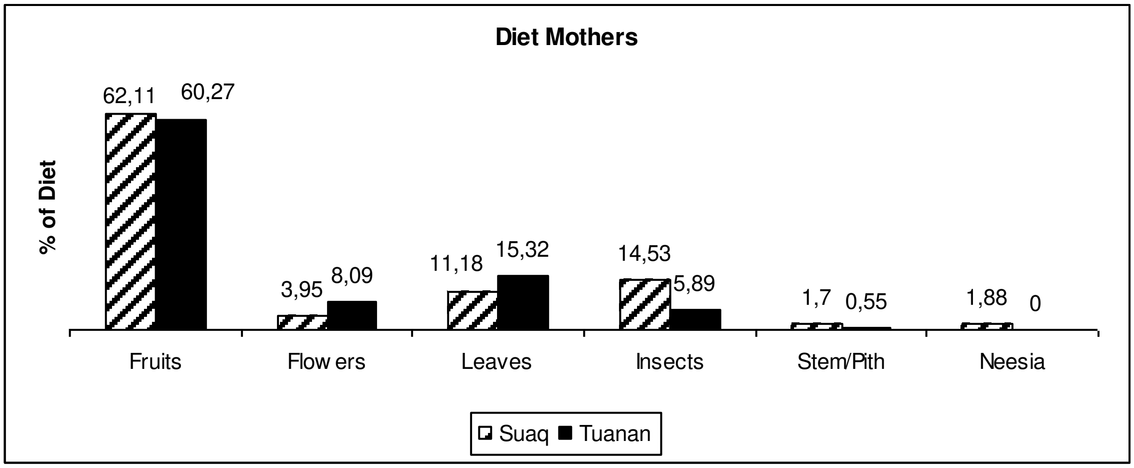

Figure 36: Different food type as % of the diet of the Suaq respective Tuanan mothers. To be noticed is that *Neesia* does not grow at Tuanan and is therefore only part of the diet of Suaq orangutans.

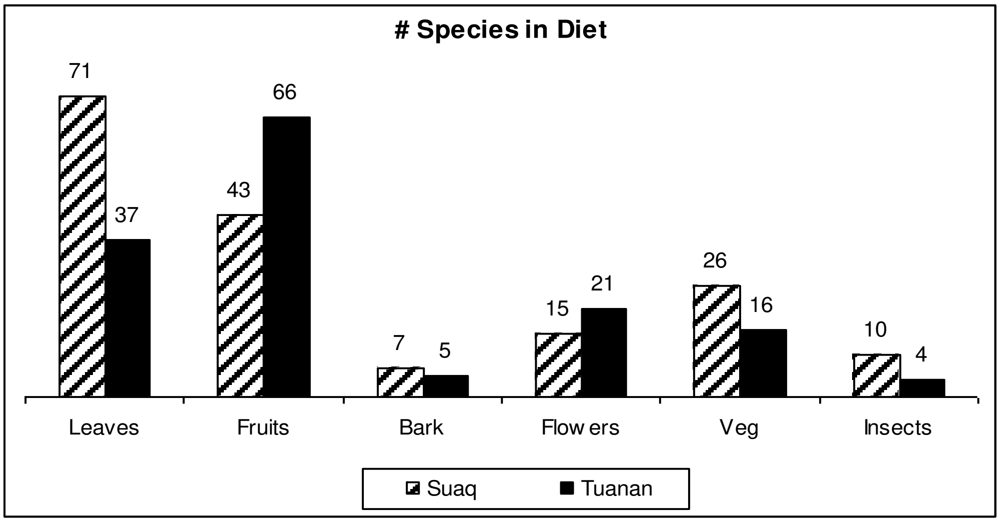

Figure 37: Number of species of different food types at Suaq Balimbing and Tuanan.

We then looked for any differences in the diet of the immatures between these two sites. Fruits were pretty much equally important in a young orangutan’s diet at both sites, irrespective of age (Figure 38). Insects on the other hand turned out to make up a larger part of Suaq orangutan diet than at Tuanan (Figure 39).

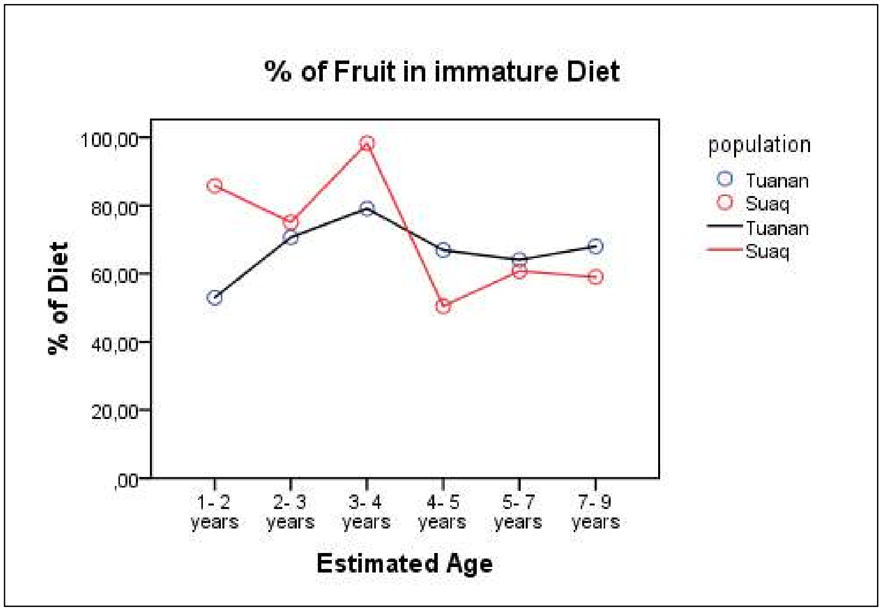

Figure 38: % of Fruit in the diet of immatures at Suaq Balimbing and Tuanan

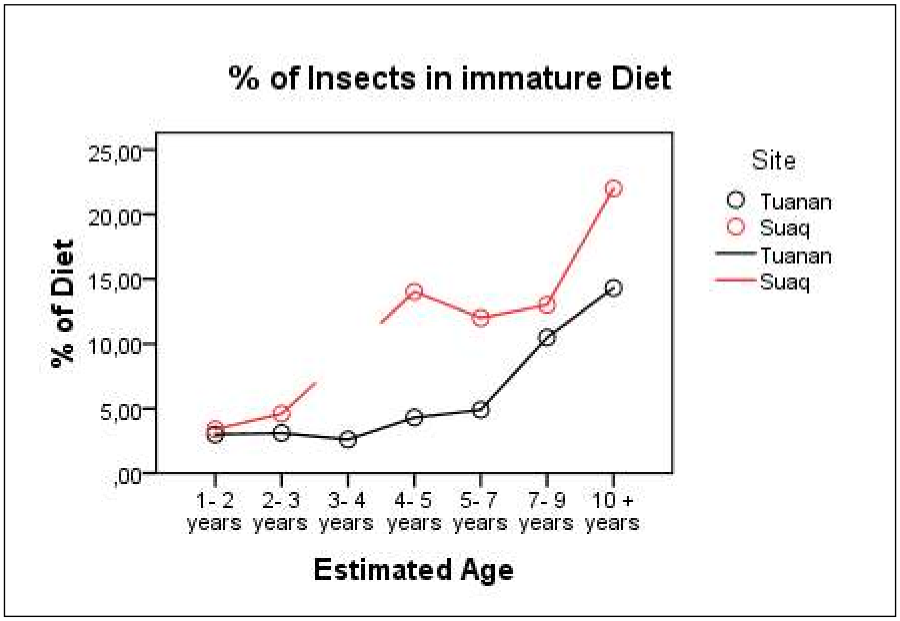

Figure 39: % of Insects as part of the diet of immatures at Suaq Balimbing and Tuanan

4.4 Food Solicitation

Begging behavior expresses infant interest in food and others activities with food. It is suggested that orangutan offspring beg for food items, they not yet master themselves, in order to gain knowledge about unfamiliar food types *(Jaeggi, van Noordwijk et al. 2008)*. A begging attempt can be anything from passively holding out a hand towards the food item of the owner or actively taking an item or a part of it from the owner. The latter, understood as tolerant theft, is most common among orangutans and results in successful food transfer. Although orangutan mothers sometimes refuse to let their infant reach the object, little is known about how and if she adjusts these allowances. The food types that infant begged for at Suaq are mostly of categories that do not constitute a large part of their diet (Figure 40). Ronaldo, the youngest focal animal mostly begged for leaves and fruits, whereas this was rarer for the other infants as they manage to feed on most fruit and leaf species on their own.

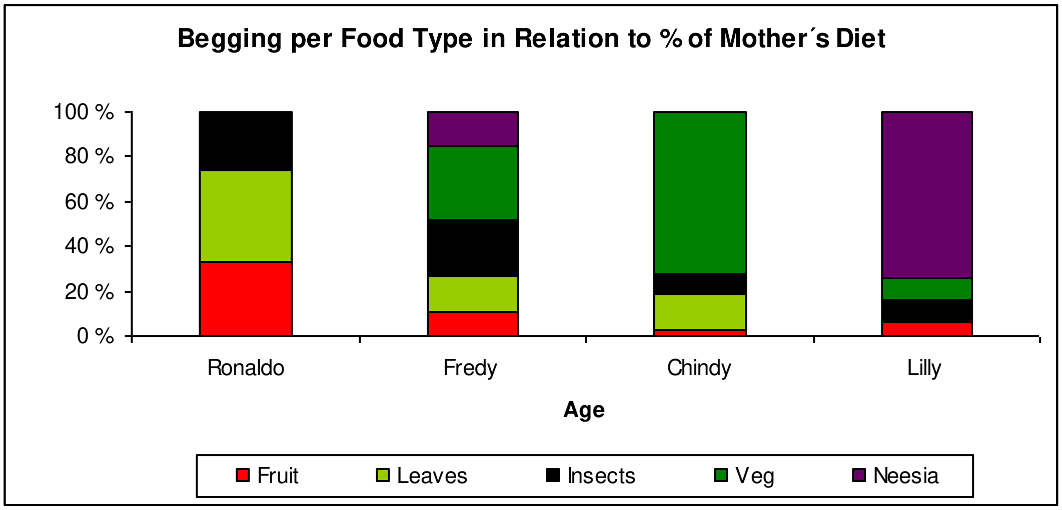

Figure 40: % of begging by different food types, corrected for how much % of the mother's diet respective food type exhibit

Food items begged for have been tested in the Tuanan population in a previous study, which showed that infants begged significantly more for embedded items than non-embedded *(Jaeggi, van Noordwijk et al. 2008).* We tested weather this also holds for immature at Suaq as well. Indeed we found a significant relationship for begging rates and embedded/ non-embedded items (see figure 24). We also found a significant linear trend towards increased begging with the number of processing steps of the food item (Linear trend, Jonckheere-Terpstra test: J = 2.702, p = 0.007) (Begging according to processing step of the food item: N = 98, proc. Step 0, Mean Rank = 43.29, Proc. Step 1, Mean rank = 47.96, proc. Step 2 = 52.12, proc. Step 3 = 62.19, proc. Step 4 = 63.17, Kruskal- Wallis test: p = 0.154, figure 41).

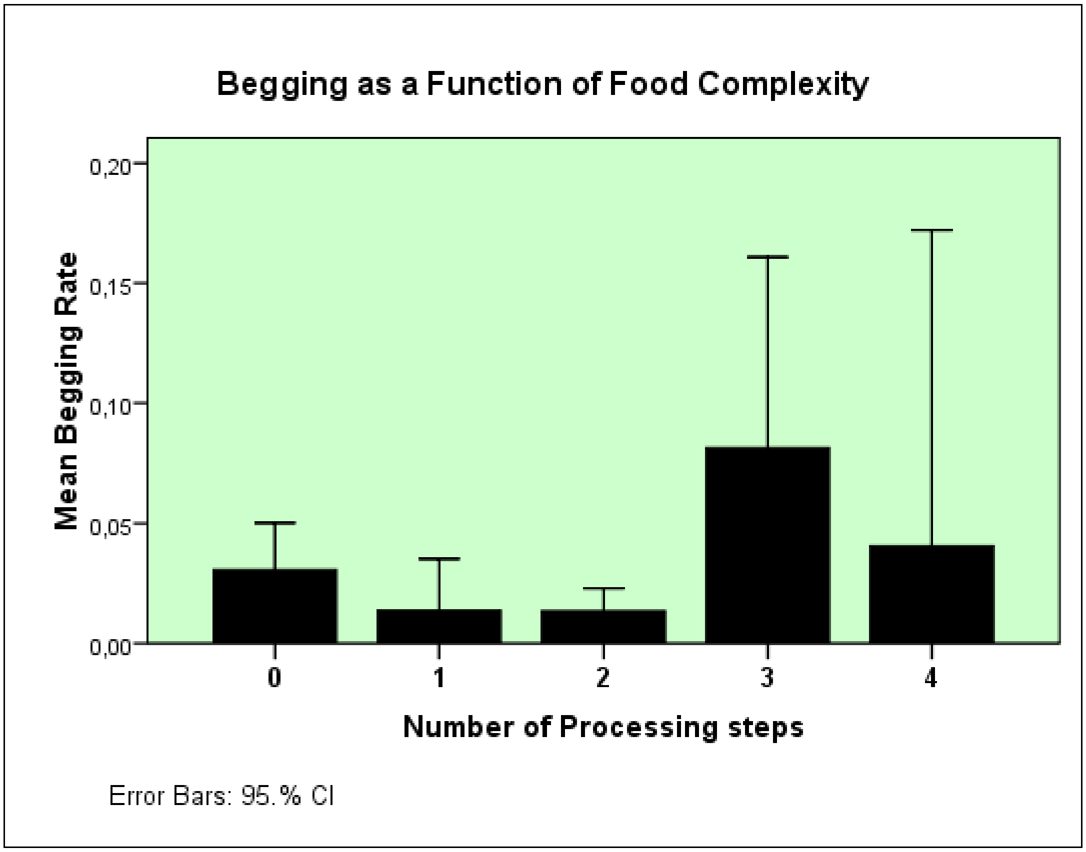

Figure 41: Begging rates according to complexity of food item.

Since both peering and begging turned out to be influenced by complexity of food item we compared peering- and begging rates for different food types. Peering rates were in general significantly higher than begging rates for all other categories than vegetation, see figure 42 (Wilcoxon signed rank: N = 79, Z = -2.717, p = 0.007). Also we calculated peering events where begging would occur within the same feeding bout and compared this to how many peering events would happen without any food solicitation (figure 43).

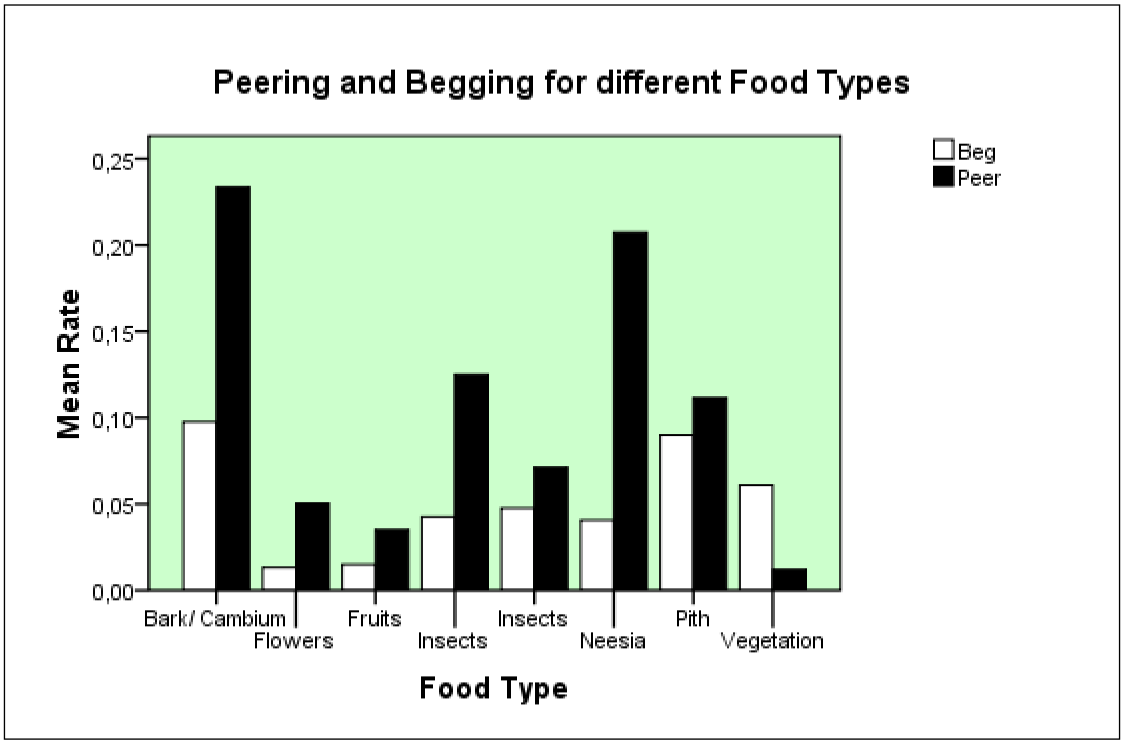

Figure 42: Peering and begging compared for different type of food.

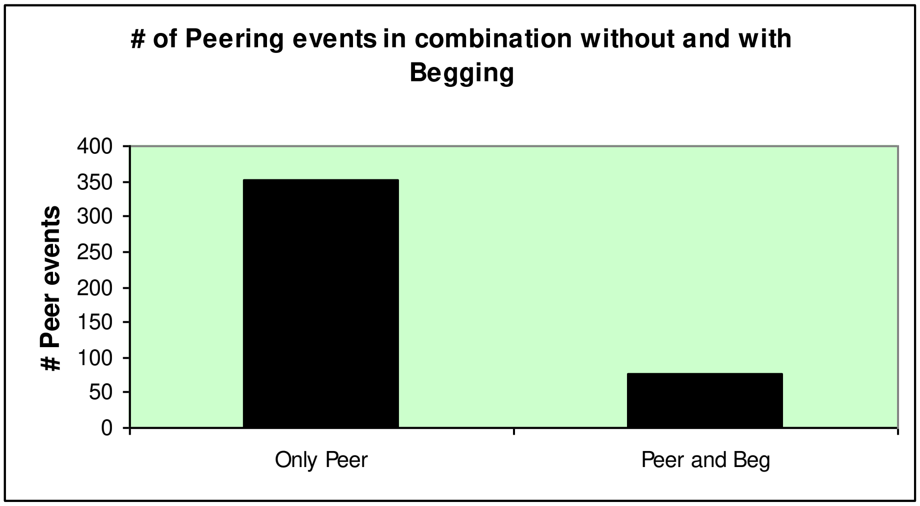

Figure 43: Number of peering events without and with begging in within the same feeding bout.

4.4.1 Comparison of begging behavior between Suaq and Tuanan

Assuming that infants reduce their begging behavior as they acquire knowledge about more food sources, we should expect begging to decrease as infants grow older. This was found for Bornean orangutans at Tuanan (Jaeggi 2005) (Figure 44), but from Suaq our results are different (Figure 45). We calculated ecological competence according to an infant's ability to find a food patch on its own and time spent feeding alone. We tested this in relation to begging behavior but found no significant correlation between these two factors (Spearman's rho, N = 4, r = -0.800, p = 0.200, figure 45). The oldest offspring, Lilly was often observed feeding alone and already practiced most feeding skills, yet her begging rate was still quite high. If we look at the items Lilly would beg for, it consisted mostly of seeds from the *Neesia* fruit, suggesting that this was one of the remaining skills she still would have to practice to reach full competence.

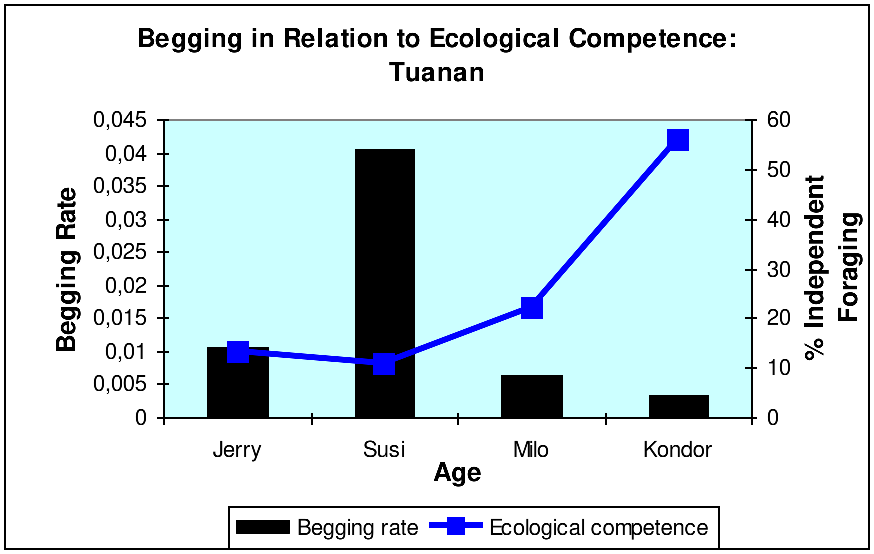

Figure 44: On left Y- axis Begging rate for Tuanan infants and on the right Y- axis % of independent foraging time.

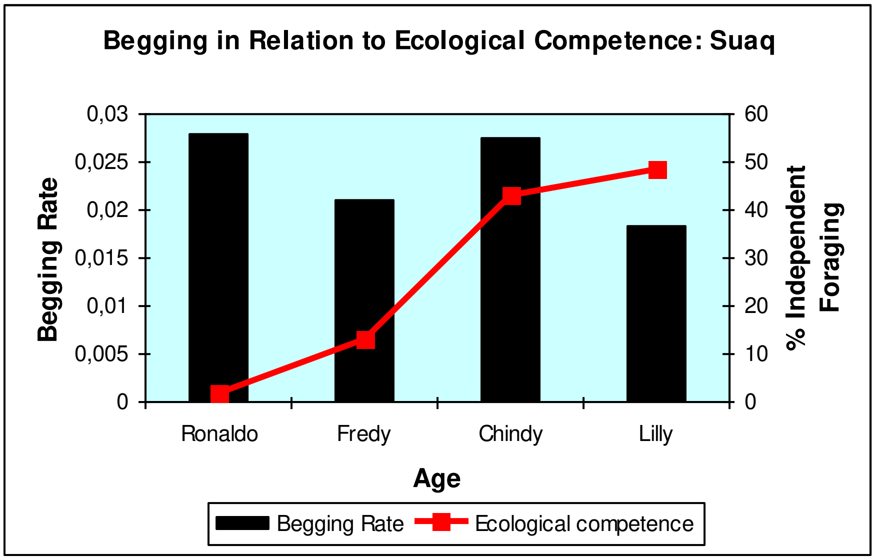

Figure 45: On left Y- axis Begging rate for Suaq infants and on the right Y- axis % of independent foraging time

Whether a mother shares or allows her offspring to obtain food from her in order for it to get familiar with the item in question rather than to provide it with nutrition, is not clearly settled. We speculate that if infants, as they get older, would continue begging for food items they already master themselves, we would expect sharing rates to go down with infant age. Sharing rate did however not go down with infant age, but followed the pattern of the begging rates (Figure 47 and 48). Thus we suggest that infants at different age stages beg for different food types (figure 46).

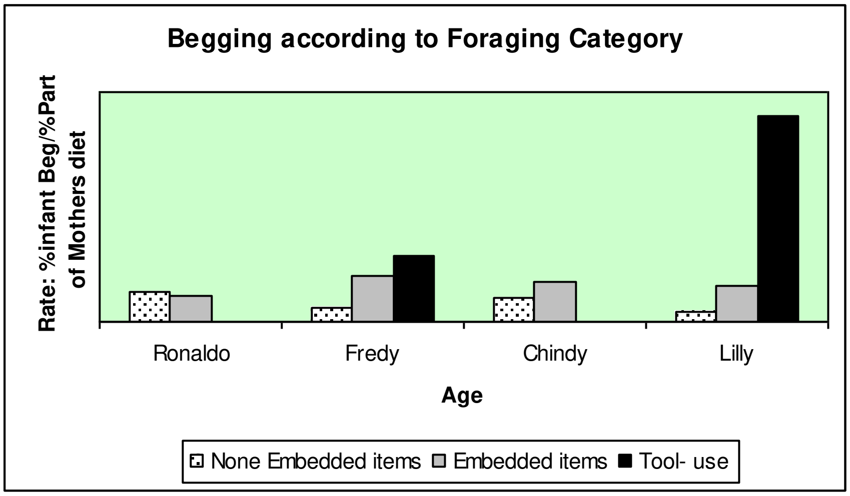

Figure 46: Begging for different food categories. Infant age increases towards right of the X- Axis.

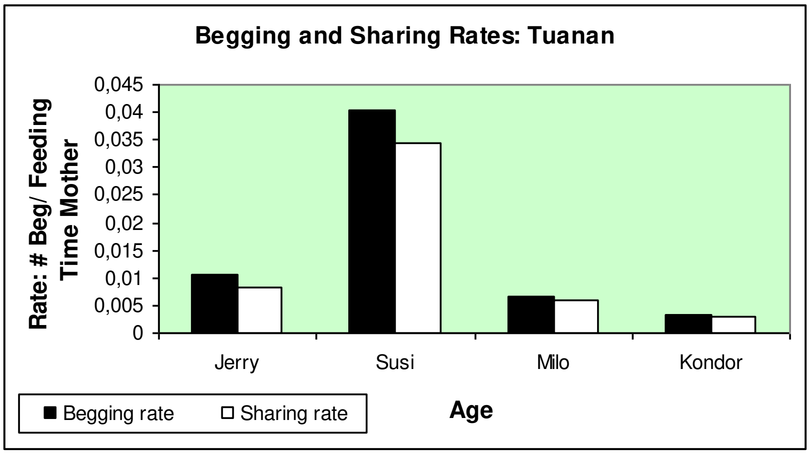

Figure 47: Begging and sharing rates for Tuanan infants

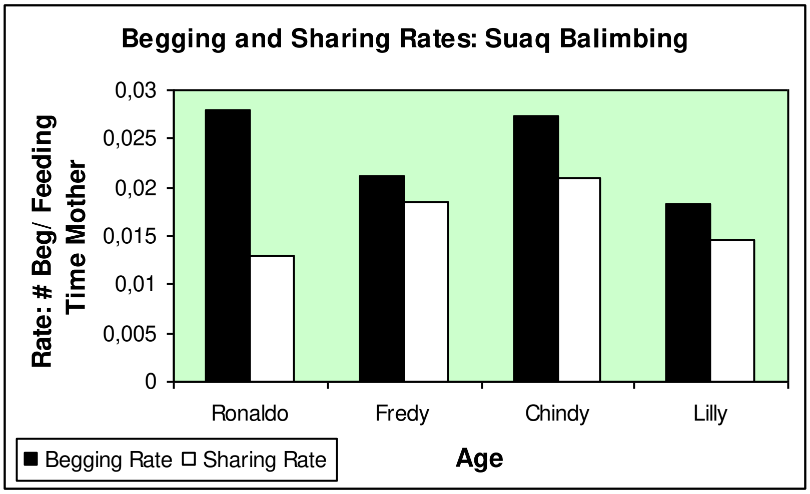

Figure 48: Begging and sharing rates for Suaq infant

Further the food begged for at Tuanan would differ from food categories begged for by Suaq immatures (Figure 49). Fruits were begged for fairly equally at both sites, whereas leaves, vegetative plant parts and seeds from *Neesia* fruit (not present at Tuanan) were begged for more at Suaq. Insects, bark and water on the other hand were begged for more frequent at Tuanan.

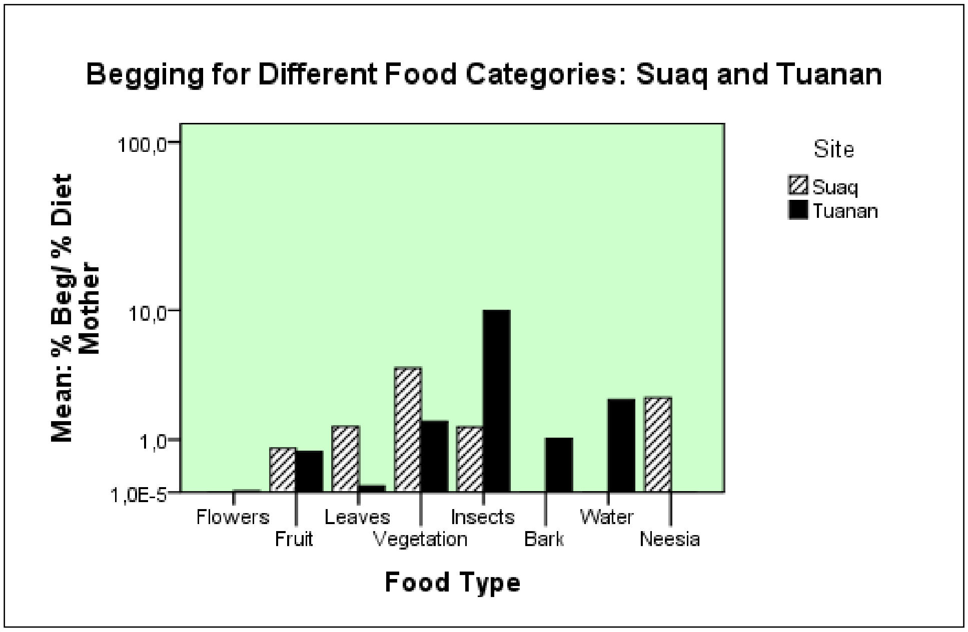

Figure 49: Different food types and their begging rates for Suaq Balimbing and Tuanan.

4.5 Independent Exploration

Whether a behavior is a result of local enhancement or of observational learning is very hard to distinguish from the fact that it could have been independently discovered by the individual itself. In this chapter we present our investigations in how exploration behavior expresses itself in young Suaq orangutans by measuring manipulative object play and try- feeding on encounter food items as well as non food items.

4.5.1 Try- Feeding

As for peering we tested try- feeding rates according to complexity of food item. This analysis contained all try- feeding events, including the ones on non food items and food items not part of mother’s diet. There was no significant difference between different processing steps (Try- Feeding according to processing step of the food item: N = 55, Proc. Step 0, Mean rank = 35.26 Proc. Step 1, Mean rank = 22.50, proc. Step 2 = 23.72, proc. Step 3 = 33.06, proc. Step 4 = 25.50, Kruskal- Wallis test: p = 0.167, figure 50).

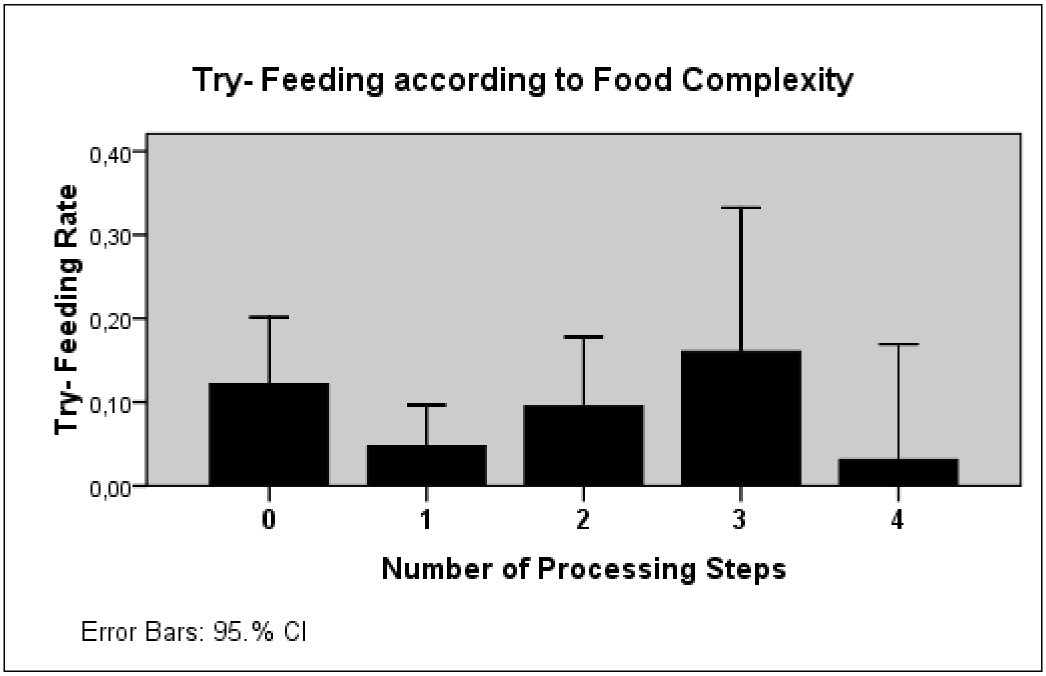

Figure 50: Try- feeding according to processing steps of the food item.

To establish whether infants try-feed on items they have not yet integrated completely to their diet, we correlated infant's diet to a try-feeding rate (Figure 51). This rate was calculated from events try-feeding divided by amount of time mother spent feeding on that item, in order to control for how many opportunities an infant would have to try-feed a certain food type. There was a significant negative relationship between these two factors (Spearman´s rho; r = - 0.516, p = 0.001, N = 39). This tells us that in fact infants mostly try-feed on food types that are not yet familiar to them.

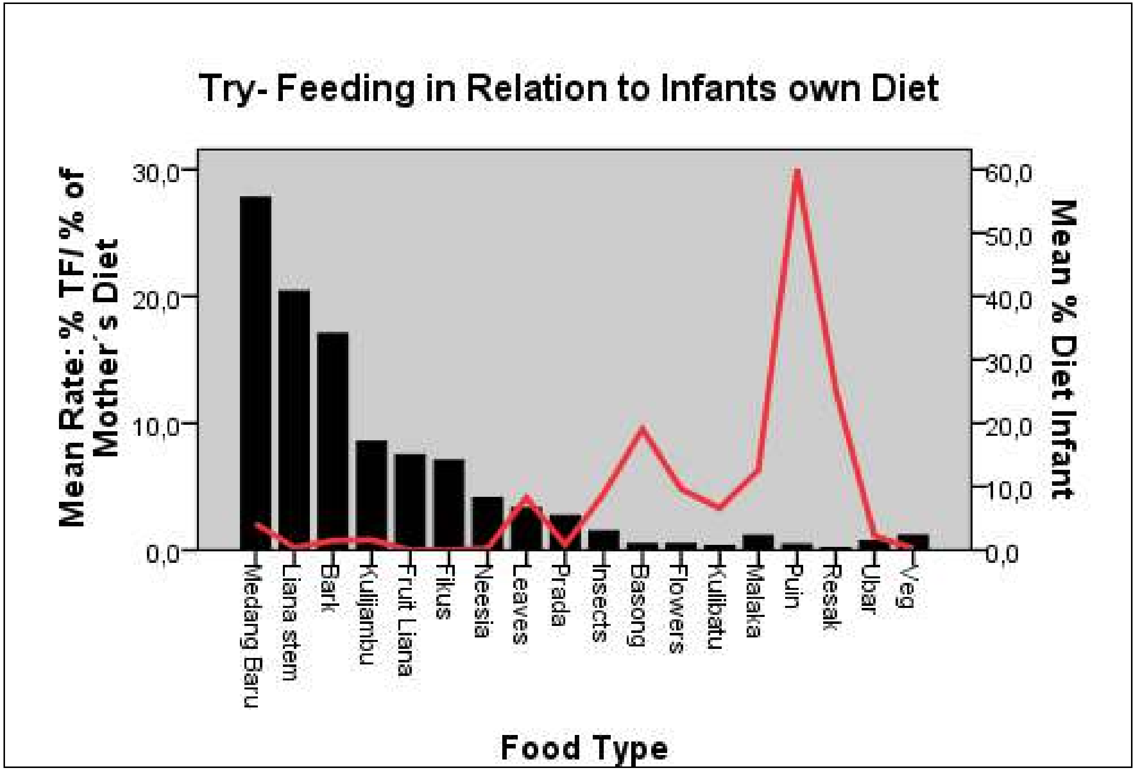

Figure 51: Try- feeding rate was negatively correlated to how large part of an infant's diet a certain food type would possess.

4.5.2 Exploring and practicing

An infant's motivation to try-feed on an item might be driven by its curiosity for novel objects, and hence express itself as an exploration behavior. But a try-feeding event can also occur simply as a result of an infant's lack of skills to ingest or process an item properly. All our recorded try-feeding events were grouped according to if the item was included in the feeding repertoire of the mother or not, the latter also included non food items that were try- fed on. We analyzed these to categories to address whether young orangutans show any interest in exploring their environment on their own, or if they simply just restrict themselves to items that are standard in their mother's diets (figure 52). Young orangutans were often observed trying out random potential food items they would encounter, as young individuals travel through the canopy after their mothers. We found no significant difference in try-feeding rate for these two categories, suggesting that apart from practicing, try-feeding express itself as an explorative behavior. (Mann-Whitney U test: Items included in Mother's diet, N $_{\text{ind}}$

= 5, Mean rank = 6.80, Items Not included in Mother's diet, N_{ind} = 5, Mean rank = 4.20, p = 0.222).

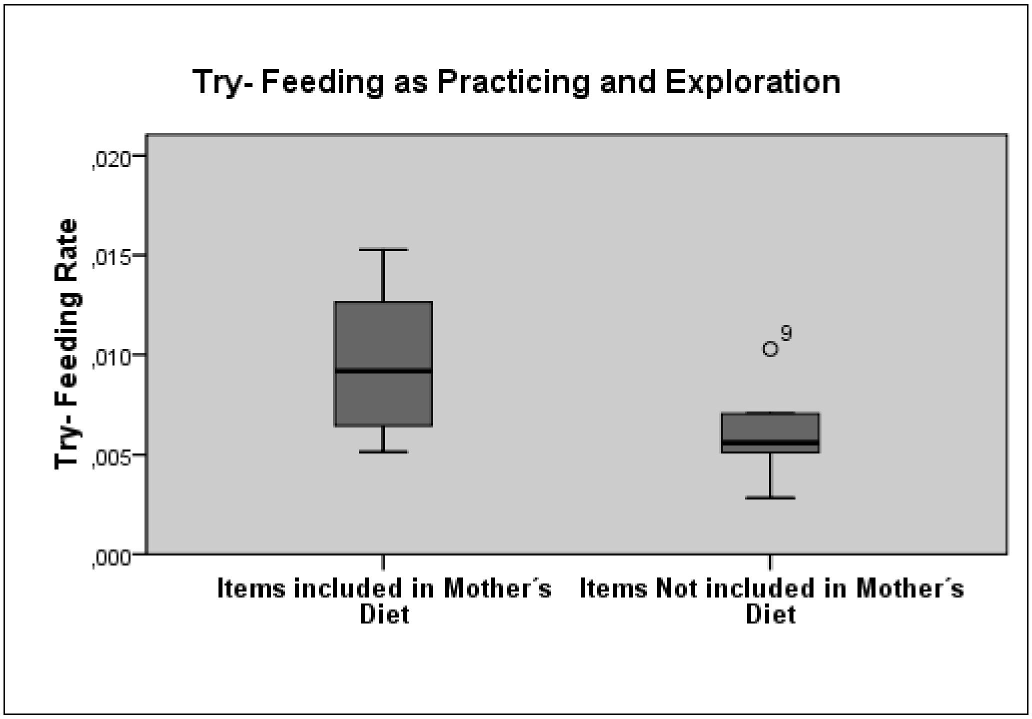

Figure 52: Try- Feeding rates on items integrated in mother's diet and items not being part of the feeding repertoire of the mother.

Of all the try- feeding events on items, included in the diet of mothers, we further analyzed whether mothers behavior has an influence of the try-feeding rates, see figure 53 and 54. We divided these try-feeding events into three categories: 1. Try-feeding on a food item independently of the activity of the mother or before mother started to feed on that food item. 2. Try-feeding on an item within one hour after mother had been feeding on that food item, but with no explicit peering event recorded. 3. Try-feeding on a food item after peering by mother feeding on that item, try-feeding within maximum one hour after recorded peering event. There were significantly more try-feeding on items included in mother's diet after close range watching of mother processing the item in question (Friedman ANOVA: Try-feeding before mother fed, Mean rank = 1.25, Try-feeding after mother fed/ without peering, Mean rank = 1.75, Try-feeding after peering, Mean rank = 3.00, N = 4, p = 0.039) (figure 53 and 54).

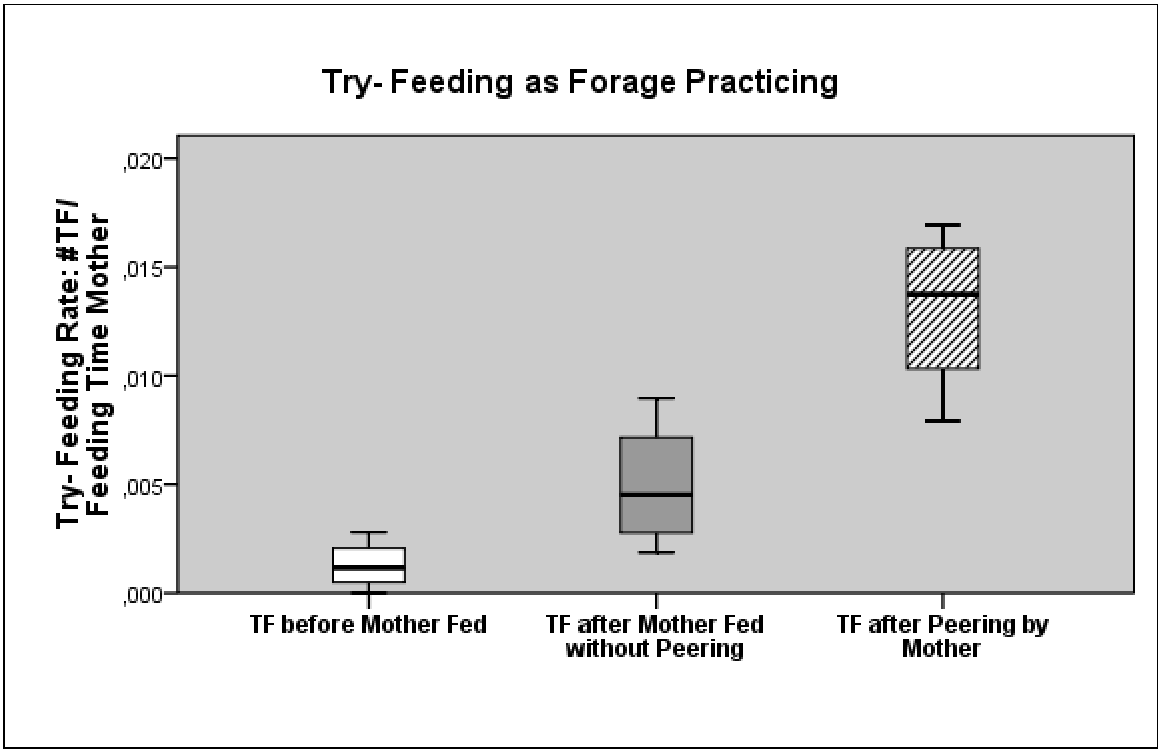

Figure 53: White plot: Try-feeding on an item independently from mother's activity or before mother fed on that item. Grey plot: Try-feeding on an item after mother fed on it but without close range watching. Striped plot: Try-feeding on an item after peering at mother feeding on that item.

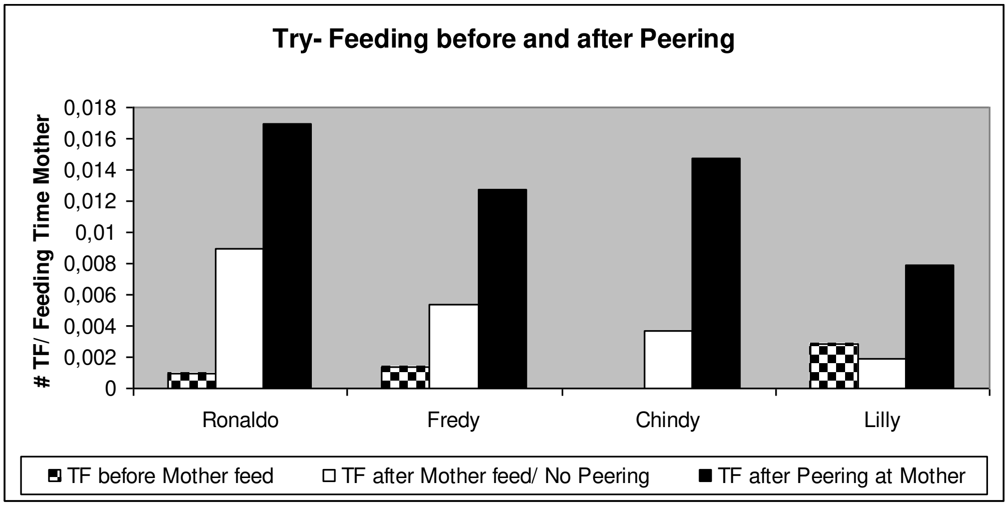

Figure 54: Try-feeding before mother fed, after without peering and after peering by mother, plotted for each infant.

Try-feeding independently from mother's activity, hence without any peering event recorded before and try-feeding after observing mother feeding would not be equally distributed for all food types, illustrated in figure 55. For vegetative plant parts, insects, bark and Neesia seeds there were a clear increase in try-feeding after peering.

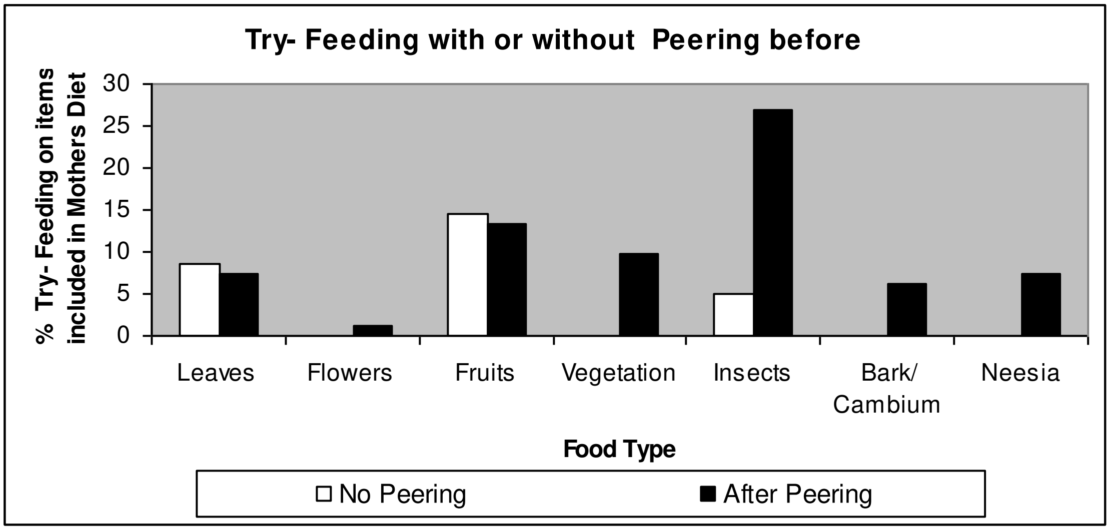

Figure 55: Try-feeding, without peering before and after peering by mother, plotted for different food types.

4.5.3 Independent discoveries

A mother potentially plays a big role in what items an infant chooses to eat. A wrong pick can be costly especially if poisonous. An infant might also not be able to recognize food sources and hence only try them out after the mother has guided them to the right feeding spot. As an infant grows older and develops locomotion skills competent enough to move around the canopy itself, it has a choice where to go. We correlated this with the ecological competence, e.g. how often would an infant recognize a food patch before the mother or how often would it be feeding alone in a patch (Figure 56). There was a significant negative correlation between feeding alone and time spent clinging to mother while moving (Spearman’s rho: r = -0.880, p = 0.021, N = 6, figure 56). In this case again we use the time spent clinging to mother’s body while moving through the canopy as an age related estimate of developmental stage.

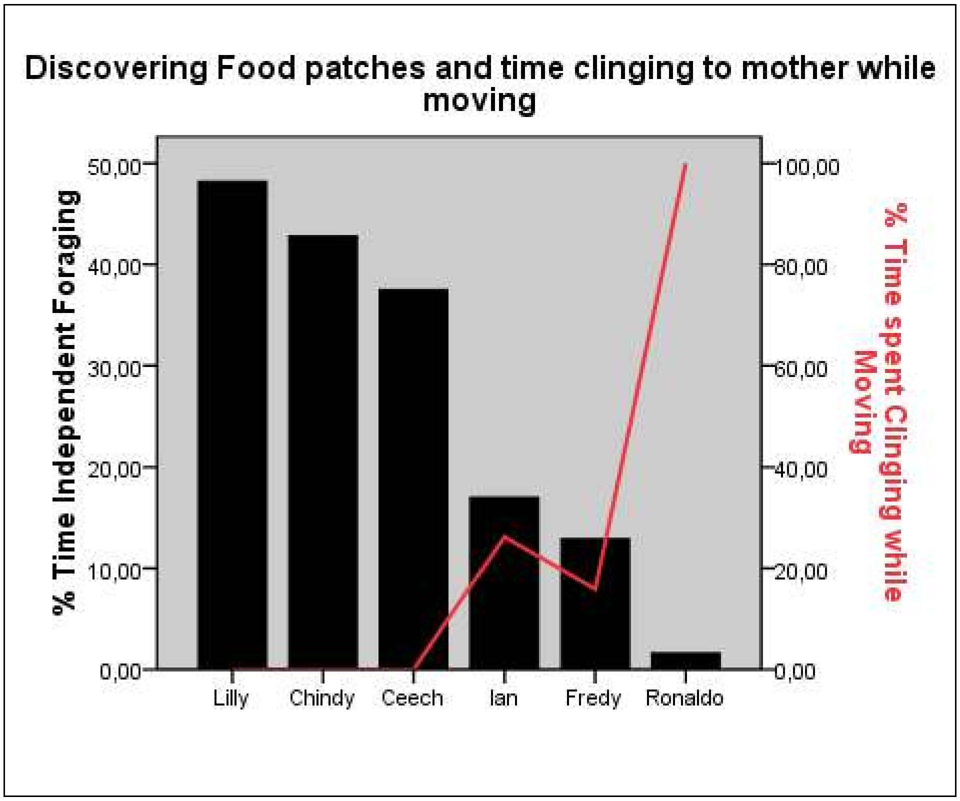

Figure 56: % time spent feeding alone in a food patch compared to % time spent clinging to mother while moving.

4.5.4 Independent exploration in Suaq and Tuanan

If cognitive behaviors are linked together we predicted that the site where we find more indications for social learning would also be the place where we found more of other cognitive mechanisms such as independent exploration and innovations. To test this for the orangutans we compared Suaq immatures to the ones at Tuanan in matter of behaviors like try- feeding and object play (Figure 57 and Figure 59). We used the same criteria as for parallel comparison of peering. Data from Suaq was recorded by Sofia Forss and Ellen Meulman and for Tuanan only data from year 2005 from Adrian Jaeggi and Lynda Dunkel were included in the analysis. We calculated a rate of try-feeding per total time followed for different kind of food types. Only try-feeding on items integrated in orangutan diet was analyzed, very few explorative try-feeding on novel food items as well as non food items were recorded from Tuanan, whether the two sites differ in this question will still remain to be answered. As we predicted try- feeding was significantly more frequent in the Suaq infants (Wilcoxon signed- ranks: Z = - 2.521, p = 0.012, N = 8). The difference was larger than we initially expected.

The same analysis was then performed on object play. Manipulative handling of objects, like liana pieces, twigs and branches did not show any significant difference between the two field sites (Mann- Withney: U = - 0.289, p = 0.081, N = 8). Playful handling of objects seems to be equally frequent in both populations and tended to decrease with infant age, see figure 58. In year 2005, the oldest infant of Tuanan, Kondor was 5,5 to 6 years old and never observed playing, more or less equally aged Lilly at Suaq would still often playfully manipulate objects.

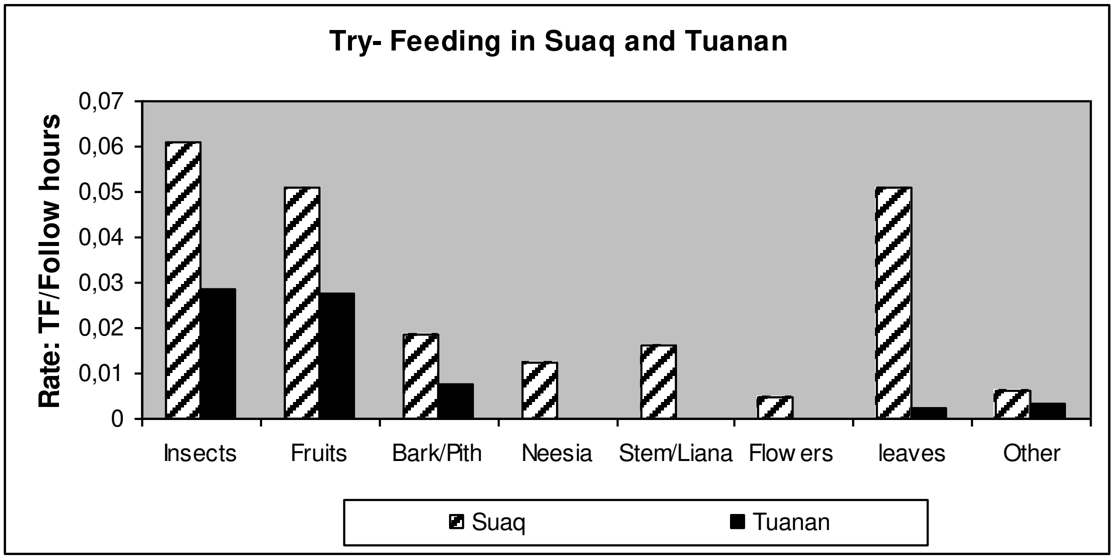

Figure 57: Try- feeding for different type of foods at Suaq Balimbing and Tuanan.

.

The previous analysis, presented in 57 regarding try-feeding were based on *ad libitum* data recorded by every observation of an infants try-feeding behavior. Additionally we calculated how much time of the focal time, were each activity is recorded every second minute, were spent try-feeding and playing with objects for Suaq and Tuanan infants. For object play these results showed no significant difference between the two sites, however try-feeding would in general take up significantly more time of a Suaq infant’s activity than an infant from Tuanan. (Mann-Whitney U test: APO: Suaq, N = 5, Mean rank = 4.9, Tuanan, N = 4, Mean rank = 5.12, U = - 0.123, p = 0.902, Try- Feeding: Suaq, N = 5, Mean rank = 6.60, Tuanan, N = 4, Mean rank = 3.00, U = - 1.960, p = 0.05, figure 58).

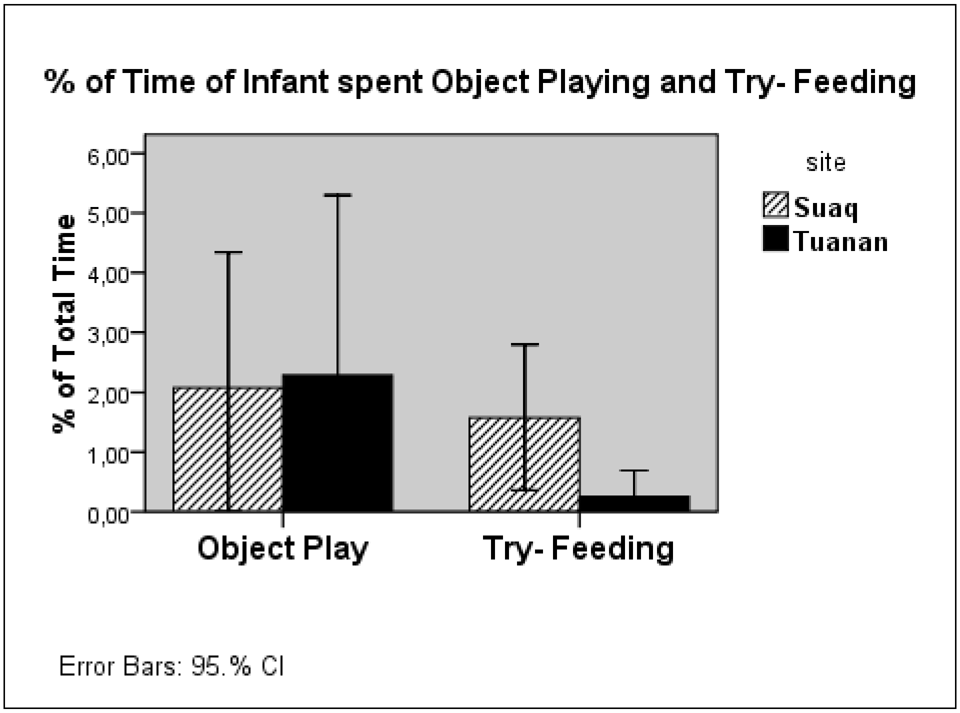

Figure 58: Percentage of time infants spent Object playing and try-feeding at Suaq Blimbing and Tuanan.

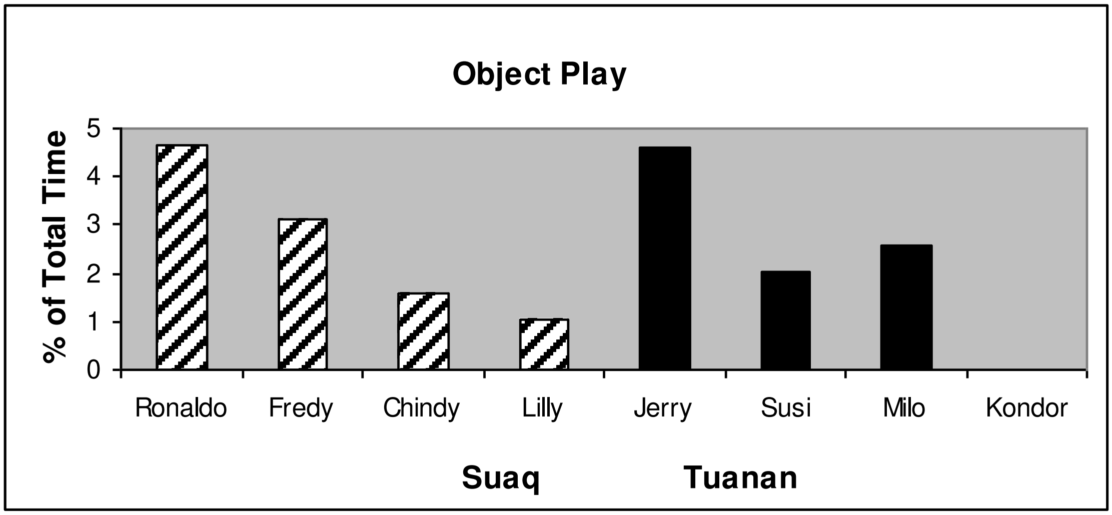

Figure 59: There was no significant difference in frequency of object play between Suaq and Tuanan immature.

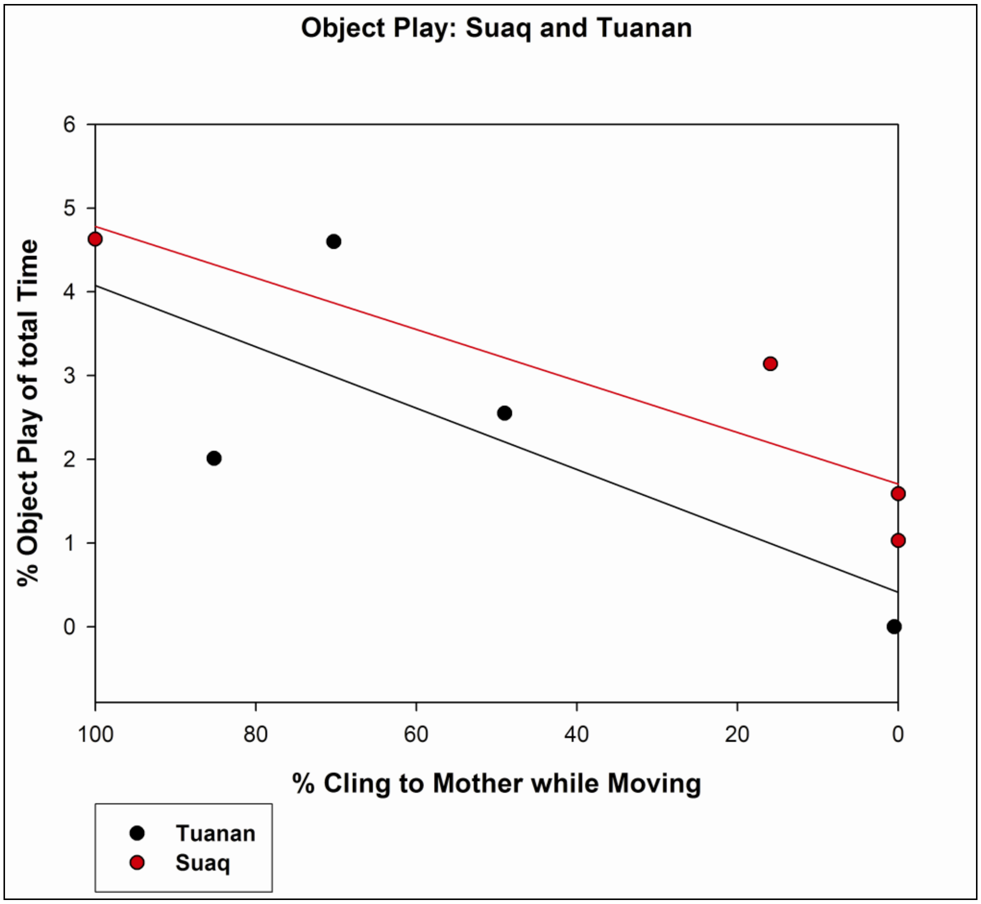

Figure 60: Object play for both study sites as a function of how much time spent clinging to mother while moving, used as an age related estimate.

As infants slowly develop in locomotion and feeding skills they also develop the ability to recognize food patches themselves. We looked at how often our focal infants at both sites would feed independently in a food patch or entering a food patch before the mother. Using an age related estimate (time spent cling to mother while moving) we assessed a univariate analysis of covariance (ANCOVA) according to percentage of independent feeding. The covariate, time spent cling to mother while moving, was significantly related to the percentage of time an infant spent feeding independently from mother: $N_{Suaq} = 6$, $N_{Tuanan} = 4$, $F = 23.695$, $p = 0.002$, but there were no significant different found between the sites $F = 2.676$, $p = 0.146$, indicating that as infants develop locomotors skills they tend to increase their independent foraging time at both studied populations. As expected the older an infant gets, the more it forages independently from the mother (Figure 61). For the Suaq infant we can see a large increase in independent foraging from the three younger individuals to the three older ones; these are also the two groups of individuals we previously classified as dependent and independent travelers.

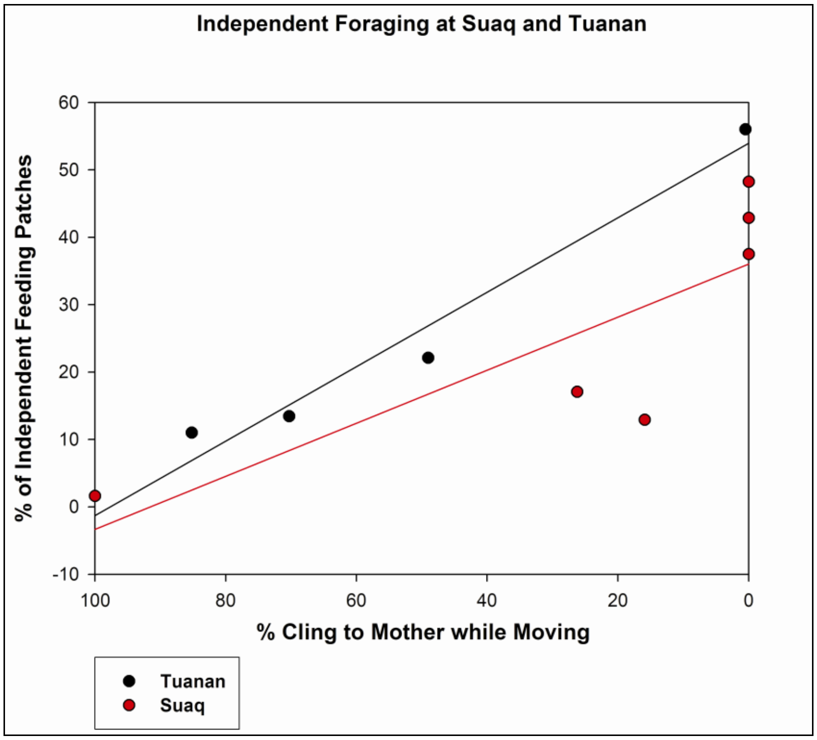

Figure 61: Percentage infant spent foraging independently from mother related to time they depend on mother by moving

5. DISCUSSION

The study of social learning in the wild requires a very different approach from the experimental one used for captive studies. The challenging aspect of approaching these types of questions in free living animals is the sheer lack of ability to control the situation. Reduced ability to choose the focal subject, time of observation and age classes are just examples of matters that have to be treated the way we encounter them in situ. The positive side is that there are no artificial situations set up or any enculturation effects, thus each behavior is observed in the natural environment where it evolved. Although the amount of research on social learning is tremendous, so far very few studies have concentrated on free living animals. This study had the privilege to do so.

In this chapter we will discuss whether our results indicate the presence of social learning in wild infant orangutans. As predicted, infants did not randomly observe any behavior of role models; instead, visual attention was concentrated onto more complex behaviors such as nest building and foraging. Furthermore, within the foraging domain we found the same tendency of increased visual attention by the infants towards adults as the complexity of feeding techniques increased. The comparison with the Bornean study sites gave us the advantage to detect how sociality and diet complexity encourage behaviors such as social biased learning and independent exploration in wild populations.

5.1 Social Associations

Compared to other great apes the orangutan is mostly described as solitary, only socially associating during reproductive phase or briefly at high level of food abundance. Sociality fluctuating with gregariousness of the population has therefore in the context of orangutan social organisation been referred to as an individual-based fission-fusion system (*van Schaik 1999*). Our results show that the infants and adolescent orangutans studied in Suaq Balimbing spent up to 75% of their total time in association with other conspecifics beyond the mother (figure 12). The same graph also presents the clear difference in sociality we found between immatures at Suaq and Tuanan. Taking a closer look at the associations formed with the infants, we found that closer distances (10m and 2m) are also more customary at Suaq than Tuanan (figure 13), again indicative of a higher social tolerance among the Suaq orangutans. Suaq immatures would actually spend most of their time in association within 10 m to the associated individual, which for a non group living species is a close proximity. The youngest infant, Ronaldo spent a high percentage (20%) of his total follow time within two meters of a party member. Due to his young age he still spent up to 50% of his time in body contact with his mother; hence the mother would also often appear within these two meters at the same time. On the other hand, the oldest infant Lilly spent only around 7% of total follow time within two meters of party members, but did so mostly alone without the mother's presence within this distance (figure 14). Moreover there seems to be a tendency for older infants to selectively spend equal amount of time within 10 m to a party member and their own mother, compared to total time respective individuals were in the presence of the infant, presented in figure 14. Also close distance to associates (within 2 m) seems to slightly increase with infant age (figure 15). This clearly greater social tolerance observed at Suaq generates opportunities for social learning, which seems to be fewer at Tuanan.

5.1.1 Formation of parties

Not only was the time spent in party higher at Suaq than at Tuanan, but so were the party sizes, shown in figure 19. At Suaq we would more frequently find two or three party members around our focal animals at the same time, whereas these analogous parties seem to be a lot fewer at Tuanan. The association measurement used, within a 50 meter distance, is regarded as non random. If it would reflect passive aggregation due to the high orangutan density (7 ind/km^2) at Suaq Balimbing, an average party size around 1.07 would be expected, calculated by Waser´s gas model (*Mitani et al 1991, van Schaik 1999*). From long term studies among different research sites it has been established that mean party size is considerable higher than random (1.5- 2.0 at the Sumatran sites; Suaq Balimbing and Ketambe). Among the Bornean sites (Kutai, Tanjung Puting, Gunung Palung and Tuanan) densities are notable lower but also party sizes tend to be lower than on Sumatra (1.05- 1.3) (*van Schaik 1999) (Mitra Setia et al 2009).* Our results are consistent with these findings and conclude that greater party sizes promotes for more opportunities for social learning.

5.1.2 Who were the associates of the infants in our study?

At Suaq the most common associates were adolescent individuals (figure 18). This number is to some extent driven by one juvenile still ranging together with her mother and younger sibling. So far data collection on both sites reflects a different image of the sociality among adolescent individuals. In Sumatra these gregarious adolescents tend to seek company, often witnessed to approach other conspecifics, whereas in Borneo this is the time when they enter the most solitary phase of their lives (*Mitra Setia et al 2009*). Due to predators such as tigers and clouded leopards, it has been argued that younger, adolescent individuals benefit from attending parties. However previous results from Suaq showed that association patterns of adolescents did not differ from other age-sex classes, so the benefits are thought to be universal and social (*van Schaik 1999*).

Both unflanged and flanged males were widely found in association with our studied immatures; sometimes even multiple males would appear simultaneously. These males were mostly tolerated around both mother and her offspring, commonly feeding together. Orangutan males range more widely (*Utami et al 2009*) and are therefore interesting party members, potentially bringing new innovations into a community. At Tuanan the percentage of time spent associated with males was much lower than at Suaq (figure 18). Certainly to a large extent a dependent infant's sociality depend on the travel pattern and decisions of its mother. Mother's with older offspring tend to increase in sociality (*van Schaik 1999*), and observations from this study also support this, since the mother with the oldest infant showed the largest number of different party members, many of them being males. Another possibly contributing reason to the different association patterns with males between the two sites, could be the frequency of forced copulations. At Bornean sites there tend to be more sexual harassment and forced copulations, especially by unflanged males (*Utami et al 2009*). This may very well influence association patterns of females, thus Suaq females may not have the same reasons to be intolerant towards an associated male. Classes expected to peak the gregariousness in orangutans are sexually active females and unflanged males, due to reproductive preferences. Mothers with unweaned infant on average keep lower associations to conspecifics (*Mitra Setia et al 2009*). As our study showed a high frequency of associations among our focal mother/ offspring pairs indicates that the social tolerance in Suaq goes beyond the sexual reproductive strategy explanations.

Our results support the suggestion, that at least in Suaq there indeed seems to exist some kind of loose community patterns and thus a social structure is present (*van Schaik 2003*). Further, the higher density of animals in the population as well as richness of food availability are most likely reasonable factors to explain the higher sociality we found at Suaq (*van Schaik 1999*). Assuming widely ranging males encounter more innovations, these being socially transmitted contributes to more opportunities of social learning at Suaq, from a wider range of individuals.

5.1.3 Feeding Tolerance

Whenever a focal individual was feeding within 10 m on the same food type as another individual it was recorded as co- foraging. Co-foraging time is regarded as indexing the opportunity for social learning. A party member could influence an individual's food choice simply by being present in, or entering a food patch first, consequently either inhibiting the focal animal to enter that patch or guide it towards that food patch, and so influencing its choice of foraging. Within a 10 m distance it is also possible for an orangutan to gather information on what species and item the associate is feeding on. We found that Suaq mothers on average would spend up to 30 % of their total foraging time within ten meters of other individuals, which potentially provides the offspring with more role models for a remarkably large part of the time (figure 16). At Tuanan such a tolerant foraging behavior was observed less than 10 % of the feeding time of the mothers. Therefore we presume that an infant raised at Suaq Balimbing is exposed to a lot more opportunities for horizontal/ oblique learning. This approach of measuring individuals close proximity while foraging has been used in other studies of social learning in the wild, indicating on opportunities to learn socially (*Perry 2009*)(*Lonsdorf 2006*). In this study we aimed to go beyond association and measured allocation of visual attention, as well as practice behavior of feeding skills.

5.2 Observational learning; its meaning and effects

Considering the expanded time orangutan infants spend in close contact to their mothers, it is to expect that they benefit from their mother as a guide for their foraging skills, especially since their feeding niche consists of a great number of species, to be classified as food or not. In order to get an insight into this opportunity for vertically learning the diet, we looked at how much of infant's attention is directed to what kind of skills, as well as for any age affect according to our grouping in dependent and independent travelers. As predicted the younger group of infants (dependent travelers) peered in general more at their mother's activities than the older group (figure 22). We predicted that if socially biased learning mechanisms are present in the wild, they should be deployed especially for more complex behaviors. These predictions are supported in our data, as we measured close-range watching for different activities of the role model. Nest building, social activities (vocalizations, social interactions such as copulation and play) and foraging would receive much more of an infant's attention than resting and moving (figure 21). Social activities may arouse an infant's attention due to the interaction with another, for the infant less unfamiliar individual. Nest building takes up very little of total activity time of orangutans, yet this behavior displays some large complexity regarding tree selection, branch folding techniques, creation of pillows, roofs and additional vocal signaling. Therefore according to our predictions it is not surprising that nest building showed the highest rate of peering events recorded in our data set. Mostly younger less inexperienced individuals would peer at their mothers while she was building a nest. Orangutan immature are competent nest builders long before weaning age, hence older infants already posses this skill (*van Noordwijk 2008*). Our oldest infant, Lilly was even observed building her own night nest sometimes, but before nightfall she would still always move into mother's nest and overnight there. Foraging contains a whole dimension of less and more complex behaviors; hence it required a more detailed analysis regarding infant observation patterns.

5.2.1 Learning what to eat

Peering rates for different food types are illustrated in figure 23. Wooden tree parts such as bark and cambium showed high peering rates; consequently these food sources requires both the ability to distinguish between edible species as well as strength and technique how to rip the bark off a trunk. The case of *Neesia* feeding was treated separately from other fruits in our results, due to the complex technical repertoire required for processing it. During focal sampling *Neesia* feeding was encountered only by three of our five mother/offspring pairs, one of them the oldest one Lilly. However, Lilly displayed a great interest in her mother processing this fruit; hence we suggest that even older offspring require close observation of this foraging method. As a mother fed on leaves and insects, infant peering rates were higher than for fruits and flowers. Insects are often hidden inside wooden plant parts and therefore possibly need some experience by the forager before found. Leaves as a food source are very easy to ingest, but in a tropical forest with a vast number of species, including some that are poisonous, it is likely that it requires some learning which leaf species are edible. Compared to fruits, leaves are expected to contain more toxic components and thus be a riskier food source. Therefore it is hypothesized that folivorous species should profit more from social learning in their selection of food (*Watts 1985; Whitehead 1986*). Our data suggest surprisingly high rates for peering by mother feeding on leaves.

5.3 Characteristics of food types and their influence on visual attention and begging behavior

5.3.1 Visibility

Hidden food sources might require information in form of social cues, whereas a more exposed visible item is not dependent on local enhancement to be found. As we predicted, our results indicate that orangutan infants pay more attention to their mother by feeding on embedded food rather than on non embedded food (figure 24). This was also true for begging for food. Processing difficulty can still vary a lot among embedded food types. Thus, to investigate these mechanisms in more detail we ranked all food items according to how many processing steps they require before ingestion. Embedded food items were of processing class two to four, and we therefore aimed to get a deeper insight also within this categorization.

5.3.2 Food Complexity as influence on observation and food solicitation

Excluding processing step zero, which contains mainly different leaf species, our results revealed a linear increase in both peering- and begging rate as food items acquire more processing steps (figure 25 and 41). Therefore we suggest that complexity of processing food is an important underlying mechanism triggering an infant's preference to observational enhancement and food solicitation. We hypothesize that the ecological characteristics of leaves, discussed earlier, are the main reason for high peering rates of this food type despite its simple processing method. More complex food items demands more watching before a complete understanding of the process is reached; thus skills such as bark/ cambium feeding, extraction of termites from dry branches as well as all tool-assisted foraging are possibly cognitively more challenging, hence taking a longer time for an infant to learn. Previous results from Tuanan have revealed the same trend towards more watching as processing difficulty increases (*Jaeggi 2006*). Since at Tuanan tool-use foraging is not present, our additional processing step four, involving all foraging activities with tools provides us with an even more complex foraging category to test for our hypothesis. As we predicted this tool assessed foraging indeed presented the highest peering- and begging rates, supporting our predictions to find peering concentrated towards more complex feeding skills. Our results are consistent with previous findings among chimpanzees. Young chimpanzees have been shown to learn tool-assessed termite fishing from observing there mothers and acquire this skill fully only in late ontogeny (*V. Lonsdorf 2005*). The most advanced food processing technique observed by wild chimpanzees to date is the nut-cracking behavior, including use of hammers, described in the Tai community, at the Ivory Coast, Africa (*Boesch 1981, Boesch 1984 and 1993*). Researches of this population claim that this foraging technique is fully learned only at adulthood (*Boesch-Achermann and Boesch 1993*), enhancing the importance of socially biased learning as well as skill practicing as the number of processing steps increases.

Begging for items that are more complex to acquire can result from the fact that the infant still lack the competence, hence it is the only way for him/her to obtain such food items. This does not exclude the possibility that begging is in effect a learning process of the item in question. Indeed in figure 40 we see that the majority of an infants begging is directed to items not establishing a large part of its diet. Furthermore, we found that only the youngest infant, Ronaldo, would beg equally for non- embedded as for embedded food types. Older infants begged for embedded items more, and especially the oldest infant, Lilly was begging most at seed extraction tool-use. The informational hypothesis behind food solicitation has been supported in all three great ape species. As in this study, orangutan infants in Borneo have been shown to beg more frequently for difficult-to-process items (*Jaeggi et al 2008*). Western lowland gorillas show similar results in decreasing food solicitation as infant age increase, hence own ecological competence increase (*Nowell and Fletcher 2006*). A captive study of mother/offspring food sharing in chimpanzees showed that edible food parts were transferred mostly after infant-initiated begging attempts; mothers on the other hand would more commonly share inedible food parts, thus of no informational benefit for the infant *(Ueno and Matsuzawa 2004).* The same pattern is found among these three species: Food solicitation is mostly infant-initiated and decreases as independent foraging and food processing competence increases. It is not completely possible to exclude the fact that begging attempts simply decrease because infants start to perform foraging on their own. During our observations at Suaq, even mothers tend to occasionally beg for food by males in association. Lisa was observed begging for *Neesia* seeds from a flanged male successfully even if she very well possesses the competence to extract the seeds on her own. Thus begging could also express itself as a test of a partner's social tolerance (*van Noordwijk and van Schaik in press*), which obviously also is the case in every mother/infant relationship.

In this study we measured both peering and begging behavior to be able to compare both of these likely informational mechanisms. In general we found much more peering incidents than begging attempts, even among the hard processed food types peering- would clearly overtake begging rates, see figure 42. If begging is predicted to be a mechanism only of informational reason we would expect it to appear in equal frequency as our peering events, however we found that very few of all peering events would actually be combined with begging attempts (figure 43). If successful, food solicitation has a nutritional benefit for the beggar, which despite informational reasons can be the motivational cue to beg for food. Peering on the other hand has no other but informational benefit for the observing individual, since in no primate species is intense watching known to be enough for obtaining food. Then why would we observe so much of infant activity time spent peering on adults processing food if it would not serve as a learning benefit? For that reason we argue that begging is likely an attributing component, but that infant orangutans at Suaq mainly acquire information about food processing by paying close visual attention to feeding role models.

5.3.3 Interest in uncommon food

A second factor that was predicted to be a potential driving factor of infant peering and begging behavior was rarity of a food item. In other words we assumed that items that an infant encounters only rarely should be of higher interest by the infant if its general diet is socially learned. This was confirmed by the two youngest infants; Ronaldo and Fredy. First we included all food items in the analysis (figure 27), secondly we tested only items of processing step 0 and 1 in order to control for food complexity (figure 28). Both analyses suggested the rarer an item is in the content of mother's diet, the more the young infants peer. For the older infants we did not establish any significant relationship between rarity and peering rates, implying that younger individuals possess less information on food sources and therefore seem to be curious and taking the advantage of watching their mothers when she interacts with food sources they may not yet have encountered very often. Older infants have more years and seasons behind them where these food items possibly were presented to them. Recall that we previously presented the fact that young infants indeed peered more than older infants, and this may very well be explained by rarity as a contributing fact that influences younger inexperienced offspring's observation rates. Among the easily processable items, different leaf species, that were really rare in mothers´ diet, received high peering rates by the two youngest infants (figure 28), suggesting that younger infants still need to observe their mother before feeding on leaves, and that this is why we found a relative high rate for processing step 0 in the food complexity analysis. We found no relationship between rarity and food solicitation, which would support the argument that begging is restricted to items were processing competence is not yet fully achieved.

Both food complexity as well as rarity has also been shown to influence infant capuchin monkey's watching behavior towards feeding adults (*Perry 2008*). Our findings among orangutans support similar mechanism to be underlying social biased learning in the wild. Fruit size was a third influential trait on observation rates among capuchins (*Perry 2008*). However, fruit size did not appear to be relevant for orangutan close-range watching and was rejected as a food characteristic influencing peering behavior.

5.4 Potential role models

For a cultural repertoire to increase and be maintained in a population, innovations need to be transmitted socially. If transmission of innovations in a semi-solitary species like orangutans is only taking place vertically from mother to juveniles, we would expect several matrilines with different foraging techniques in a single population. Indeed we do find individual differences between mothers when it comes to diet preferences and techniques. But why then are the most complex foraging behaviors, such as the seed extraction tool- use as well as tree hole tool- use, not restricted to a few individuals but found and used by the whole population of orangutans at Suaq? It is more likely that at some point in time this cognitively demanding innovation was found and spread throughout the population, compared to the possibility that each individual orangutan came up with tool- use on its own or that the inventor's matriline expanded and displaced all others over time. Hence we assume that orangutans are horizontal learners beyond the vertical mother- infant relationship. When is this horizontal transmission pattern taking a start; already as an infant, in the adolescent stage of life or is most information transferred between adults? Among our study population at Suaq we discovered that infants would use opportunities to peer by a party member more or less equally often as they use these opportunities by mother (figure 29). Opportunities were measured as time < 2m, and then compared to how many actual peer events were recorded by that individual in that time. Especially the two older infants, Chindy and Lilly would tend to peer more toward other individuals than own mother, in relation to opportunities they had to do so. These two infants also grouped as independent travelers already master the locomotion skills required to move around the canopy alone, hence have the choice whether they approach a party member or not. Therefore we claim that as an infant grow older its interest in activities of others increases. Figure 30 shows that most approaches before a peering event were initiated by the infant. Chindy for example was observed leaving a 50 m distance to her own mother behind her, to approach Lisa and Lilly where she would observe feeding behavior of both party members, indicating a strong interest in what others do.

5.5 Comparison between two socially different populations; Suaq Balimbing and Tuanan

By reason of the clear differences in sociality we found between Suaq Balimbing and Tuanan, we expected this to influence essential social learning procedures such as peering and begging behavior. During data collection on these questions at Tuanan, there was hardly any event recorded where an infant would be involved in such a close range watching of a party member, although this would frequently happen with its mother. Thus for our comparison we looked at peering at the mother at both study sites and found that not only would Suaq infants be more interested in others, but they would also pay more attention to their own mother compared to an offspring of Tuanan (figure 31). For begging we found four cases of begging by a party member at Tuanan, whether at Suaq 8 % of all food solicitation events would be between the offspring and any other individual but the mother. For both sites embedded food types were peered at much more than non-embedded (figure 32), suggesting the same influential factors playing a role for peering among young orangutans in general. However, Suaq infants performed more peering per se.

Another interesting fact arose as we compared begging- and food-sharing rates between mother/offspring pairs at both sites. At Tuanan begging and sharing rates decreased as infant age increased (Figure 44). At Suaq the results were different; there was no clear decline in begging and sharing rates according to infant age (figure 45). These findings are consistent with our argument that there are more skills to learn before reaching independency at Suaq; therefore infants continue to beg for items that are still not integrated into their ecological competence (Figure 40 and 46). For example Lilly was observed attempting tool-use at tree hole independently of mother's activity, although she was never seen using tools for *Neesia* seed extraction without mother feeding on the same. Most begging of Lilly was indeed found when her mother was processing *Neesia* with a tool. Thus, it is likely that this is one of the last skills she had not yet mastered and hence still depended on peering and begging in order to reach her own competence. This result once again does not exclude the possibility that begging attempts on more difficult-to-process items can be biased by an attempt to obtain the food source per se rather than collecting knowledge about it.

5.5.1 Diet differences

To address why these differences in peering behavior between Suaq and Tuanan infants, we compared the diets between these two populations. Figure 36 reveals different categories of food; fruits were almost occupying equally large parts of mother's diet at Suaq and Tuanan. All other food types show certain differences, flowers and leaves being more common among Tuanan mothers and insects, pith/stem and of course *Neesia* fed upon more at Suaq. Further we compared the number of species in each food category in the feeding repertoire of both orangutan populations (figure 37). Interestingly it turned out that even though Tuanan mothers fed more on leaves, the number of leaf species included in the diet of the population was almost twice as diverse at Suaq. Given the potential risk of poisoning due to leaf feeding mentioned above, there is supposed to be more of social learning found in folivorous species (*Watts 1985; Whitehead 1986*). Whether we can see such a difference within the same species is debatable, but the results suggest that indeed the diet of Suaq orangutans contains more informational demanding food sources. Additionally we found that at Suaq orangutans would extract more food out of different vegetative plant parts, such as liana stem, pith, epiphytes etc. Tuanan's diet list contained a higher number of species of fruits and flowers, which are in general easy accessible food sources and thus do not possess the characteristics, presented previously, of what we find be promoting peering behavior.

The ecological intelligence hypothesis suggests that natural selection would promote intelligence in species with a more challenging feeding niche or fluctuating seasonality (*Byrne, Mellars et al. 1996*). We considered this regarding our two orangutan populations in this study, with the background fact that orangutans at Tuanan are exposed to food scarcity and low fruit availability to a larger extent than their Sumatran relatives (*Marshall et al 2009*). Additionally, the knowledge of fallback items for Tuanan orangutans during food scarcity are bark and vegetative parts (*Haag 2007*). According to the EIH, Tuanan orangutans should experience a stronger selection pressure to extract more species of these food types but we found the opposite: Suaq orangutans feed on a more diverse range of species of these items, although they are hardly ever exposed to low food availability. We therefore reason it is not the ecological environment that favored the development of a broader feeding repertoire at Suaq, but the greater sociality found among that population.

Figure 34 and 35 implies that infants at Tuanan overlap a large part of their mother's diets sooner than at Suaq. Yet this contributes to our findings for a more diverse feeding niche to learn at Suaq. Infants at both sites seem to acquire fruit as part of their diets at an equal time scale (figure 38), whether insects tend to occupy a slightly larger part of Suaq infant's diet in comparison to Tuanan (figure 39). This is well possible to be due to the fact that mothers at Suaq also consume more insects in comparison to Tuanan mothers, hence the result we found among the infants reflecting the diets of the mothers. These analyses were made on estimated ages, but this should not affect the results since the curve for insect feeding by Suaq infants tend to be higher despite a possible misestimating of a couple of years. Diet composition increased in diversity as well as complexity as infants grow older. In figure 33 we can conclude that Ronaldo, Fredy and Ian engage in very little insect feeding in their diet. Insects feeding classified as processing step 3 would then enlarge in the part of the diet of the two oldest unweaned infants; Chindy and Lilly. Further the two adolescent females; Ellie and Tina showed an even stronger increase of insect feeding and thus the percentage of this skill would by then reach that of any adult.

5.6 Independent Exploration

A behavior can be a result of social learning or an own discovery or even a mixture of both: through an observation of someone else, an individual can later be triggered to explore a behavior independently. Therefore it is difficult to separate whether a behavior is indeed socially learned or if it is an independent exploration. Independent exploration has not been very well studied in the wild, due to the fact of difficulty gaining such data without an experimental approach. In this study, try- feeding behavior and manipulative object played by young orangutans was measured and used to approach these questions. Characteristics of food types that were found to have an influence on both peering and begging behavior were tested for try- feeding as well. For embeddedness it seems like try- feeding would be more frequent on embedded items than non-embedded but not as clear as for peering and begging (figure 24). There was no significant difference in try- feeding for the different processing categories (figure 50). Furthermore, try-feeding was more frequent on items, which were not establishing a large part of the infant's own diet (figure 51). These results suggest that try-feeding on food may be driven partly by different mechanisms than peering and begging behavior.

5.6.1 Explorative try-feeding

As mentioned previously social learning can only be fulfilled by an individual's own opportunities to practice a certain skill, moreover try-feeding can also be an attempt to become familiarized with and explore the environment. For this reason we investigated whether items included in mother's diet, or items not included in mother's diet (also partly consisted of non food items) were more frequently try-fed on. Although try-feeding on items that were part of mother's diet was more common we could not establish any significant difference between these two categories, suggesting that try-feeding can be interpreted as practicing of skills where competence is not yet reached, but also partly as an expression to explore novel objects. This would also explain why there was no linear trend found among the processing step of food items, because infants seem to explore items such as leaves, epiphytes and other plant parts they encounter as they move after their mother through the canopy. These items are mostly easy accessible and of processing step 0- 1. For example infants were often observed to try- feed on leaves from tree species were mother were feeding on fruits, but the leaves were not a part of mother's diet. This implies that orangutan infants, as well as observed in human babies, have a need during their ontogeny to discover and get familiar with objects by tasting them and handling them with their mouth.

5.6.2 The role of practicing

By observations in the wild such as in the case of *Neesia* seed extraction tool-use, it is still not ensured that the observing animal actually is learning by true imitation or emulation *(Boesch and Tomasello 1998) (Tomasello 1996) or through another process.* The individual observing such a tool- use act can recognize the subject and the object the model is handling in the context of the outcome, here seeds extracted. It can then, by encountering the same situation itself, use this information about subject, object and the outcome, but only by privately practicing through trial- and error- process discover the way to the outcome independently. A *Neesia* fruit is big and deep enough that the actual poking actions of the tool to the seeds are necessarily hidden to the observer, who therefore will have to practice and get familiar with the feeding technique on its own. Thus social learning is a repeated sequence of observations and practice. As an illustrative example in humans, an East-Asian raised child may observe its parents feeding with chopsticks, but not until the own experience with handling the sticks will it acquire the technique how to successfully eat with them. If we expect try-feeding as practicing and emulation of foraging skills observed by the model, it should be more frequent after peering. This was clearly supported in our data. Of all try-feeding events on items included in mother's diet, i.e. the ones infants are expected to practice on, try-feeding rates were highest within an hour after a close observation of mother handling that item (figure 52). Very few try-feeding events of this kind would appear before mother fed on an item. Try-feeding on items after mother started to feed on it, but without explicit peering, was higher than try-feeding independently from activity of mother. These results imply that infants to some extent refer to mother's feeding activity before trying it and furthermore are triggered by close observation to try out and practice a skill on their own. This same pattern was established by each of our infants in the analysis (figure 53). More convincing and contributing to the-need-of-practice hypothesis, the food types for which try-feeding after peering indeed was the case were vegetative plant parts, insect feeding, bark/cambium feeding and *Neesia* seed extraction. All these skills were classified as processing step 3 or 4, hence indeed the ones we would expect to require some individual practicing before full competence is reached, see figure 54.

Finally, we looked at how much mobility might play a role in infants feeding behavior. As infants develop locomotion competence to move between trees independently of mother, their time of independent foraging would also increase (figure 56), since at that stage of ontogeny an infant is no longer totally bound to its mother's food patch but possess the freedom to move into any food patch of own choice. We concluded that this independence of travel ability seemed to play an important role in infant development, since the independent travelers were the ones peering more by party members, hence show a curiosity and interest in exploring their environment. In summary we can conclude that try-feeding on items that are part of the orangutan diet is an individual evaluation and practice of these foraging techniques i.e. influenced by observational learning, but that to some extent try-feeding would also appear as a spontaneous exploration of items encountered in the infant's environment. The latter, seen as a precondition for innovativeness, is to be further investigated.

5.6.3 Try- Feeding and Object play at Suaq Balimbing vs Tuanan

Also these explorative behaviors were compared between infants from Suaq Balimbing and Tuanan. Manipulative object play was not significantly different between sites, suggesting orangutan offspring in general show a predisposition to play around with encountered objects (figure 58 and 59). Try- feeding was tested for different food types and compared between sites. Suaq immatures execute significantly more try- feeding than Tuanan infants, for all food categories (Figure 57). These results follow same pattern as previously described peering comparisons, and thus validate that Suaq infants tend to be more involved in learning mechanisms than their Bornean relatives also in the context of independent exploration. A broader variety of diet choice that a Suaq infant can observe with its mother may require more practicing, in form of try-feeding, before they reach ecological competence, leading to a delay in diet overlap as described earlier. Also it is possible that the amount of dietary inputs an infant experiences might be reflected in its own explorative behavior, and thus social learning, in form of observing a more diverse diet encourage individual exploration. The lower overlap in diet of infants of the same age at Suaq than at Tuanan, may reflect the greater dietary complexity in the feeding repertoire at Suaq. The overall physical development seems to be similar among immatures at both sites, thus the weaning age at Suaq is at a later stage than at Tuanan (van Noordwijk et al 2009). We hypothize that this extended time around mother at Suaq could be due to social learning and the reach of foraging competence, however this is an interesting aspect for future research.

6. GENERAL CONCLUSION

In this study we attempt to approach social learning mechanisms of wild living orangutans from various different perspectives. Our final conclusions and predictions are summarized in this chapter.

Assuming orangutans as well as other great apes, including humans, rely on social learning for the acquisition of dietary competence, all necessary predictions were met. Complexity of diet as well as the processing of food proposes necessity of observational conditioning before competence is reached. Time for such social learning is present in all great apes due to late weaning, and even the longest in orangutans. In general compared to gorillas and chimpanzees, orangutans live sort of a solitary life and so provide their offspring with only one role model, the mother. However, orangutan and chimpanzee social organizations tend to differ depending on which populations are studied. Female orangutans at Ketambe were argued to be as solitary as females of an east African chimpanzee population at Kanyawara (*Wich et al 1997*). Among chimpanzee communities it has been found that the more time individuals spent together the more foraging behaviors are represented in their feeding repertoire (*van Schaik, Ancrenaz et al. 2003*). Our study supports this among orangutans as well. Caused by a higher social tolerance among the orangutans at Suaq Balimbing, in comparison to Tuanan, young individuals there get used to the presence of other individuals from an early age on. This may well express itself as lower neophobia and higher interest towards conspecifics among Suaq immatures. We show that young orangutans raised at Suaq Balimbing have a larger feeding repertoire to learn, hence that they indeed are more frequently involved in social learning, as suggested by close range observation and food solicitation, in comparison to conspecifics at Tuanan. Furthermore, our study supports the idea that the presence of multiple role models makes for cleverer individuals, in the sense of extractive-foraging skills. Infants in our study were exposed to horizontal and oblique learning opportunities, and moreover displayed interest in these potential role models. A population exposed to more social interactions of these kinds maintains more skills for individuals to learn, consequently even if an infant does not directly imitate and adapt a behavior from a stranger, its mother is more likely to possess more technical foraging skills, than a mother in a strict solitary population. We also show that infant observation is not aimed randomly but selectively at complex behavior such as social interactions, nest building and food processing. Our predictions that increases in forage difficulty requires more learning, were confirmed by higher observation rates for more advanced food processing. During early ontogeny we found that rarity has an influence on what an infant pay attention to, but this declines as the feeding repertoire becomes more familiar with age. Furthermore we show that social learning involves multiple steps before completed. Young individuals' increased practicing, in form of try-feeding after close observation, showed how observation and enhancement induces exploration and self-discovery.

We also found that indicators of social learning are seen more commonly in the more social population but also explorative behaviors express themselves to a larger extent there. This suggests that cognitive behaviors most probably are linked to each other. Therefore we suggest that the larger repertoire found at Suaq Balimbing is due to a combination of more observational learning as well as more exploration. Independent exploration is a precondition for innovations to emerge, which is a further requirement for cultural traditions to spread. Within this loop of processes we find social learning as an adaptation, enabling individuals to reach a higher competence in their feeding niche. Young orangutans at Suaq and Tuanan grow up in two socially different structures, and so the foraging behavior of the infants will be expressed according to the learning opportunities they are exposed to.

By implicating all these underlying mechanisms of socially biased learning found in the wild, we at last want to highlight the ecological validity that is missing from captivity studies. Social learning as a cognitive trait found among wild living apes can help us understand the evolutionary history of human cognition. Increased intelligence has been suggested to be favored among highly social primate species (*van Schaik and Pradhan 2003*): the model suggests that where selection on social learning is high, innovativeness indirectly improves as well due to the cognitive link between them, whereas selection on innovativeness would not promote social learning. Hence I believe that social learning as a result of evolution through natural selection is possibly the dominant mechanism leading to further cognitive abilities and also the high level of intelligence of humans.

7. ACKNOWLEDGEMENTS

First and far most I would like to thank my supervisor Carel van Schaik for giving me an opportunity to work in a field of biology I could only dream of when I first started my studies, and for introducing me to a fascinating and challenging topic that really grew into my heart. I also dedicate a great thank you to Maria van Noordwijk for all helpful advice, discussions and for extracting information out of the Tuanan data base, as well as for sharing Pongoland with me.

I am truly grateful to Universitas Nasional (UNAS) in Jakarta, Indonesia for their support and collaboration, special thanks to Mr. Tatang Mitra Setia and Dewi Suprobowati for all their help and to Sri Haryati for being my counterpart in the field. I thank The Indonesian Institute of Science (LIPI) and the State Ministry of Research and Technology (Ristek) for permission to carry out research in Indonesia. Further I thank Direktorat Fasilitasi Organisasi Politik dan Kemasyarakatan, Departamen Dalam Negri, The Department of Forestry and Nature Conservation (PHKA) and Taman Nasional Gunung Leuser (TNGL) departments in Jakarta, Medan as well as great thanks to the local office in Tapaktuan for all their permissions for me to work in the national park. For permission to work at Suaq Balimbing I would also like to thank Badan Pengelolaan Kawasan Ekosistem Leuser (BPKEL) and Yayasan Leuser Ekosistem (YLI). I specially thank YLI for letting us researchers stay at their camp and all their help with everything. A special thanks to Paneco and Sumatran Orangutan Conservation Programme (SOCP) for their sponsoring and help with so many things, especially Ian Singleton, Santi Delavita Lubis, Didik Prasetyo, Asril, Sisilo, Nuzuar, Deva and Melda. I also would like to thank SOCP for investing and building of the new camp, which I hope will see many days of promising research in the future.

I would like to dedicate a great thank to Ellen Meulman and Andrea Gibson, I could not have wished for better field companions to share our beloved swamp with. Thanks for making my field experience an inspiring and joyful time of my life, for friendship and great collaboration and for so many unforgettable moments. I am also especially grateful to all our field assistants; Mahmuddin, Fikar, Izumi, Zahari and Bangzul, for the great work they performed, for sharing their knowledge about the forest and for friendships and sharing of their different culture, which enriched my life so largely. I am very thankful to Pak Izahk and Pak Samsuar and their families, for all their help and advices and for hosting us in their homes as family members. Also I would like to thank Sahrul and Armas for providing us with food and company at camp, Hermanysiah for data collection and interest in our research.

At the University of Zurich I am really grateful to Adrian Jaeggi for all his contributing discussions and help, to Eric Willems for his professional statistical advice and helpfulness, Brigitte Spillmann, Moritz Fritz, Sina Kreicker and Corinne Ackermann for their support and friendship. I would like to thank Marcus Gisi for technical help and Claudia Zebib Brunner for administrative organization. I am really grateful to Claudine Largo for the help with formatting. I also like to truly thank Simon Townsend for proofreading and correcting my work. I also warmly thank my parents for always believing in me, supporting me and giving me the freedom to follow my dreams, and to Jacquline Frias for visiting me during my field work, only a true friend makes it through a swamp like Suaq voluntarily.

Finally I would like to thank the A.H. Schultz Foundation and the University of Zurich for financial support, the Anthropological Institute and all its coworkers.

This study was conducted in the framework of the Memorandum of Understanding between UNAS and the Anthropological Institute (AIM) of the University of Zurich.

8. CITED REFERENCES

Boesch, C. and Tomasello, M. (1998). "Chimpanzee and human cultures." Current Anthropology 39(5): 591-614.

Boesch-Achermann, H. and Boesch, C. (1993). "Tool Use in Wild Chimpanzees: New Light From Dark Forests". Current Directions in Psycological Science.

Byrne, R. W., Mellars, P. et al. (1996). Modelling the Early Human Mind, McDonald Institute Research Monographs, Cambridge.

Byrne, R. W., Whiten, A. et al. (1988). Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans, Clarendon Press, Oxford.

Castro, L. and Toro, A. M. (2004). "The evolution of culture: From primate social learning to human culture." The National Academy of Science of the USA 101(27): 10235- 10240.

Dewar, G. (2004). "Social and asocial cues about new food: cue reliability influences intake in rats." Learning and Behavior 32: 82- 89.

Dunkel, L. (2006). "Development of ecological competence in Bornean orangutans (*Pongo pygmaeus*): With special reference to difficult-to-process food items." Diploma thesis University of Zurich.

Fragaszy, D.M and Visalberghi, E. (1996). "Social Learning in Monkeys: Primate "Primacy" Reconsidered". Social Learning in Animals, The Roots of Culture. Heyes, C.M. and Galef, B.G. Jr. Academic Press.

Galef B.G., J., Dudley K.E. and Whiskin. E.E. (2007). "Social learning of food preferences in ´dissatisfied` and uncertain Norway rats." Animal Behaviour 75: 631- 637.

Galef, B. G. and Laland, K.N. (2005). "Social learning in animals: Empirical studies and theoretical models." Bioscience 55(6): 489-499.

Haag, L. (2007). Response to Food Scarcity. A comparative study of white-bearded gibbons (Hylobates albibarbis) and Bornean orangutans (Pongo pygmaeus wurmbii). Anthropological Institute and Museum, University of Zurich.

Hill, K. (2009). "Animal "Culture"?". The Question of Animal Cultures, Laland, K.N and Galef, B.G. Harvard University Press.

Horner, V., Whiten, A. et al. (2006). "Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children."

Proceedings of the National Academy of Sciences of the United States of America 103(37): 13878-13883.

Jaeggi, A. V. (2005). The role fo social learning in the acquisition of foraging skills in wild Bornean orangutans (*Pongo pygmaeus*). Anthropological Institute & Museum. Zurich, Masterthesis University of Zurich.

Jaeggi, A. V., Dunkel, L.P. et al. (2007). "The role of social learning in the acquisition of foraging skills in wild Bornean orang-utans (*Pongo pygmaeus*)." American Journal of Physical Anthropology Supplement 44: 135-135.

Jaeggi, A. V., van Noordwijk, M.A. et al. (2008). "Begging for information: Mother-offspring food sharing among wild Bornean orangutans." American Journal of Primatology 70: 533-541.

Lefebvre, L. and Giraldeau, L.A. (1996). "Is Social Learning an Adaptive Specialization? Chapter 6: Social Learning in Animals: The Roots of Culture." 107- 128.

Lonsdorf, V.E. (2006). "What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? Animal Cognition 9:36-46

Marshall,A. et al. (2009). Developement of Independence. Orangutans Geographic Variation in Behavioral Ecology and Conservation S. S. U. A. Serge A. Witch, Tatang Mitra Setia and Carel P. van Schaik, Oxford University Press**:** 189- 203.

Marshall, A.J.. and e. al (2009). The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans, Are Sumatran forests better orangutan habitat than Bornean forest? Orangutans Geographic Variation in Behavioral Ecology and Conservation. S. S. U. A. Serege A. Witch, Tatang Mitra Setia and Carel P. van Schaik, Oxford University Press.

Mitra Setia, T et. al. (2009). Social organization and male- female relationships. Orangutans Geographic Variation in Behavioral Ecology and Conservation. S. S. U. A. Serge A. Witch, Tatang Mitra Setia and Carel P. van Schaik, Oxford University Press.

Nowell, A. A. and A. W. Fletcher (2006). "Food transfers in immature wild western lowland gorillas (*Gorilla gorilla gorilla*)." Primates 47(4): 294-299.

Perry, S. and Manson, J.H. (2008). "Manipulative monkeys, the Capuchins of Lomas Barbudal". Harvard University Press.

Perry, S. (2009). "Are Nonhuman Primates Likely to Exhibit Cultural Capacities like Those of Humans?". The Question of Animal Culture, Laland, K.N and Galef, B.G. Harvard University Press.

Rapaport, L. G. and G. R. Brown (2008). "Social Influences on Foraging Behavior in Young Nonhuman Primates: Learning What, Where, and How to Eat." Evolutionary Anthropology 17: 189- 201.

Stoinski, T. S. and A. Whiten (2003). "Social learning by orangutans (*Pongo abelii* and *Pongo pygmaeus*) in a simulated food-processing task." Journal of Comparative Psychology 117(3): 272-282.

Thornton, A. and K. McAuliffe (2006). "Teaching in wild meerkats." Science 313(5784): 227-229.

Tomasello, M. (1996). Do apes ape? Social learning in animals: The roots of culture. San Diego, Acad Press, Inc.**:** 319-346.

Tomasello, M. (1999). "The Cultural Origins of Human Cognition." Harvard University Press, Cambridge, MA.

Tomasello, M. and J. Call (1997). Primate cognition. New York, Oxford Univ Press.

Ueno, A. and T. Matsuzawa (2004). "Food transfer between chimpanzee mothers and their infants." Primates 45(4): 231-239.

Utami, A. S. S. et. al. (2009). Male- male relationships in orangutans. Orangutans Geographic Variation in Behavioral Ecology and Conservation. S. S. U. A. Serge A. Witch, Tatang Mitra Setia and Carel P. van Schaik, Oxford University Press.

van Noordwijk, M.A. et al (2009). Development of Independence. Orangutans, Geographic Variation in Behavioral Ecology and Conservation. Wich, S,A. , Utami, A.S.S, Mitra Setia, T., van Schaik, C.P. Oxford University Press.

van Schaik, C. (2004). Among orangutans: Red apes and the rise of human culture. Cambridge, MA, Harvard University Press.

van Schaik, C. (2006). "Why are some animals so smart?" Scientific American 294(4): 64-71.

van Schaik, C. P. (1999). "The Socioecology of Fission- fusion Sociality in Orangutans." Primate Socioecology 40(1): 69- 86.

van Schaik, C. P., M. Ancrenaz, et al. (2003). "Orangutan cultures and the evolution of material culture." Science 299(5603): 102-105.

van Schaik, (2009). Geographic variation in the behavior of wild great apes: is it really cultural? The Question of Animal Culture: Laland, K.N. and Galef, B.G. Harvard University Press.

Watts, D. P. (1985). "Observations on the Ontogeny of Feeding-Behavior in Mountain Gorillas (Gorilla-Gorilla-Beringei)." American Journal of Primatology 8(1): 1-10.

Whitehead, J. M. (1986). Development of feeding selectivity in mantled howling monkeys, Alouatta palliata. Primate ontogeny, cognition and social behaviour. D. G. Else and P. C. Lee. New York, Cambridge University Press**:** 105-117.

Whiten, A. and C. P. van Schaik (2007). "The evolution of animal 'cultures' and social intelligence." Philosophical Transactions of the Royal Society B-Biological Sciences 362(1480): 603-620.

Wich, S. A., H. de Vries, et al. (2009). Orangutan life History variation. Orangutans Geographic Variation in Behavioral Ecology and Conservation. S. A. Wich, A. S. S. Utami, T. Mitra Setia and C. P. van Schaik, Oxford University Press.

Wich, S. A., Sterck, E.H.M and Utami, S.S (1999). "Are Orang-Utan Females as Solitary as Chimpanzee Females?". Folia Primatologica 70:23-28

www.unesco.or.id

www.aim.uzh.ch/orangutannetwork.htm

9. APPENDIX

9.1 Example of food items with different processing steps:

Processing step 0: Example: Liana leaves, food item ready to ingest whole as it is

Processing step 1: Example: Ripe Kulijambu fruit, food item has only to be bitten up, and ingested as whole.

Processing step 2: Example: Malaka fruit,
food item has two steps before ingestion, first bitten up fruit flesh is then eaten and fleshy substance around seeds, which then are spit out.

Processing step 3: Example Cambium, food item has to be bitten loose from trunk or stem, then ripped off and chewed on before finally spitted out.

Processing step 4: Example Neesia tool- use extraction, first a tool is being processed by peeling of a twig or stick, then by poking with the tool multiple times into the center of the fruit seeds are processed out of inner layer of the fruit.

9.2 Geographic variation in likely cultural behaviors among orangutan sites.

	site	**Suaq**	**Ket**	**GP**	**TP**	**Sab**	**Tua**	**Ku**	**LK**
	island	**S**	**S**	**B**	**B**	**B**	**B**	**B**	**B**
	(sub)species	**P.a.**	**P.a.**	**P.p.w.**	**P.p.w.**	**P.p.w.**	**P.p.w.**	**P.p.m.**	**P.p.m.**
#	**habitat**	**psw**	**dry**	**dry**	**psw**	**psw**	**psw**	**dry**	**psw**
c1	Snag riding: Ride on pushed-over snag as it falls, then grab on to vegetation before it crashes	A	A	A	**C**	R	**H**	A	A
c2	Kiss-squeak with leaves: Using leaves on mouth to amplify sound, then drop leaf	A	R	**C**	A	R	**H**	**H**	A
c4	Leaf wipe: Wiping face with fistful of squashed leaves, then drop (in kiss-squeak context)	A	A	A	**C**	A	A	A	A
c9	Scratch with stick: Using detached stick to scratch body parts	A	A	A	R	R	R	**H**	A
c10	Auto-erotic tool: Using tool for sexual stimulation (female and male)	A	**C**	A	A	A	A	P	A
c11	Raspberry: Spluttering sounds associated with nest building	**C**	A	A	A	**C**	A	A	**H**
c12	Symmetric scratch: exaggerated, long, slow, symmetric scratching movements with both arms at same time	**C**	R	A	A	A	A	A	A
c13	Twig biting: Systematically passing ends of twigs used for lining of nest past the mouth (sometimes including actual bite) during last phase of nest building	**C**	A	P	A	**H**	**H**	A	A
c14	Leaf napkin: Using handful of leaves to wipe latex of chin	A	R	A	A	A	A	**C**	A
c15	Branch as swatter: Using detached leafy branches to ward off bees/wasps attacking subject (who is raiding their nest)	**H**	**H**	R	R	R	A	**H**	**H**
c16	Leaf gloves/cushions: Using leaf gloves to handle spiny fruits or spiny branch, or as seat cushions in trees with spines	E	**C**	E	R	E	E	A	R
c17	Tree-hole tool-use: Using tool to poke into tree holes to obtain social insects or their products	**C**	A	A	A	A	A	A	A
c18	Seed-extraction tool use: Using tool to extract seeds from the protected fruits of *Neesia* sp.	**C**	E	A	A	E	E	E	A
c19	Branch scoop: Drinking water from deep tree hole using leafy branch (water dripping from leaves)	**H**	A	A	A	**H**	A	A	A
c24	Slow loris eating: Capture and eat slow loris hiding in dense vegetation	**H**	**H**	A	A	A	A	A	A
c25	Nest smack: smacking sounds associated with nest building	A	A	A	A	R	**C**	?	A
c26	Carry leafy branch to different tree in which subject starts to build nest using carried leaves as lining, pillow or cover (Tuanan: *Campnosperma*)	A	A	A	R	R	**H**	?	A
c27	Branch cushion: Covering (non-spiny) big branch(es) with few leaves or leafy branches, then sit or lie on it	A	**H**	R	**H**	**H**	**C**	?	A

	site	**Suaq**	**Ket**	**GP**	**TP**	**Sab**	**Tua**	**Ku**	**LK**
	island	**S**	**S**	**B**	**B**	**B**	**B**	**B**	**B**
	(sub)species	**P.a.**	**P.a.**	**P.p.w.**	**P.p.w.**	**P.p.w.**	**P.p.w.**	**P.p.m.**	**P.p.m.**
#	**habitat**	**psw**	**dry**	**dry**	**psw**	**psw**	**psw**	**dry**	**psw**
c28	Throat scrape: deep throat sound made by female towards offspring	A	A	A	R	A	**H**	?	A
c29	Moss cleaning - Cleaning hands with moss	A	A	A	A	**H**	A	?	A
c30	Chewing leaves into pulp then smearing foam over body (selected parts chosen)- till fur all wet	A	A	A	A	**H**	A	?	A
c31	Male and female use the same nest to spend the entire night (during consortship)	A	A?	R	A	A	A	?	**C**
c32	Tooth cleaning: Chewing and spitting out leaves after eating (sticky?) fruit	A	A	**H** (?)	A	A	**H**	?	**C**
c34	Using *Asplenium* fern to rest or sleep in	A	R	A	A	A	A	?	**C**
c38(ex-i14)	Coercive hand-holding: male firmly holds female's hand/wrist for long period of time during consort	A	A	A	R	R	**H**	?	R
c39 (ex-i17	Water play (wild splashing) on ground	E	E	A	P	R	**H**	?	A
c6	Bunk nests: Build a nest a short distance above the nest used for resting (during rain)	A	A	A	P	R	R	A	**H**
c7	Sun cover: Building cover on nest during bright sunshine (rather than rain)	A	**H**	A	A	A	R	**C**	**C**
c8	Hide under nest: Seek shelter under nest for rain	A	R	A	R	A	R	**C**	P
c21	Bouquet feeding: Using lips to pick ants from fistful of dry, or fresh, or rotting leaves (nests)	**C**	**C**	**C**	**C**	A	**H**	A	**H**
c23	Dead twig sucking: Breaking hollow (dead) twigs to suck ants from inside	**C**	**C**	A?	**C**	**H**	**H?**	A?	A
c33	Copulation on female's nest	A	**H**	**C**	R	A	R	?	R
c35	Nest as social refuge: female on nest left alone by otherwise coercive male	P	P	P	P	**H**	A	?	A
c36(ex-i7)	Biting through vine to swing Tarzan-style across gap	R	R	R?	R	R	**H**	A	A
c37(ex-i13)	Biting through vine to release tree for swaying to reach adjacent tree	R	A	R	A	R	**H**	?	A

Table from Chapter 21: Orangutan cultures revisted (Carel P. van Schaik, Marc Ancrenaz, Reniastoeti Djojoasmoro, Cheryl D. Knott, Helen C. Morrogh- Bernard, Nuzuar, Kisar Odom, S. Suci Utami Atmoko and Maria A. van Noordwijk), Orangutans Geographic Variation in Behavioral Ecology and Conservation, 2009.

Notes and explanation of codes:

Sites are ordered from west to east. Sites are Sua= Suaq Balimbing; Ket= Ketambe; GP= Gunung Palung; TP= Tanjung Puting; Sab= Sabangau; Tua= Tuanan; Ku= Kutai, Mentoko area; LK= Lower Kinabatangan.
Islands: S= Sumatra; B= Borneo.
Habitat: dry= dry-land forest, usually mixed riverine and lowland dipterocarp; psw= peat-swamp forest.
Numbers in first column refer to numbers in van Schaik et al. (2003 and van Schaik et al. (2006); new variants numbered from c24 on. The numbers follow van Schaik et al. (2003) (see also Russon et al., chapter 20).
Cell entries: C- customary= shown by all or most relevant individuals at a site; H= habitual, shown by multiple individuals; P= present with unknown prevalence, usually meaning rare; R= rare, i.e. low prevalence; A= absent; E= absent for clear ecological reason.

9.3 Number of cultural and non-cultural variants per site.

site	**Sua**	**Ket**	**GP**	**TP**	**Sab**	**Tua**	**Ku**	**LK**
island	S	S	B	B	B	B	B	B
(sub)species	*P.a.*	*P.a.*	*P.p.w.*	*P.p.w.*	*P.p.w.*	*P.p.w.*	*P.p.m.*	*P.p.m.*
habitat	psw	dry	dry	psw	psw	psw	dry	psw
Number of very likely cultural variants (C, H)	8	5	3	3	6	10	4	5
Number of likely cultural variants (possibly hidden universals)	2	4	2	2	2	4	2	3
Innovations that are not cultural at this site	4	13	12	17	17	11	2	7
Total number of recorded innovations	14	22	17	22	25	25	8	15

Table from Chapter 21: Orangutan cultures revisted (Carel P. van Schaik, Marc Ancrenaz, Reniastoeti Djojoasmoro, Cheryl D. Knott, Helen C. Morrogh- Bernard, Nuzuar, Kisar Odom, S. Suci Utami Atmoko and Maria A. van Noordwijk), Orangutans Geographic Variation in Behavioral Ecology and Conservation, 2009.

Note: Time of observations differ largely between sites, which affects the number of cultural variations recorded per site. At sites with long term research going on observers has been trained to record these variations for a longer time (Ketambe, Sabangau, Tuanan and Tanjung Putting) which of course gives these sites a high number of total recorded variants. Research at Suaq was interrupted for more than ten years, thus Suaq still has a high absolute number and the highest relative proportion of variants (*van Schaik et al 2009*). Ongoing studies at Suaq will probably establish more data for these variations.