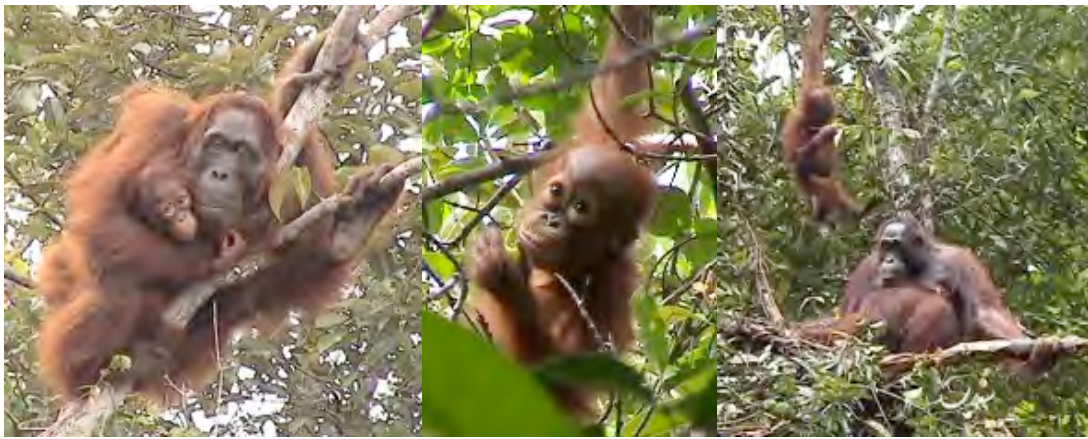# Development of Ecological Competence in Bornean Orangutans (*Pongo pygmaeus*): with special reference to difficult-to-process food items.

Diploma Thesis of Lynda P. Dunkel

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Abstract

Orangutans have among the slowest life history of all primates, and their inter-birth interval is the longest among all mammals, on average 9.4 years long (for the Sumatran subspecies). This makes them an interesting species to test the main hypothesis that aims to explain inter-specific variation in life histories. The focus of this study on Bornean orangutans is on the immature period to test on the one hand the Needing-to-learn hypothesis, which suggests that a long period of immaturity is required to learn all the skills to succeed as a reproducing adult, and on the other hand the alternative hypothesis called Needing-to-grow-strong hypothesis, which suggests that young individuals are too small, thus not strong enough to forage competently at an adult level, and first need to grow big and strong to reach this competence. The results show that very young infants already feed on very hard food items and thus the Needing-to-grow-strong hypothesis is rejected. At least for reaching feeding competence, the Needing-to-learn hypothesis is tested for food selection competence as well as for the foraging efficiency competence, whereas the range-use competence can't be tested by the observations of available mother-infant pairs. The feeding competences are both reached before or shortly after weaning age, which leads to the rejection of the Needing-to-learn hypothesis for feeding competence. Since no conclusion can be drawn yet about the range-use competence, further research has to be done on this subject, before we can conclude for sure if the Needing-to-learn hypothesis is rejected or supported.

Key words: orangutan, life history, needing-to-learn, foraging competence, immaturity, hardness of food items

1. Introduction

1.1. Life history and its variations among great apes, including humans

Primates have a slow life history, but with considerable inter-specific variations (Read & Harvey 1989). This means late age at first reproduction, high life expectancy, long inter-birth interval and a small litter size after long gestation. The orangutan has among the slowest life histories of all extant mammals with the highest inter-birth interval (e.g. Harvey et al. 1987; Knott 2001) with an average of 9.3 years (for *Pongo abelii*, Wich et al. 2004), which indicates late weaning and thus slow infant development.

The orangutan's extreme position in the life history spectrum makes it an interesting species with which to test the main hypotheses that aim to explain inter-specific variation in life histories. Since human life histories are in some respects even more slowed-down than those of the great apes (Blurton-Jones et al. 1999), insights into the determinants of great ape life histories may also enhance our understanding of the changes during hominid evolution. As in several recent attempts to explain life histories (Ross & Jones 1999; Kaplan et al. 2000), the duration of the immature period is the focus of attention. Table 1 gives a brief comparison of three life history traits in orangutan, chimpanzee and human.

	Orangutan (Sumatra)	Chimpanzee	Human mean value of Ache, Hiwi and !Kung females
Age at first reproduction (years)	15.4	14.3	19.7
Max. lifespan (years)	Up to 58	50	80
Inter-birth Interval (years)	9.3	5.8	3.5

Table 1: A comparison of three life history traits in orangutans (Wich et al. 2004), chimpanzees (Boesch and Boesch-Ackermann 2000) and human hunter-gatherers (Kaplan et al. 2000) shows how humans differ from the other two.

Compared to great apes, humans have a later age of first reproduction as well as a longer maximum lifespan. On the other hand their inter-birth interval is shorter than that of great apes and they possess a unique feature, the menopause.

To explain these variations in a mammalian life history we should focus on the pre-reproductive period. There is one main hypothesis to explain the long duration of the pre-reproductive period and hence the long dependency

of orangutan infants to their mother. This hypothesis can be tested by observations on a single species.

1.2. Main hypothesis to explain the long period of immaturity: Needing-to-learn hypothesis (Ross & Jones 1999)

The hypothesis, also known as the skill learning hypothesis proposes that life history is driven by the duration of development, which in turn is set by the amount of skills the developing individual needs to master (Bruner 1972; Pagel & Harvey 1993). It predicts that all skills concerning ecological performance have to be acquired to reach improved adult survival and especially reproductive performance.

These skills are usually thought to concern ecological competence, especially feeding, but may also refer to the capacity to deal with social pressure. The hypothesis would attribute taxonomic variation in the duration of immaturity to variation in the complexity of the species' life style, in particular its foraging niche. This hypothesis can explain the long delays before breeding in many birds, which reach adult body size around fledging (MacLean 1986) (Fig. 1)
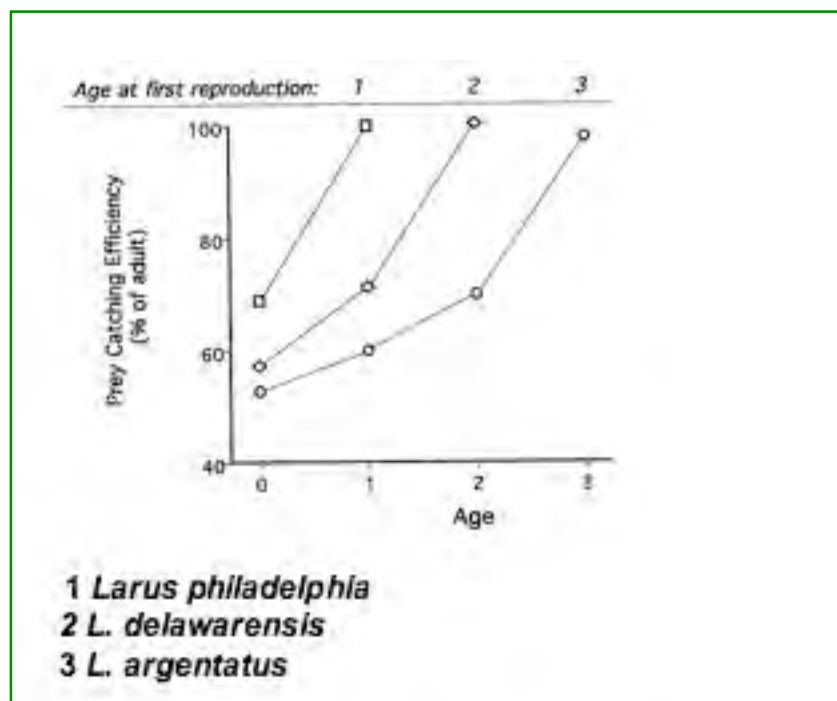
Fig.1: Age of seagulls in relation to Prey Catching Efficiency.

As can be seen in Fig. 1, three different species of seagull reach total prey catching efficiency at different ages, as some need more time to learn. Age at first reproduction coincides with reaching 100% prey catching efficiency.

Similarly, the great apes have been characterized as occupying a cognitive foraging niche that is, they require specific skills to exploit their environment. They learn their complex foraging skills such as tool use at slow rates (e.g. Boesch & Boesch-Achermann 2000). The slow attainment of competence may be due to the

strong social component. Learning often shows an alteration between periods of observational learning, as seen in the close attention juvenile apes pay to the processing techniques of older role models (e.g. Myowa-Yamakoshi & Matsuzawa 2000), and periods of individual practice. Begging for food items from adults by infants is a commonly observed behaviour (King 1994, Fragaszy et al. 1997). However true food sharing that is the voluntary donation of food by one animal to another (King 1991) seems to be rare among primates (Altman 1980)

However there are also other hypotheses, which can explain this long period of immaturity (van Schaik et al. in press). Charnov's (1993) adult mortality hypothesis is a demographic model and suggests that the decrease in adult mortality sets the age at first reproduction. The juvenile risks hypothesis and its variants links large brain size to slow development and thus late maturation (Janson & van Schaik 1993; Deaner et al. 2003).

Even though these hypotheses may explain the general life history pattern of great apes they are unlikely to explain the differences between them.

1.3. Why are orangutans good candidates to test the Needing-to-learn hypothesis?

As mentioned before, orangutans have one of the slowest life histories of all mammals. They have the longest inter-birth interval, which means the longest period of exclusive dependence on their mother. The arboreal lifestyle in combination with low productivity prevents a mother from association with two offspring (van Noordwijk & van Schaik 2005) as she provides not only nutrition but also transportation, which is important for arboreal apes. Mothers also give protection against conspecifics and predators. Not to forget the numerous skills that offspring can learn.

At the infant's age of weaning, females lose their biological suppression of ovulatory activity and soon conceive a new offspring. At this time the older infant will be on it's own most of the time. Sometimes, though, weaned immatures visit their mothers and new siblings or form groups with other weaned immatures (van Noordwijk & van Schaik 2005).

The solitary lifestyle is a key difference to the gregariousness displayed by other apes, such as the chimpanzees and gorillas. Weaned individuals can stay in the group or join another group and follow to food sources and learn more feeding techniques. Because offspring can continue to stay with their mother, learn from her and get protection after weaning, their mothers can wean earlier.

Other important aspects why orangutans are good candidates to test the Needing-to-learn hypothesis are that they need to acquire a complex foraging competence. Their diet is rich in species (Rodman 1988) and food items range from fruits, leaves, piths and flowers to insects and bark. Their foods are often extracted and require processing by hands, teeth (e.g. Rodman 1977; Rijksen 1978) or tools (van Schaik et al. 1996; van Schaik & Knott 2001) before ingestion. Tool use is seen in Suaq Balimbing (Sumatra) but not in other sites, which could be explained by culture (van Schaik 2006) Skilled extraction or processing may be especially important for the vegetative foods that serve as fallback foods during food scarcity (Russon 1998).

The third point is that they inhabit large home ranges (Knott 2001; Rijksen 1978, Rodman 1988; Russon 1998; van Schaik et al. 1996; van Schaik & Knott 2001) of over 1000 ha for adult females and over 4000 ha for sexually mature males. The optimal exploitation of these ephemeral foods requires locating other patches of the same species, which in turn requires substantial memory of a species' distribution in the home range and knowledge of the degree of a food species' degree of intra-specific phenological synchrony.

The Needing-to-learn hypothesis concerning ecological competence has three main components:
 (i)   *What* to eat: food selection competence reflects the ability to recognize edible food items.
 (ii)   *How* to eat it: foraging efficiency reflects the skills with which foods are processed.
 (iii)   *Where* and *when* to eat it: range-use competence, reflects the ability to select appropriate foods and to remember their location if they are seasonal or ephemeral.

Food selection competence can be estimated by the degree to which immatures feed independently and before the mother starts on particular food sources. Feeding independently means that an infant feeds alone on a food item its mother isn't feeding on, without regard to the distance between both, it might be that the mother is resting or the infant feeds away from the mother, mostly within 20 m in another feeding patch. Foraging efficiency is estimated by the rate of intake of particular food items, which should increase faster for food items that are easy to harvest, and by the similarity of feeding techniques. Range-use competence can be estimated by the tendency to feed independently on food items when not near the mother. It is predicted that young individuals foraging independently from their mother (or other tolerant role models) are less capable of selecting feeding sites or locating suitable food sources, less likely to incorporate favoured food items in their diet, and are more likely to experiment more with foods. This will lead to a different diet composition, relative to expectation. But this competence can only be estimated through observations on weaned immatures.

The Needing-to-learn hypothesis predicts that all three aspects of foraging competence increase with age and, critically, that they tend to reach stable values around the age at first reproduction, i.e. around or beyond adolescence, or even continue to rise during early adulthood (Fig. 2).
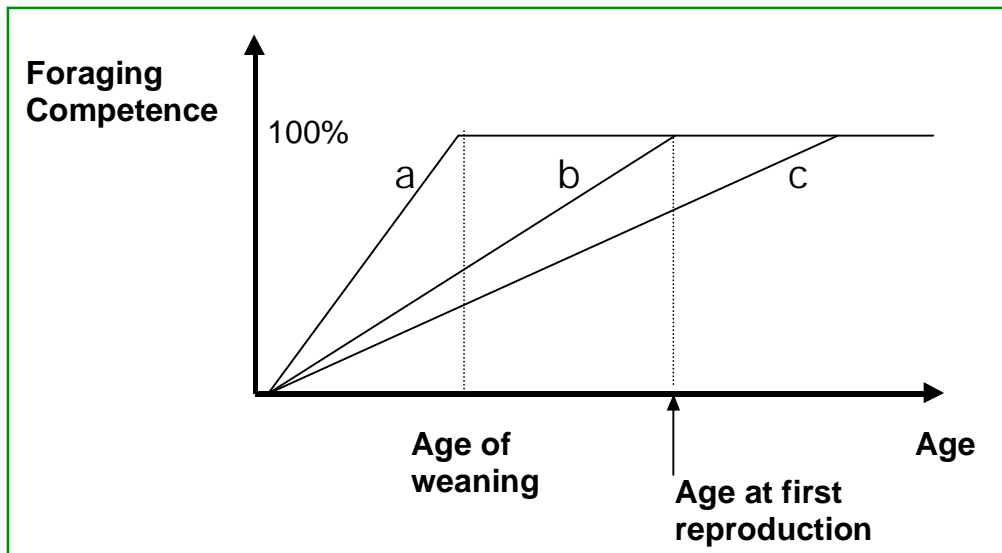
Fig. 2:
-   a) rejects the Needing-to-learn hypothesis, if foraging competence is reached well before age of first reproduction.
-   b) or c) support the Needing-to-learn hypothesis, if foraging competence is reached around or after sexual maturity (van Schaik pers. com.)

It is unlikely that all aspects of ecological competence are equally effected by age. Nonetheless, if all three components of foraging competence peak well before sexual maturity is reached, the Needing-to-learn hypothesis can be rejected. The Needing-to-learn hypothesis is also not supported if mixed results are obtained, especially if the more slowly maturing skills involve foods that require adult-level strength to harvest. However, mixed outcomes may still support the hypothesis if a relatively late emergence of food selection competence and foraging efficiency concern major staple foods, critical fallback foods (as shown by phenological information on food scarcity), or foods with unusual nutrient density (as shown by nutrient density). In that case, overall range-use competence should also emerge late in relation to reaching sexual maturity.

An alternative hypothesis to explain delayed foraging competence with, is the Needing-to-grow-strong hypothesis.

1.4. Alternative: Needing-to-grow-strong hypothesis

The Needing-to-grow-strong hypothesis suggests that the delay in foraging competence is due to infants' small body sizes, rather than incomplete skills. Infants being small, thus less strong are not able to forage competently because they can't open hard foods or pull out plants which are anchored in a substrate, thus the hypothesis is correlated with body size and growth.

Although, delayed foraging competences due to the Needing-to-grow-strong hypothesis doesn't exclude simultaneously learning, while waiting to grow up. Even if a weak individual can't forage at an adult level it might learn, for example through observations and use the skills only when adult body size is reached.

The needing-to-grow-strong hypothesis can be estimated by taking hardness measurements of food items and measurements of the strength needed to pull food items out of a substrate.

Hardness depends on the amount of force required to break the sample at first bite with the front teeth, mostly the canines (Vincent et al. 2002). Fruits can be grouped into hard or soft based on the structural properties of the outer skin. Some are encased in thin exocarps and contain soft flesh, whereas others exhibit more durable coverings and relatively harder contents (Dumont 1999).

Hardness may have an important impact on food selection. A lot of individual strength is required to bite a hard food open or to pull a well-fixed plant out of a substrate. In comparison, foods which are soft and easy to-pull-out can be harvested with little strength. One hypothesis will test whether young infants with small body size are strong enough or not to open hard food items.

If the hardness of edible food items plays a role in food selection in younger and thus smaller and/or weaker individuals, then it seems likely that younger individuals are not yet able to forage on hard foods (Fig. 3). Age and hardness of the food items should be positively correlated. This correlation can be directly tested, by plotting hardness against age.
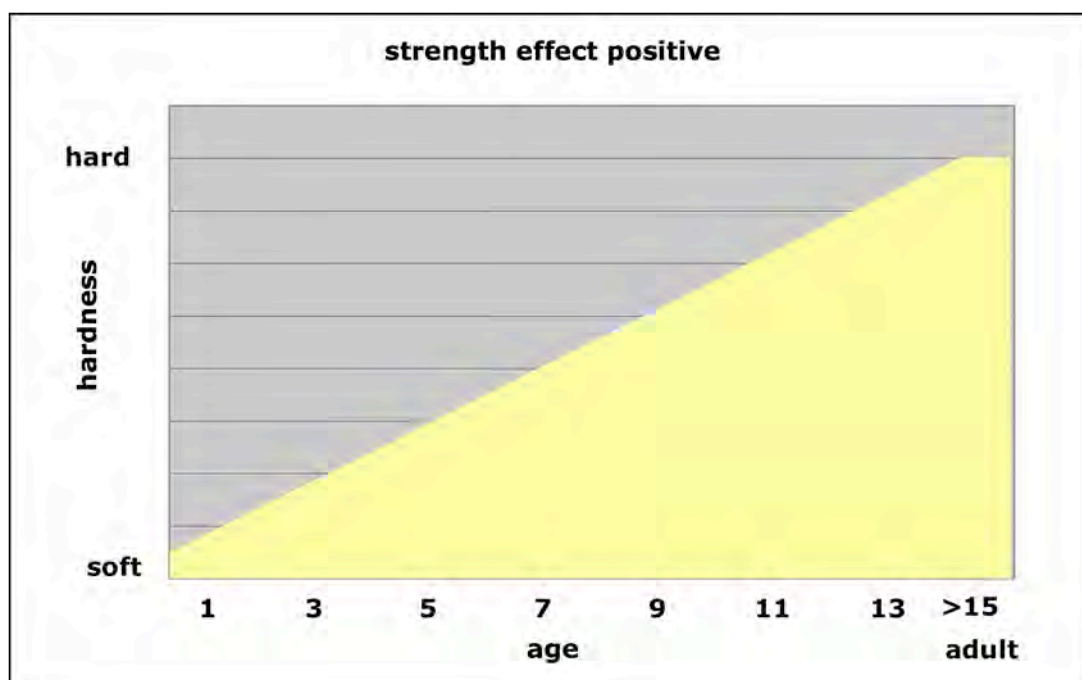

Fig.3: If all data-points are located in the yellow triangular area, this would mean that young infants don't feed on hard food yet, due to lack of strength.

Further, in the case that infants already eat some hard foods, we can still estimate a strength effect by looking at the infant's time spent on hard food to that spent on soft foods relative to their mother's time spent on hard and soft foods. We expect that infants spend more time on soft food items relative to their mothers.

Another estimate can be done by looking at the infants' selection of food, while feeding independently. We expect that infants select rather soft foods if a strength effect is present.

1.5. Significance for understanding human origins

Human life history shows some features that are slowed-down relative to those of great apes, later age at first reproduction and longer life span (Table 1). It also shows unusual features like a faster inter-birth interval, weaning age of the immature is about 2.5 years (Kennedy 2005), and menopause in females (Hawkes et al. 1998). Does Charnov's general life history hypothesis or a variant of the Needing-To-Learn hypothesis best explain human life history? The Adult Mortality model simply notes, as mentioned before, that the enormous increase in human life expectancy caused the lengthening of the pre-reproductive period (Blurton-Jones et al. 1999; Hawkes et al. 1998).

The competing model is the "Embodied Capital" hypothesis (Kaplan et al. 2000), which is similar to the Needing-to-Learn Hypothesis. It assumes that foraging yields in humans increase until well into adulthood. Immatures are weaned clearly before they are able to find and process sufficient food, this stage is subsidized by adults.

If the Needing-to-learn hypothesis is supported for orangutans, whose foraging behaviour requires highly developed skills, it is possibly that early hominins' period of immaturity was set by the complexity of its foraging niche. When the niches became even more skill intensive for the subsequent hominins, their maturity had to be delayed.

By contrast, if the Needing-to-learn hypothesis is rejected for orangutans, there would have been abundant room for increasing skill intensity of foraging before requiring greater delays in maturity, and adult subsidies are more likely to have different origins and functions. That outcome would increase the plausibility of the more demographic models, suggesting that the driving factor was a reduction in adult mortality, perhaps brought about by increased technological sophistication and thus avoidance of predation and starvation.

1.6. This study was designed to test the following hypotheses:

Hypothesis 1: Lack of strength rather than lack of skill is the reason that immatures don't forage at adult levels. If there is a strength effect concerning foraging in immature orangutans, we expect that:
- Hard foods are not eaten by young infants but by older individuals.
- If young immatures eat some hard foods, then they feed for a shorter time on hard foods than on soft foods.
- While feeding independently, infants select soft foods rather than hard foods.

Hypothesis 2: The food selection competence is fully acquired around the age of first reproduction, thus we expect that:
- The similarity of diet for mother-infant pairs increases with age.

- The number of events where the infant feeds independently or before the mother increases with age.

For the Needing-to-learn hypothesis the results would depend on how difficult to process food items are

For the Needing-to-grow strong hypothesis the results would depend on how hard the food items are.

Hypothesis 3: The foraging efficiency can only be estimated for the Needing-to-learn hypothesis and is fully acquired around the age of first reproduction, thus we expect that:

- The similarity of feeding techniques between mother and infant increases with the infant's age and is fully acquired at the age of first reproduction.
- Feeding rates increase with age and reach stable adult value at the age of first reproduction.

The range-use hypothesis can only be estimated by the observations of weaned immatures, because infants always stay in close association to their mothers (van Noordwijk & van Schaik 2005). But in this study we focused mainly on mother-infant pairs, therefore didn't test for the range-use competence.

2. Materials and Methods

2.1. Study site

Data collection took place from December 2004 until July 2005 at the Tuanan study site (2° 09' S; 114° 26' E) inside the Mawas Reserve in central Kalimantan; Borneo, Indonesia. The study started in the wet season and ended at the beginning of the dry season. There was high fruit abundance during the whole research period of the eight months. Various forest types, mainly arranged along a gradient perpendicular to the Kapuas river are present, from white sand or seasonal swamp on mineral soils near the river to forests on increasingly thick peat farther inland. Most of the area has been subject to formal and informal selective logging.

Most of the orangutans are habituated as they have been followed since mid 2003. The study area is divided into grid cells by trails at ca 200 m distance. Some trails are provided with a boardwalk to quickly reach the morning nests, which can be located anywhere from near the camp to distances of over 2 km.

The area supports an average orangutan density of 4.25 ind/km^2 (van Schaik et al. 2005). Thirty-five individuals were identified and catalogued.

Photo 1: View of the Camp and the 726 ha study area (right), close to a trail (left) leading to the Kapuas river.

2.2. Orangutans

The study focused above all on mother-infant pairs, but data have also been collected for independent immatures and adult individuals. Subjects were four fully habituated mother-infants pairs and 3 independent juveniles, of which one female showed highly proceptive sexual behaviour (Table 2). Un-flanged and flanged males were also taken into consideration in order to analyse sex differences.

Mother	Immature	Sexe	Immatures' birthdate
Jinak	Jerry	M	I 2003
Sumi	Susi	F	II 2002
Mindy	Milo	F	II 2001
Kerry	Kondor	F	II 1999
?	Lolo	F	II 1998
?	Nanio	M	I 1997
?	Juni	F	II 1994

Table 2: Overview of main focal animals of this study. I 2003 means first half of the year, whereas II means second half of the year. These are estimated ages.

Picture presentation of the focal animals:

Photo 2: Jinak with her son Jerry, who is the youngest of all focal animals.

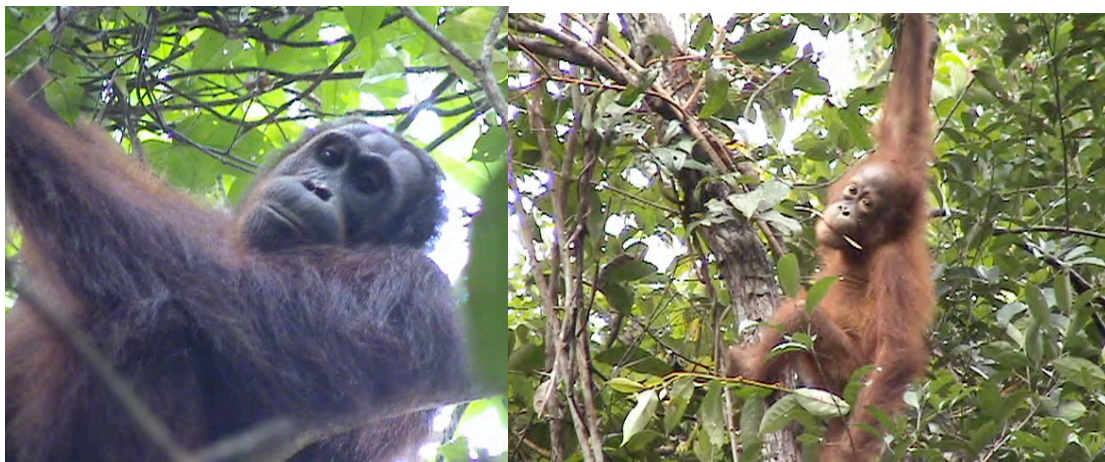Photo 3: Sumi with her daughter Susi.

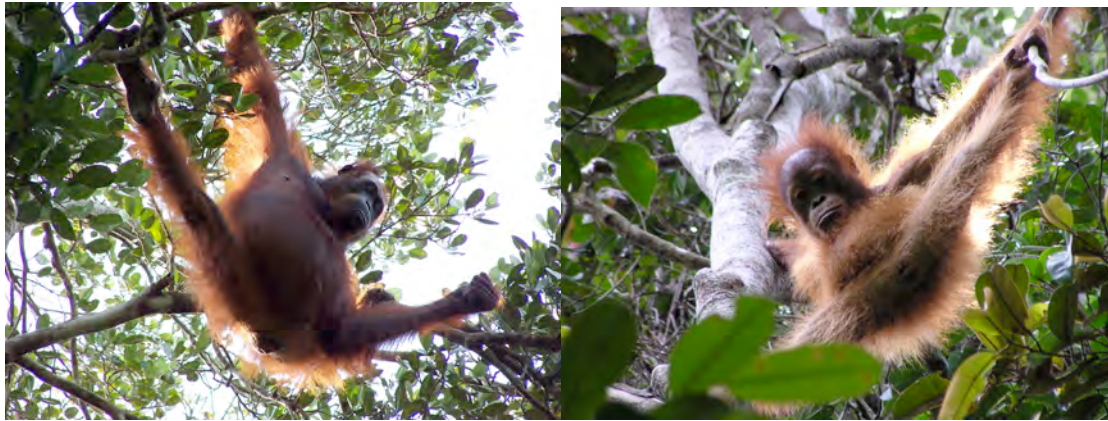Photo 4: Mindy with her daughter Milo.

Photo 5: Kerry and her daughter Kondor. She was the oldest dependent infant and got weaned during the data collection.

Photo 6: Lolo an independent juvenile female. She was estimated to be only one year older than Kondor, but lives alone. She was never seen in association with her mother.
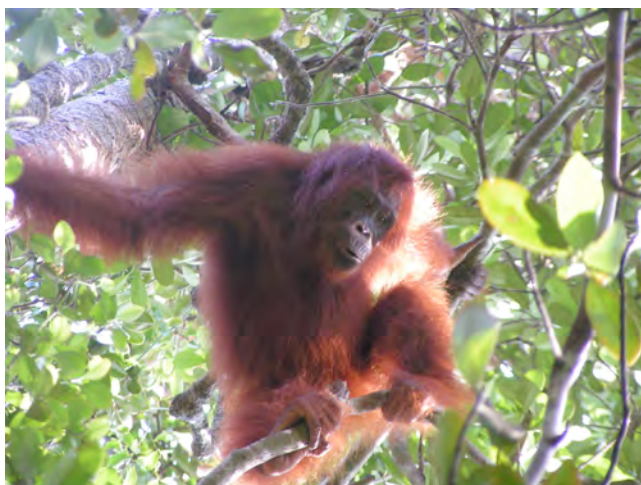

Photo 7: Nanio an independent juvenile male.

Photo 8: Juni was a nulliparous female. (She gave birth on 10.2.2006 to her first offspring). She showed highly proceptive sexual behaviour during the data collection period.

The estimates of immatures' ages were done by Carel van Schaik and Serge Which, when they first encountered the individuals in 2003. Both are experienced researchers of Sumatran orangutans. Some adjustments were made to these age estimates with the help of picture comparisons and facial morphology (cf. Kuze et al. 2005). We analysed infant size relative to mother size in old and recent photographs, and compared this relative size among infants (see appendix 7.1). For example, the size of Kondor in 2003 was similar to that of Milo in 2005, which leads to the conclusion that they are separated by two years. In doing so, we assume that infants are on approximately similar growth trajectories. This assumption may be incorrect for Susi who seemed to have more or less the same size as Jerry, but seemed to be retarded in her growth due to her mother's bad condition. However, she was more advanced in locomotory and feeding skills when first encountered in 2003 than Jerry at the same time and therefore her estimated age was six months older than Jerry's.

Kondor was last seen being nursed by her mother in January 2005 and considered weaned from the age of 5.5 years. Furthermore, she started to sleep more often in her self-built evening nest, contrary to sharing the nest of her mother. Her mother Kerry showed since January 2005 a highly sexual activity and often copulated with males, whereas females with dependent offspring don't show any sexual activity. Thus it is possible that Bornean orangutans get weaned earlier than Sumatran orangutans. (Bornean 5-6 years, Sumatran 7-8 years)

2.3. Methods

The orangutans were studied using focal animal sampling (Martin & Bateson 1993). Firstly, individuals had to be identified and if they were seen for the first time, they were described and photographed. Information on activities, height, food item, patch residence times, range-use, mother-infant distances, general associations (parties <50m) distance and social behaviour

were recorded every two minutes during whole day nest-to-nest follows using established methods (van Schaik 1999, see website: www.aim.unizh.ch/orangutannetwork). These methods are standardized across sites, allowing comparisons. The plant species identifications were provided by staff of the station in the Wanariset herbarium near Balikpapan, East Kalimantan.

In addition to the standard Focal sheet, feeding techniques were described with the terminology of Russon (1998) as well as video-taped. Feeding rates (item/sec or sec/item method) of food items were measured (van Schaik & van Noordwijk 1988: Knott 1998) either directly in the field or from video tapes. Feeding rates were estimated by recording the handling time between picking up a fruit until picking up a subsequent fruit (van Schaik & Knott, 2001).

Data on active sharing, where an individual voluntarily donates food to another begging individual (King 1991), which seems to be rare among primates (Altman 1980), and data of passive sharing, which is defined as tolerated theft (Brown et al. 2004; Feistner 1989), between mother infant pairs or party members were collected. Distances for party members were recorded in distance classes. A party started if an individual approached another orangutan within 50 m. All instances of approach and retreat for 10 m and 2m between two orangutans were recorded. A party ended when the distances between the individuals in association exceeded 50 m. Moreover, the order, in which mother and infant started to feed in a feeding patch were carefully noted. These data, together with time budgets, allow estimation of the various measures of relative foraging competence.

Hardness of food items

All food items ever seen ingested but also those food items avoided were collected, identified and photographed. The focus of this study is on one physical property of food items: The hardness (= the resistance of the surface of a material to permanent deformation). Foods that have relative resistant surfaces are hard; solids having surfaces that deform easily are soft (Strait 1997). Three Methods were used to estimate the hardness of the different food items.

The first method involved manual testing of food items by myself. The categories range from very soft to very hard food items. Very soft can be squeezed with two fingers, soft can be opened with one hand, moderately hard can be opened with two hands, hard can be opened with teeth, very hard can only be opened with a tool. For food items, which were pulled out of a substrate we used the following categories: Easy when the item can be pulled out with one hand; Moderately difficult when the item needs two hand with force and difficult when the item needs more than one person or a tool to be pulled out of a substrate.

The second method of assigning a hardness class was the use of a Hardness tester tool, a Durometer, usually used for hard rubber, named Shore-D Durometer Model HD3000 from Hildebrandt.

The Durometer was held in a vertical position above the food item to be tested for pressure resistance. Then it was pressed down without shock until the entire presser foot (∅ 18mm) was in full contact with the specimen with the indentor passed through the outer skin. The dial hand showed the actual Shore hardness. The drag pointer gave the maximum reading, ranging between 0 and 100, which were converted into mN with help of a converter list (e.g 10 = 4450mN).
The indentor diameter was 0.79 mm. Each food item was measured 50 times, that is 5 measurements on 10 food items.

indentor   presser foot

Finally, a self-built tool was used to measure hardness of food items. It was a redesigned spring-scale. A thicker tip (∅ 2.5 mm) was pushed into the outer layer of a fruit. A special marker around the scale indicated how many grams were needed to permeate the fruit. It ranged between 0 and 10 kg. Each species was measured ten times.
With both tools, I only tested the outer layer of food items, because I was only interested in the hardness of the skin, which had to be opened and removed by orangutans for most of the fruits. Leaves or flowers were not tested, as they were soft and easy to process anyway. Bark was difficult to test with the tool as well.

marker to indicate the force needed
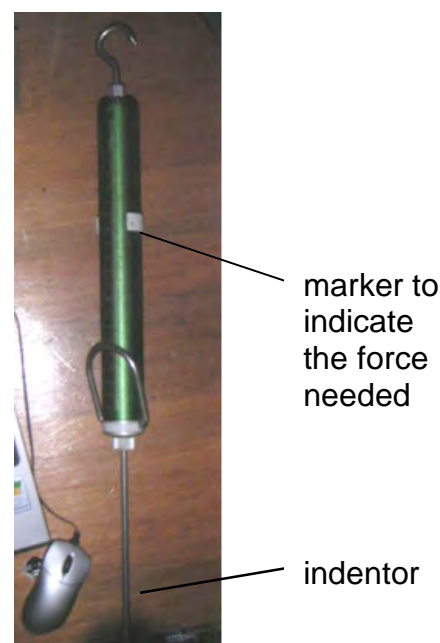
indentor

2.4. Statistical analyses

The results refer to data collection on 122 days of nest-to-nest follows with a total amount of 1209 hours of observations on mother-infant pairs. Another 28 days with 213 hours of observation were made on independent immatures. This data collection was done by three observers in the period from December 2004-July 2005 (see below).

As in other studies of great ape development, we had low statistical power, due to relatively small numbers of individuals, in this case four mother-infant pairs.

A Spearman correlation was done to test how similar both tool methods were. To simplify, hardness measures were classified in 9 categories. The results on hardness relative to the different categories were analysed with the help of Spearman's rank correlations.

Most of the data-points represent whole days. Feeding rates represent the average over the whole research period, without respect to possible change with age during that period. All analyses done on feeding rates are very preliminary analyses, as the data on feeding rates were scarce.

For the comparisons of the immatures with different ages, linear regressions were generated. The dependent immatures were always tested among them or relatively to their mothers. Unfortunately data of independent immatures are scarce, as they weren't encountered often enough to compare their foraging behaviour to the other individuals. Statistical analyses were performed using the software SPSS 12.

Inter-observer reliability

All results of the foraging competence are based on data collected by only three observers from about eighteen. These are data collected by Adrian Jäggi, a student from the University of Zürich and Ganda, a local assistant and of course my own. As we all focused mainly on mother-infant and other immature individuals, we often worked together, thus I could regularly check for the similarity of our data collection. Feeding rates were difficult to measure, as orangutans feed high up in trees and are often hidden behind dense foliage, thus data were scarce. The hardness measurements were only done by myself.

3. Results

The results of the analyses for the strength effect, the food selection competence and the foraging efficiency are presented below.

3.1. Hardness of food – Can the infants eat it?

The hardness results can be used to estimate the strength effect. All hardness measurements were done by myself, thus no inter-observer reliability questions came up.

3.1.1. Selection of the best method to measure the hardness of foods

Firstly, I had to select the method, which was best for further analyses on food item hardnesses. The manual method was ignored, because it was too imprecise (see methods).
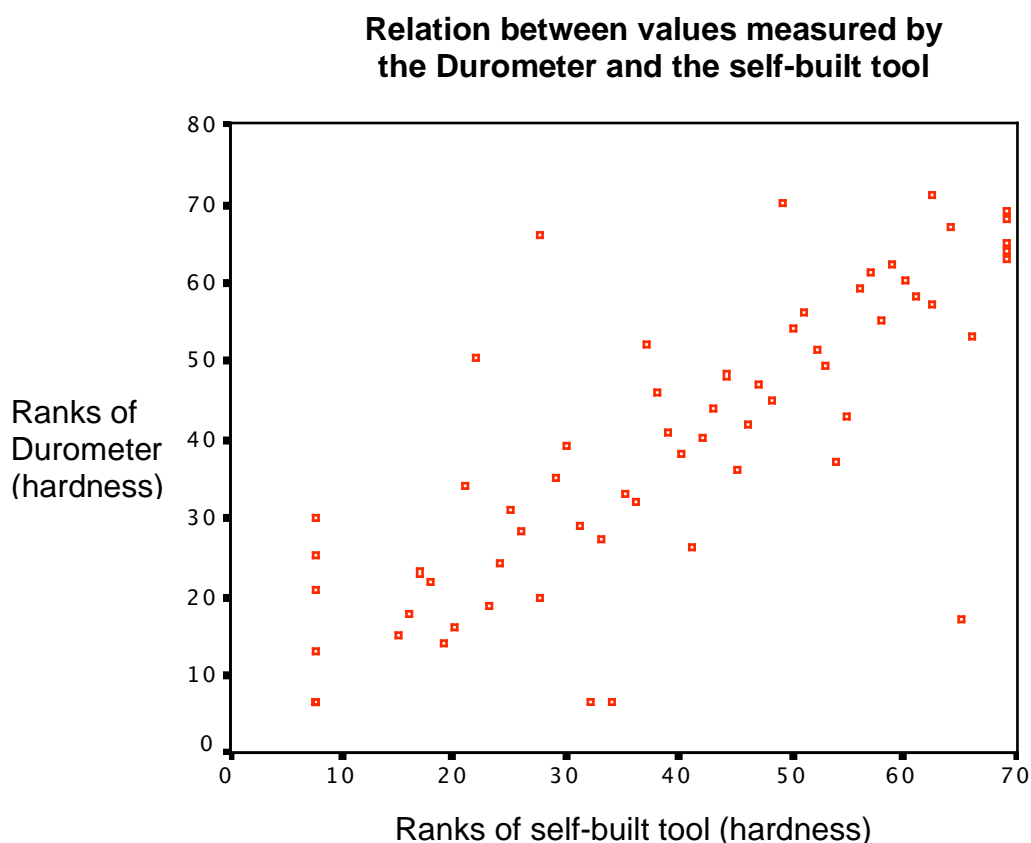
Relation between values measured by the Durometer and the self-built tool

Fig.4: Rank of Durometer against rank of self-built tool. Spearman's correlation, coeff of 0.839, p<0.01, N=71, 2-tailed.

The measurements taken with both methods are positively correlated. Since the self-built tool's indentor has a diameter of 2.5 mm, which is more similar to an orangutan's tooth than the tiny tip of the Durometer, further analyses are based on the measurements done with the self-built tool.

Hardness differences in orangutans' food items

There were large hardness differences among the various food items. The following graph shows the box-plots of the hardness of all measured food items. We see a higher variation for harder food items than for softer ones (Fig. 5).

**Box-plots, which represent the
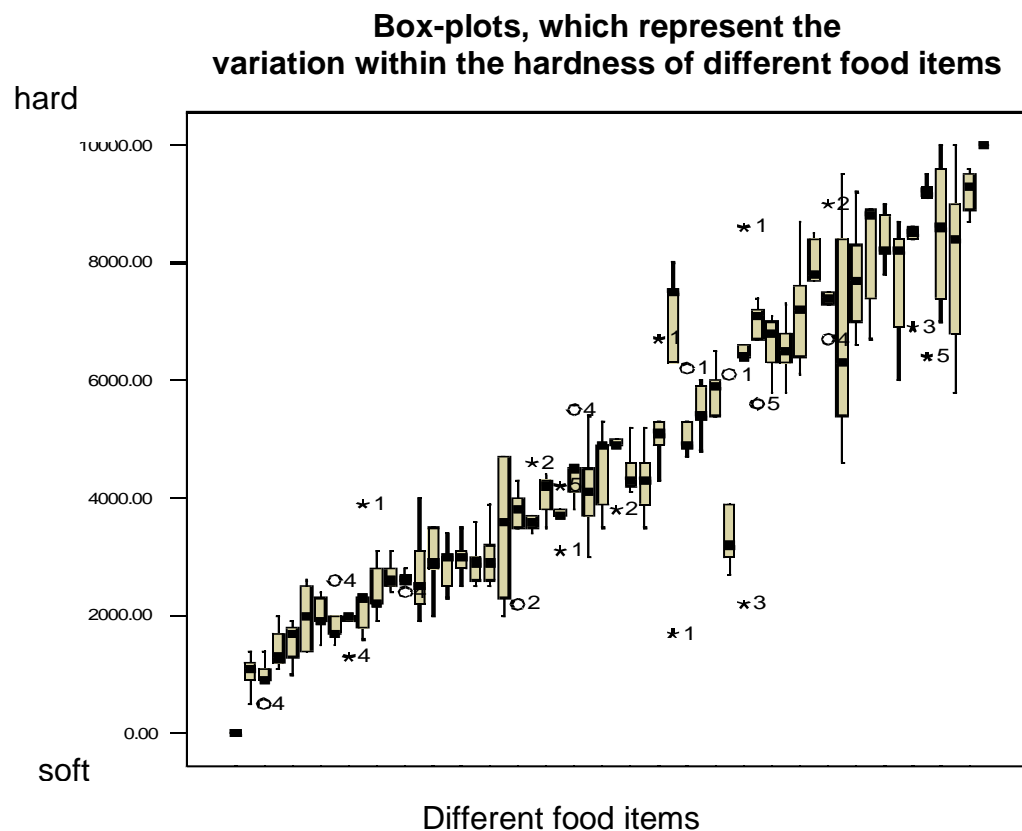variation within the hardness of different food items**

Fig.5: Boxplots of the hardness, measured with the self-built tool for different food items. x-axis: different food items, mostly fruits ranked by average hardness values; y-axis: hardness in grams taken by the self-build tool.
For each food item ten measurements were taken. The numbers in the plot refer to the outliers. (e.g. 4 means that the fourth measurement was an outlier.)

The different food items include fruits (FR), young leaves (YL), mature leaves (LV), flowers (FL), insects (INS), pith and other vegetations (VEG), bark including cambium (BK) and other stuff, among other soil, charcoal, epiphyte (OTH).

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As I was interested in the effects of hardness on food selection, food items were classified into different categories of hardness to be used for further analyses. Since the hardness of flowers, leaves and barks could not be measured with one of the tools, I generated nine hardness categories. Whereby, flowers and leaves were put into the "softest category (cat.1) and barks into the hardest one (cat.9). In overall 126 food items were included into the nine different hardness categories. It was possible for one fruit species to be put into two different hardness categories, e.g. the ripe fruits in a softer one and the unripe fruits in a harder one (see appendix 7.2. table 4). The categories range from 1 (very soft) to 9 (very hard) (Fig.6). All these categories are significantly different from each other (p<0.05; Wilcoxon).
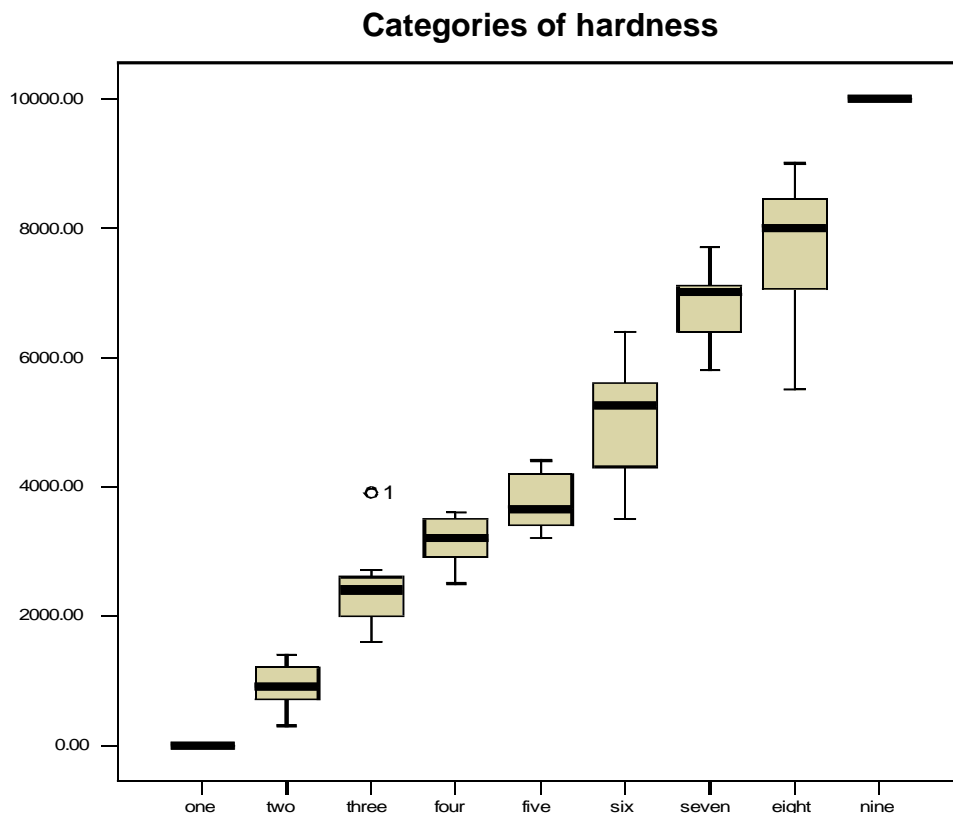
Categories of hardness

Fig.6: The different box-plots display the variation within each hardness category. Number 1 above the boxplot 3 shows a single outlier measurement of one fruit.

3.1.2. Are hard foods avoided by infants?

There is no evidence that food items were avoided due to hardness. For instance, the diet of Jerry, the youngest infant, included items from the hardest to the softest categories. All infants foraged on food items from almost all hardness categories (Fig.7).
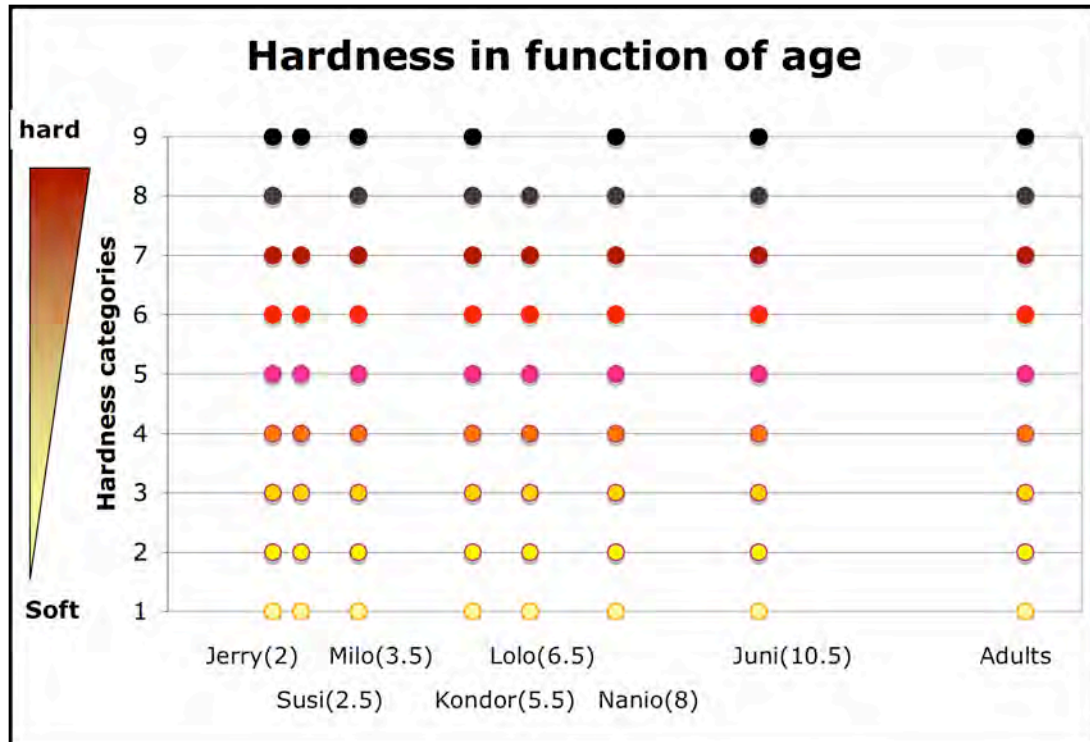

Fig.7: x-axis: Immatures with their estimated ages. y-axis: hardness categories ranging from 1 (soft) to 9 (hard). Data points represent food items in this hardness category eaten by the individuals. Adult males and females are all included in one class.

3.1.3. Do infants feed less long on hard foods compared to their mothers?

Since all infants fed on hard food items, we can test for the hypothesis that infants feed less long on hard food items than on soft food items compared to their mothers.

The time that all infants spent on food items of different hardness categories were compared to their mothers' time spent on these food items. We could see that the mothers' and infants' time spent on food items of the different hardness classes are alike (Fig. 8).
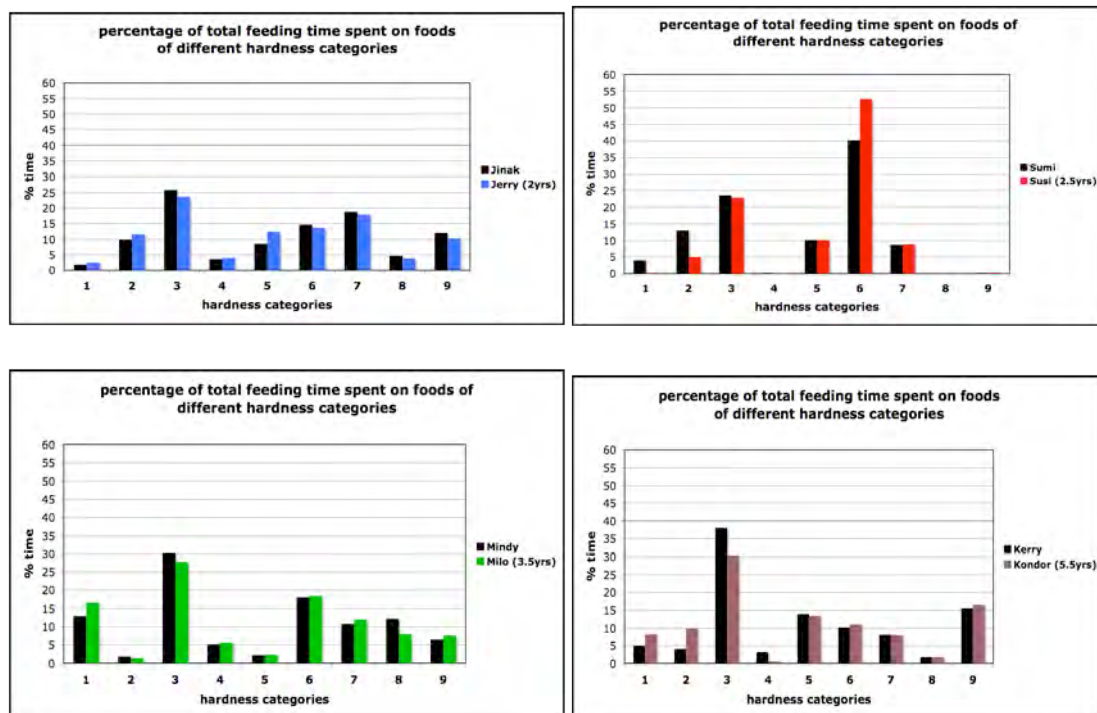
Fig. 8: Percentages of total feeding time spent on food items of each hardness category for all four infants compared to their relative mothers.

Jerry and Milo show a close similarity to their relative mothers, whereas Susi seems to feed more on category 6 and less on soft foods than her mother. Kondor, the oldest infant seems to feed more on soft foods than her mother does, but she also spends as much time as her mum on hard foods.

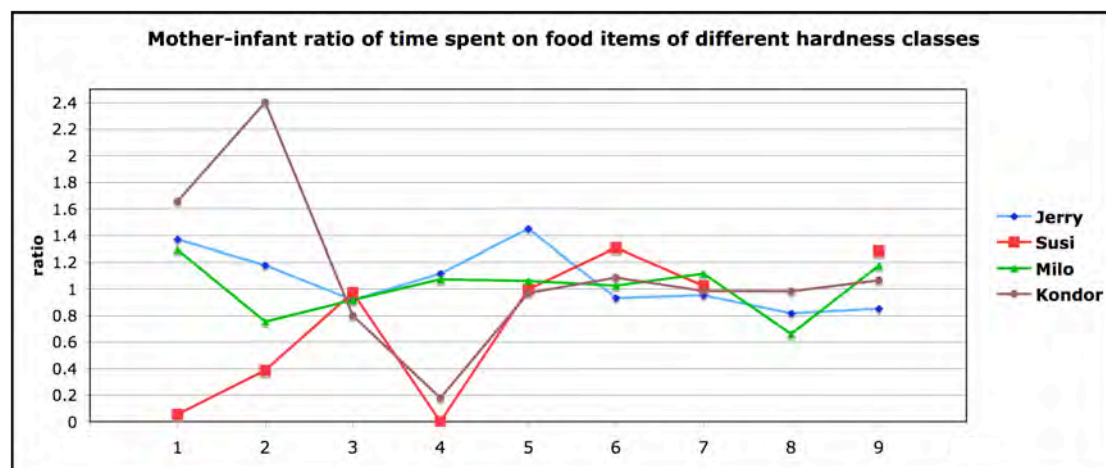For a better overview the ratio mother-infant time was calculated and plotted (Fig. 9).

Fig. 9: Ratio of time spent on food items of different hardness categories between mothers and infants

Jerry shows a significant decrease (p=0.05; Spearman's rho rank correlation) towards feeding more on soft than hard food items compared to his mother, but the data-points range very closely around 1, thus no real tendency towards a strength effect can be seen. In contrast, there is a positive correlation between hardness and time (p=0.021) for Susi, which means that

Susi showed a preference for harder foods compared to her mother. This surprising result can be explained by the fact that Sumi, her mother was missing the two lower canines, and therefore probably avoided hard foods. No correlation between hardness and time spent on foods of different hardnesses was found for Milo (p=0.966) or Kondor (p=0.637).

It can be concluded that infants did not spend more time on soft foods than on hard foods.

3.1.4. Independent foraging

For foods eaten independently by infants (i.e. not in close proximity with the mother and usually on a different tree or feeding close to the mother while she was not feeding at all), a different constellation of food items is recognized.
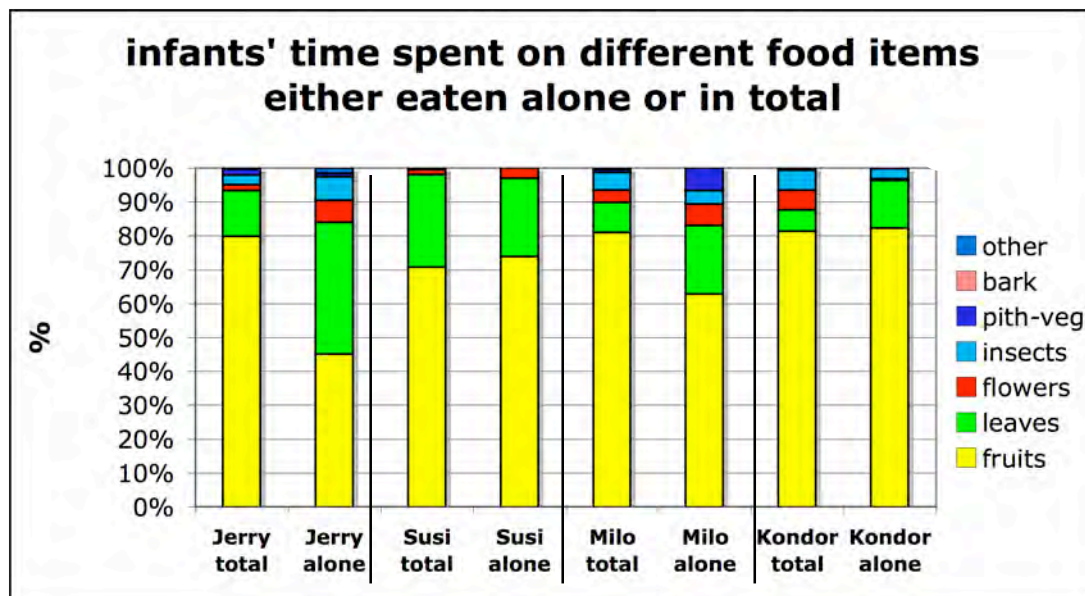

Fig.10: This graph shows the percentage of time spent on each food item. Alone means that the immature ate food while mom was not in close proximity or was not eating. Total refers to all occasions of the immature's feeding irrespective of mother's activity (cf. Fig. 15).

Fig. 10 shows that Jerry and Milo fed less on fruits than on leaves or flowers, when feeding independently, which would lead to the assumption that infants preferred soft food items like leaves or flowers.

The percentage of time infants spent on foods of different hardness categories when feeding independently was compared to the percentage of time they spent on these foods of different hardnesses when feeding together with the mother (Fig. 11).
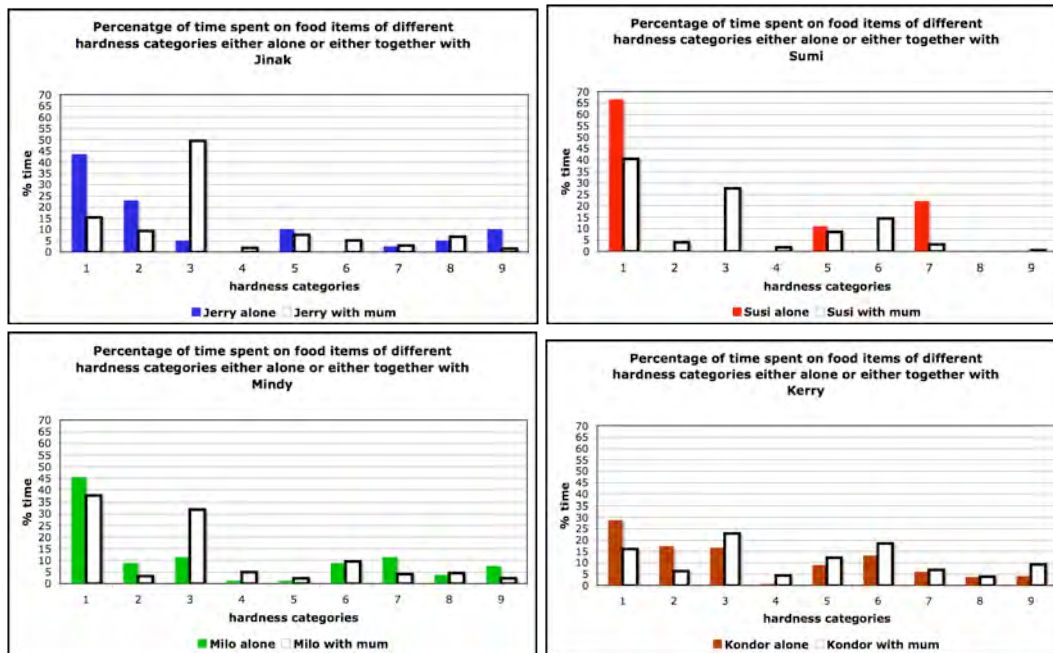
Fig. 11: Comparisons of percentage of time when infants are feeding alone and feeding with mother.

For a better overview a ratio was calculated, i.e. the percentage of time spent on food of different hardness classes when feeding alone was divided by the percentage of time spent on these foods when feeding together with the mother (Fig. 12).
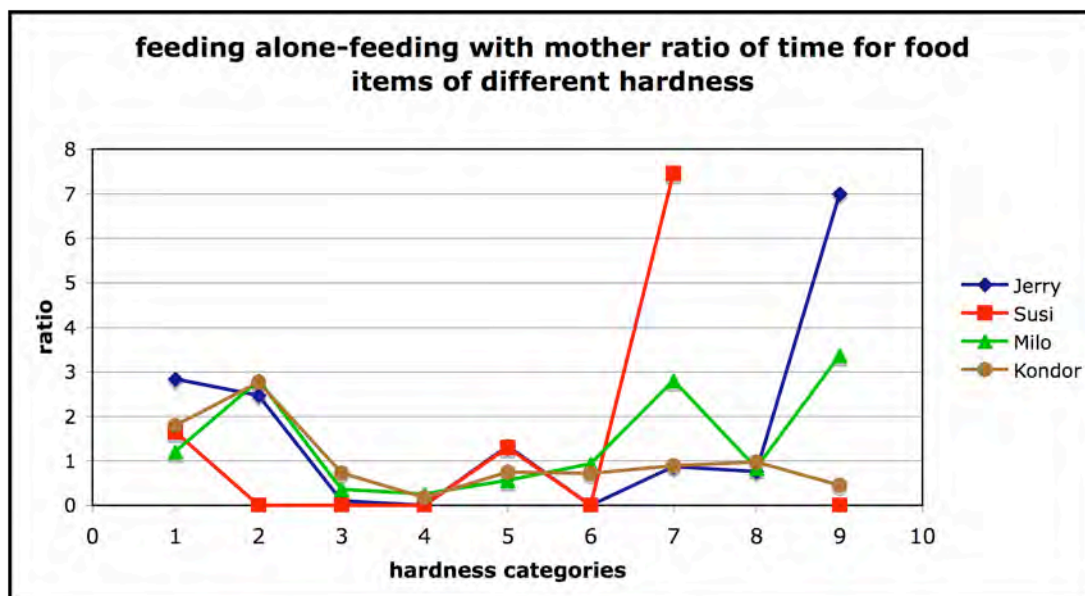

Fig. 12: Ratio alone and with mother feeding time in function of the hardness categories.

The results do not show any trend for infants selecting preferentially soft food items when feeding independently. (Spearman's rank correlation: Jerry 0.966, Susi 0.846, Milo 0.472 and Kondor 0.286). This might suggest that the infants did not know where the good feeding patches were located.

3.2. Food selection competence – Do the infants know what to eat?

3.2.1. Percentage of time feeding

Fig. 13 displays the average percentage of time spent on feeding activities for all infants, mothers and weaned immatures, as well as one unflanged and one flanged male. We can see that that the average time spent on foraging by adults ranges between 50%-65% of their daily activity budget, and that independent immatures already reached the adult feeding time range.
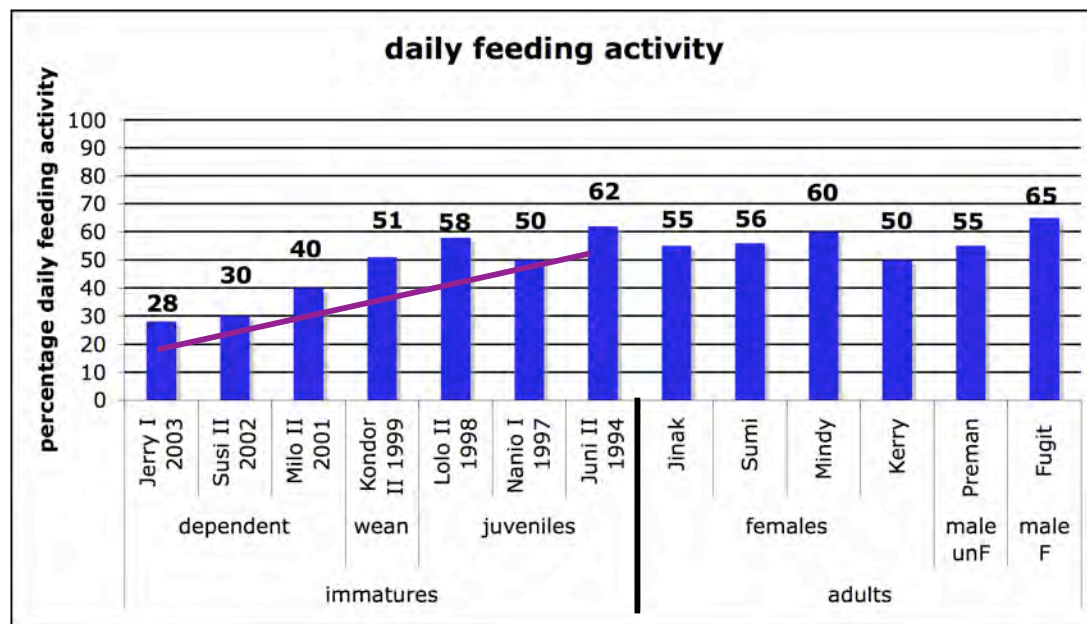

Fig.13: The graph represents the percentage of time the individuals spent foraging. Percentages are based on total daily activity recorded. Feeding while clinging to the mother and nursing were included in the infants daily feeding time.

Moreover there is a significant increase over age for all immatures, from Jerry to Juni (line, p=0.004). In other words, as infants grow older they spend more time on feeding.

Infants' daily feeding time compared to that of their mothers'

We can compare their feeding time with that of their mothers' (Fig.14). The infant Kondor, who was weaned during the data collection period, reached 100% of her mothers feeding time. The youngest infant Jerry already reached the 52% mark of his mother's daily feeding activity by the age of two.
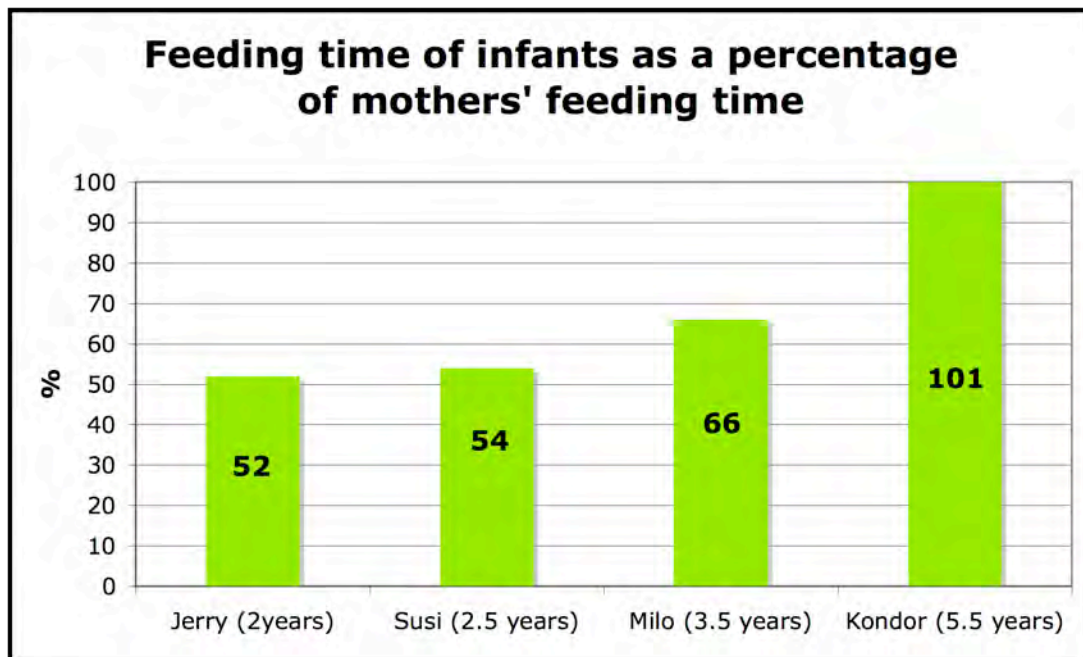
Fig.14: Daily feeding activity of infants compared to that of their mothers'

3.2.2. Similarity of diet
Similarity of time spent on different food items between mothers and infants

Another key aspect to test for the food selection competence concerns the similarity of mother-infants time spent on different food items. The result (Fig.15) shows a higher similarity in time spent on different food items *within* mother-infant pairs than *among* mother-infant pairs.
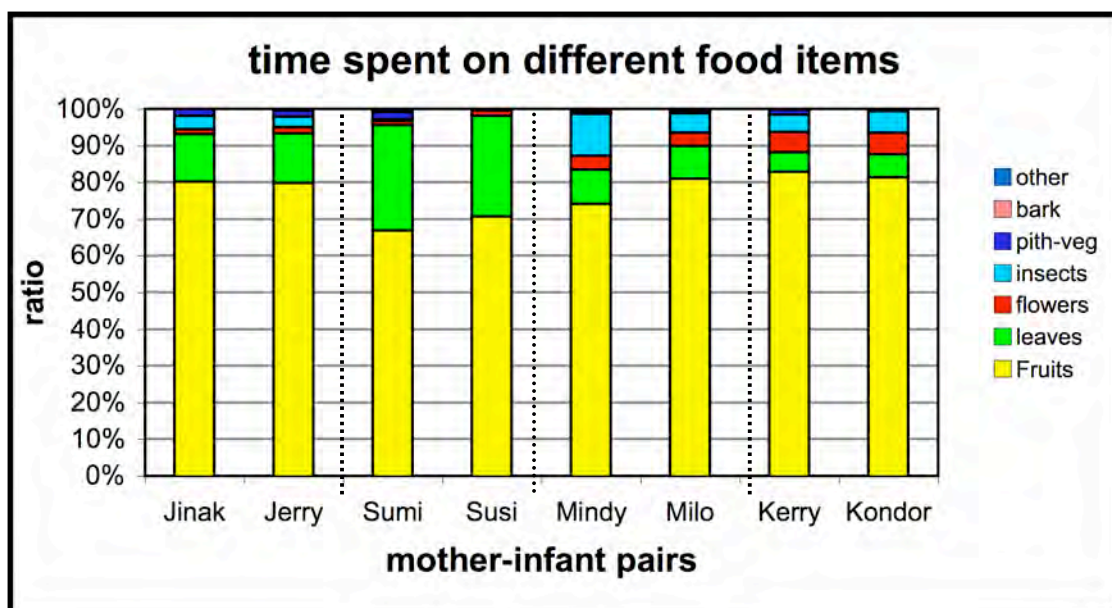

Fig.15: Ratio of time spend on different food items for mother-infant pairs
For overview of other immatures, unflanged and flanged males see appendix 7.3
Fig.21.

Similarity of diets between mothers and offspring

Table 3 gives an overview of the number of food items individuals fed on, as well as the amount of food items that were only eaten either by the mother or the infant. The column "both" refers to the amount of food items included in both mother's and infant's diet. The last column represents the overlap in food items eaten by mothers and offspring, expressed as the percentage of infants' total number of food items divided by that of the mother.

Diet variability

	Total number of food items	Either mother or infant	both	Overlap in food items eaten by mothers and offspring
Jinak	64	9	55	
Jerry	56	1	55	86 %
Sumi	55	14	41	
Susi	42	1	41	75 %
Mindy	71	4	67	
Milo	69	2	67	94 %
Kerry	69	1	68	
Kondor	70	2	68	99 %

Table 3: Overview of food items eaten by mother-infant pairs

The data show that there is a high similarity of foods in the diet of mother-infant pairs. For example, around the age of 2 years Jerry was already eating approximately 86% of the food items eaten by his mother (Fig 16). Moreover, Kondor had a 99% overlap with her mother's diet at the age of 5.5 years. These results could even be higher, considering that we only followed the animals ten days in a row and then did not follow them for one month. Consequently, it is likely that during this long absence the infants fed on the food items that were reported as only eaten by the mothers. Taken together, these findings suggest that the diet of orangutans starts in early age to be similar to that of the mothers.
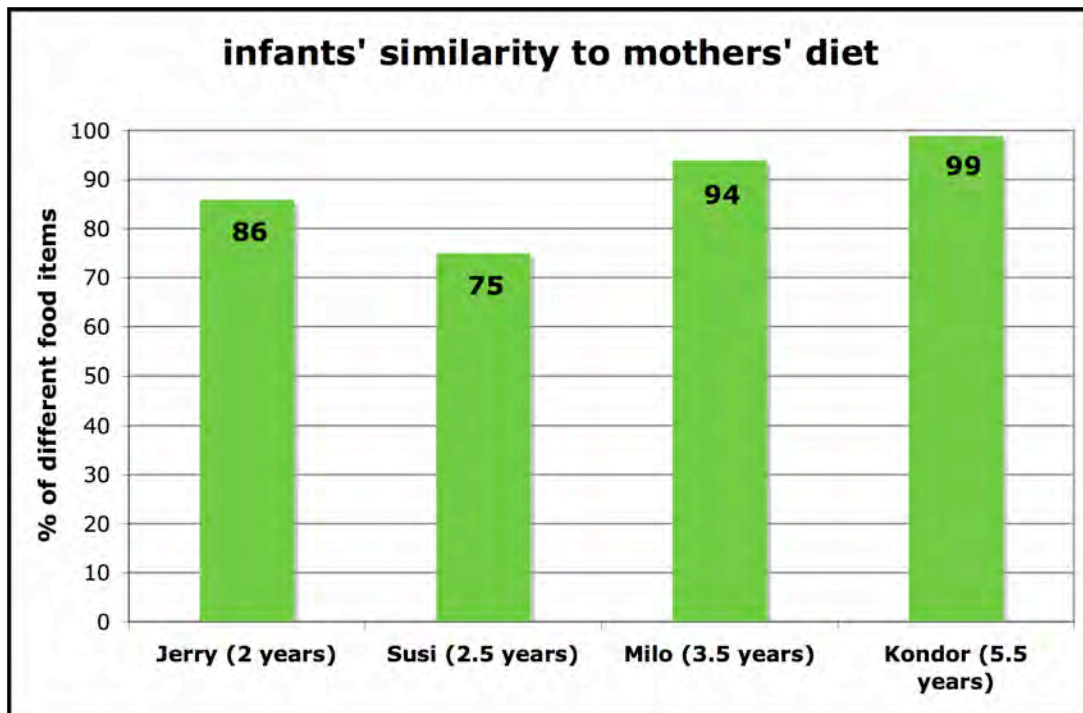
Fig.16: This graph represents the percentage of the number of different food items eaten by infants compared to the number of different food items eaten by their mothers.

3.2.3. Independent food selection

An important aspect to test for the food selection competence is to analyse how often an infant fed independently, including the number of events where an infant started feeding before its mother after both arrived at a feeding patch. Fig.17 represents the number of events where infants fed independently compared to the total number of food patches visited per day.

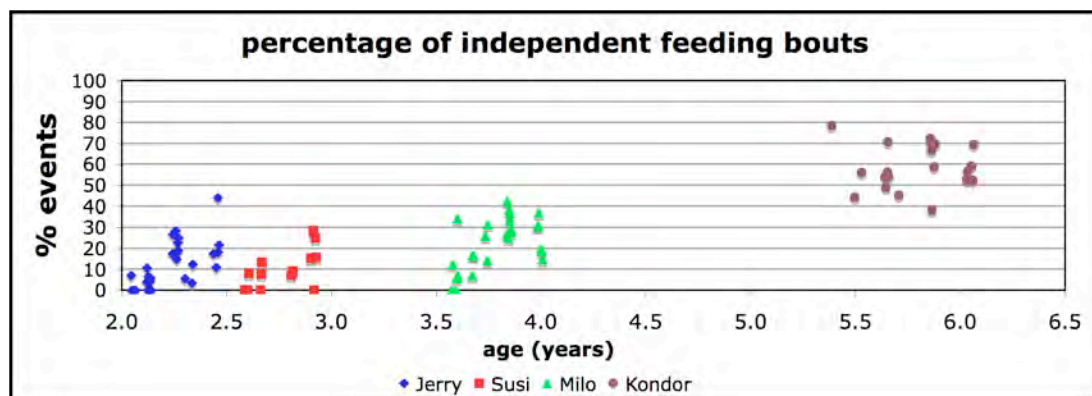Fig.17: The reach of the 100% mark would mean that the infants always feed independently. The data-points represent one day.

The data show that fully dependent infants feed more often independently as they grow up. In fact, the three fully dependent infants, Jerry, Susi and Milo showed a significant increase in independently feeding over time, but still fed more than 60% simultaneously with their relative

mothers. The oldest infant Kondor ate between 40%-70% of all food patches visited on her own and reached stable values.

3.3. Foraging efficiency - how efficient do infants forage?

The results of the foraging efficiency included the analyses of different feeding techniques as well as the feeding rates.

3.3.1. Feeding techniques

No large differences in feeding techniques could be observed among the individuals of the orangutan population at the Tuanan site including mother-infant pairs. All individuals used the same feeding techniques to pick, open or process the same food items. The youngest infants used the same feeding techniques to forage on a food item than their mothers did.

3.3.2. Feeding rates

The results on feeding rates presented here are based on very few samples. Therefore they can only be considered as preliminary results. Infants' feeding rates increase with age, as shown by the following two graphs (Fig. 18&19). Interestingly, among the infants Milo seemed to be slower than the two younger infants.
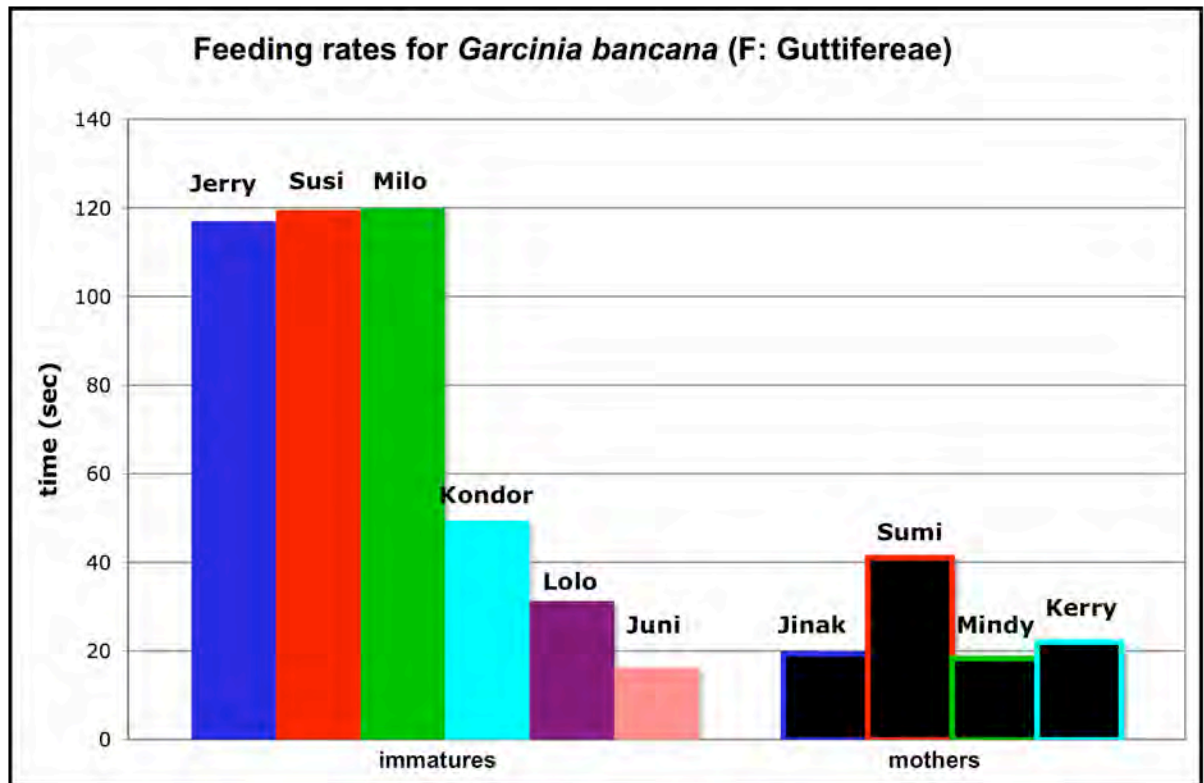
Fig.18: Time (sec) needed on average for all individuals to pick, open, process and eat one fruit of *Garcinia bancana* (local name :Mangis hutan daun kecil). Measurements of feeding rates spanned the time from the moment that they started to look for fruits in a tree to the last seed spat out of a fruit.
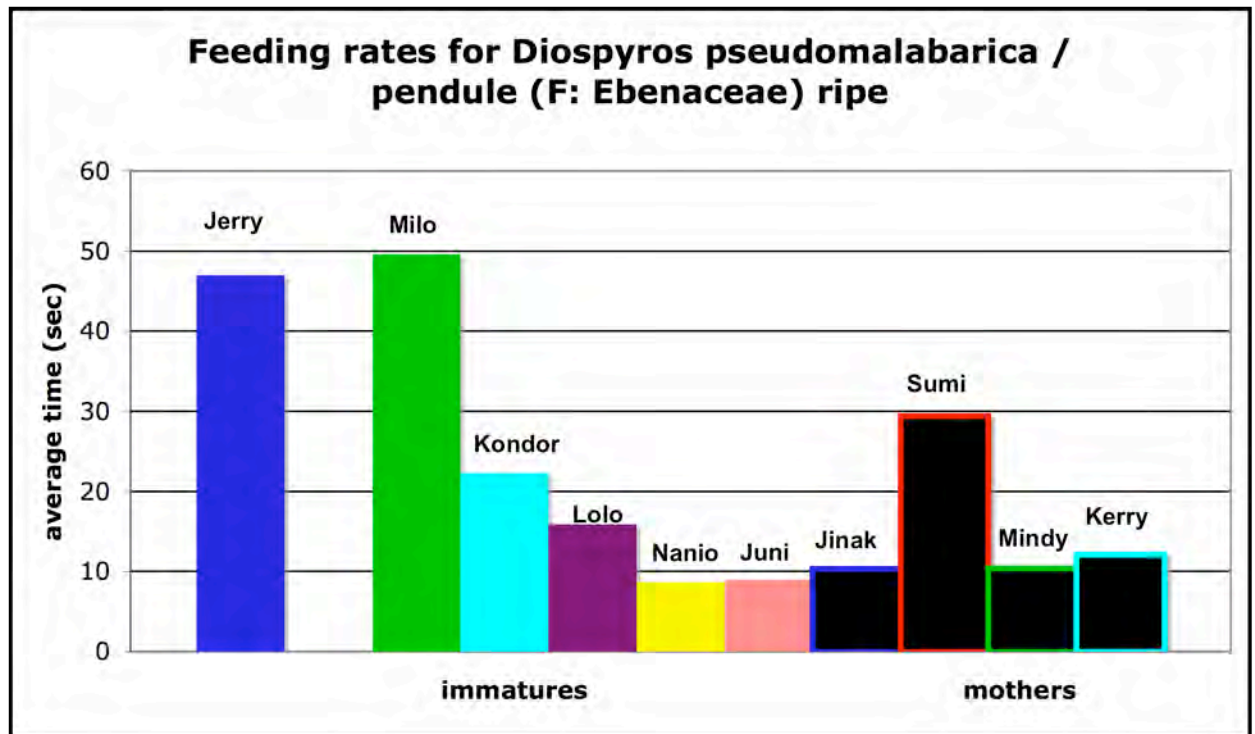
Fig.19: time (sec) needed to pick, open, process and eat one fruit of Diospyros pseudomalabarica /pendule (local name: Tutup Kabali) Unfortunately no feeding rates were taken for Susi on this fruit, which is represented by the gap.

These two figures show that the feeding rates of all mothers were similar. An exception was Sumi, the mother of Susi, who was much slower than other adults. This might once again be related to the fact that Sumi was missing the two lower canines, thus decreasing her feeding rate relative to the other mothers. All infants were much slower than their respective mothers, whereas Kondor was the fastest.

4. Discussion

The discussion will include the three main aspects analysed before, which are the strength effect on foraging behaviour, food selection competence and foraging efficiency. It will also briefly mention what these results mean for human origins and give an overview of the objectives and results.

4.1. Hardness of food

4.1.1. Selection of the best method to measure the hardness of foods

The hardness of food items was assessed using three different methods. The manual method using categories was excluded due to lack of precision. It allowed classification in only four different categories. Nevertheless results of this method enabled double-checking for the main used method. For food items being pulled out of a substrate no differences could be observed. All were located in the "easy category" as all could be pulled out easily with one hand.

Both tool methods showed a highly significant correlation. Since the 2.5 mm thick indentor of the self-built tool, rather resembled an orangutan tooth than did the tiny indentor (ø 0.9) of the Durometer, all analyses were done using results of the self-built tool. Food items showed a high degree of variation in their hardness, particularly in the case of hard foods as opposed to soft foods. Lucas (1979 & Lucas and Luke 1984) placed foods into three texture categories: hard-brittle, tough-and/or-soft and juicy fruits. But my study used more categories and referred to the results from the redesigned hardness tool. Food items were placed into 9 hardness categories ranging from very soft 1 to very hard 9 (for a description of all categories please see appendix 7.2 table 4).

4.1.2. Are hard foods avoided by the infants?

Contrary to our expectations on the effect of strength, which predicted that young infants wouldn't eat hard foods because of lack of strength, all infants, even the youngest and smallest fed on food items of all nine hardness categories. The infants did copy their mothers diet seemingly irrespective of hardness of the food items.

4.1.3. Do infants feed less long on hard foods compared to their mothers?

The hypothesis predicted that the infants would feed less long on hard foods than on soft foods compared to their mothers. The results gave no indication that infants fed for shorter periods of time on hard food items compared to their mothers' feeding time on the same food items. Susi even

showed a significant increase in feeding time for hard food items compared to her mother. This was probably due to her mother missing the two lower canines, and therefore may had avoided hard food items, which led to this unexpected result. Thus, in Susi's case the comparative result may have been due, more to her mother's food choice than her own.

In conclusion, no hardness effect could be detected. The infants did not seem to have problems with hard food items, thus fed as long on hard as on soft foods.

4.1.4. Independent foraging

The expectation, that infants, while eating independently, would rather select soft food than hard food, could be rejected: No significant effect was seen for harder or softer food items.

The results (Fig.10) displayed that the younger infants, while feeding away from their mothers, seemed to feed less on fruits but more on leaves and flowers. This was the case for Jerry and Milo. The likely explanation was the ease in finding and harvesting such foods, rather than softness per se. Most of these foods, like leaves, were widely distributed in the forest. Flowers were known to have an appealing taste but provided less energy than other foods, and were thus preferred by infants but not mothers. Kondor seemed to know already better where to find good fruits, which were important for her diet, as she fed as much alone as together with her mother. Susi fed very little independently. She showed a similar diet alone and in total.
Food items eaten either only by the infant or only by the mother didn't show a difference in their hardness. Both fed on hard and soft foods.

Combining these results, it seems that contrary to expectation, hardness isn't a key aspect concerning foraging development in immature orangutans.

4.2. Food selection competence

Food selection competence requires, as mentioned before, the knowledge about what can be eaten, what food species and which parts of them are edible.

4.2.1. Percentage of time feeding

The duration of an infant's daily feeding activity was less than that of adults, probably due to their smaller body size and dependency on lactation. Kondor, whose estimated date of birth was in the second half of 1999 and was weaned with 5.5 years of age in early 2005, reached the 100% border of her mother Kerry's feeding time per day, although her intake was lower because she ate more slowly, which was also seen for weaned gorillas (Watts and Pusey 1993). Kerry, her mother, spent only 50 % of her daily activity on feeding. This low percentage relative to that of other adults could be explained by her sexual activity during that period and the increased amount of time spent with a male. As we have seen in Fig. 14, e.g. the youngest infant Jerry reached 52% of his mother's daily feeding activity at the age of two years approximately. Dependent infants were smaller in body size and still nursed,

hence they needed less food. They spent a lot of time doing auto-play, either alone or with objects, while the mother was feeding (see appendix 7.4 Fig. 22).

4.2.2. Similarity of diet

An infants' diet matched that of its mother very closely. This was because different foods were not randomly distributed in space and so mother-infant pairs, being close together, were likely to consume the same food items (table 3). The infant Kondor fed a lot on her own but always in association, that is < 50 m away from her mother Kerry. Mother-infant's diets were similar, whereas between mother-infant pairs variation was displayed. For example, Sumi preferred leaves, so her daughter Susi also fed more on leaves than did other infants.

The infants stuck mostly to their mother's diet. As orangutans forage on a wide range of food types, they would be likely to commit errors by selecting toxic food, if they followed a trial-error process. Therefore it is likely that they eat what they see their mother or other orangutan feeding on, to avoid ingesting noxious foods. As an example: All orangutans in Tuanan liked to feed on *Leucomphalos callicarpus* (F: Leguminoseae). They ate leaves, flowers and the seeds of the fruits, when they were unripe. Sumi and Susi were the only known individuals not eating the *Leucomphalos* fruit at all. They were selectively picking the leaves out of the tree full of fruits. It was an easy to harvest and soft fruit. Susi imitated her mother by not eating the fruit. Reports of adults actively preventing young from ingesting items that adults have learned to avoid are rare (Galef & Giraldeau 2001).

These results suggest that food selection competence is a socially learned competence. Infants experimented rarely with unknown foods, and if so than just to try it, but they did not include it in their diet. It will be interesting to see if Susi, after weaning, will learn to eat *Leucomphalos callicarpus* fruits from other individuals.

The data show that at the age of weaning infants ate everything that their mothers ate, though at the age of 2 years Jerry already ingested 86 % of food included in his mother's diet.

Mothers varied in their number of different food items that composed their diets. Sumis diet was composed of 55 different food items from 46 different species. By contrast, Mindy included 71 food items out of 57 plant species in her diet.

Some food items were only ingested either by the mother or by the infant. But the time spent on such foods was quite limited. Moreover, in the case of these items and during the period of observation, individuals were normally only observed to eat it once or twice. The one exception is Sumi, who was observed spending over 600 minutes on the fruit *Mezzettia umbellata* (Fam.: Annonaceae) of which her daughter didn't eat during the period of this study. We don't know anything about the reasons why Susi didn't eat it. Since all other immatures did eat it.

4.2.3. Independent food selection

The results show an increase over age for dependent immatures feeding independently, which is evidence that infants know what they can eat. But if they fed independently they only ate food, which they ate already before but together with their mothers. As an example, Kondor seemed to have attained such knowledge based on Kerry's diet. She was eating 99% of the mother's diet at the time of this study. It is possible that all infants would eat more often independently if they were not hindered by their small body size to move efficiently in the canopy (see appendix 7.5).

In conclusion, the food selection competence seems to be fully acquired before age of weaning. It would be of interest to compare weaned immatures' diet to that of their mothers, to look for further horizontal social learning concerning food selection competence. For such comparisons, paternity analyses to ascertain genetic relationships among individuals would be useful information.

The current study was done in a period with a good supply of food (van Schaik & Wich, in prep.) It would be of interest to do the same study once more in a period of fruit scarcity, when orangutans eat mostly bark and other fall-back foods (Knott 1998). Southeast Asian rainforests are known for their highly fluctuating production (Wich & van Schaik 2000), thus in addition to their regular diet when food is abundant, immatures need to learn what to eat during scarcity as well.

4.3. Foraging efficiency

4.3.1. Feeding techniques

Mothers and infants had the same feeding techniques for all food items. This was also the case for all other individuals in this population. During the study, no large differences were observed. Infants already knew how to open foods in order to reach the inside, like flesh or seeds. The only difference was that infants, being smaller, needed more bites to open a larger fruit, whereas adults could do this with only one bite.

Termites represented a special case. They posed a challenge to some individuals. Termites live mostly in dead tree branches, which are often found on the ground. Orangutans had to first find this dead wood and then open it to see if there are termites living in it. Some individuals, such as Mindy or Juni, seem to be real experts in termite finding. Other individuals aren't that talented and took an advantage from others' knowledge. For example Jinak was observed taking termite rich branches away from Juni, who didn't seem to mind her taking it away. All infants, including the oldest Kondor, beg their mothers or other individuals, most of the time, for a piece of dead wood with termites. Besides, Kondor, who spent a lot of time away from her mother, but still in hearing range, ran to her mother as soon as she heard the sound of a breaking dead tree, probably hoping that she might get some termites. She often tried feeding on dead branches, without success despite having frequently observed her mother eating termites. This seems to be a particularly difficult task.

The infants used the same feeding techniques as their mothers as soon as they fed themselves on certain food items. The development of the competence for feeding techniques correlated with the food selection competence. As the infants fed early in life on all foods, their mothers were feeding on, they developed also quickly the competence for feeding techniques needed to forage on these foods.

4.3.2. Feeding rates

Foraging efficiency can be measured, by looking at feeding rates. These were slowed down for all four infants for all food items compared to the adults. The reason might have been an insufficient efficiency. Milo showed a higher slow down in feeding rates compared to the other infants, which could be explained by a personal efficiency deficit.

The feeding rates of the two independent immatures, Juni and Nanio, were similar to those of the adults (small sample size). Sumi represented an exception as being quite slow compared to other adults. She wass old and lacked the two lower canines what made it difficult to bite large food items open.

Even if we can trust these analyses only as a preliminary result, it seems that orangutans have already acquired the full knowledge necessary for food processing by the time they wean, although subsequent improvement of feeding technique efficiency occurs after weaning age, which was also the case for the Sumatran orangutans of Suaq Balimbing who were able to use tools of the local repertoire (van Noordwijk & van Schaik 2005)

4.4. Comparison with chimpanzees and what does it now mean for human origins?

Orangutan infants are not slower in development than chimpanzees, who wean about 2-3 years earlier, but then stay 2-3 years longer in close proximity to the mother than do orangutans (van Noordwijk & van Schaik 2005). Van Noordwijk & van Schaik (2005) argued that early weaning of infants before full ecological competence is reached in humans and chimpanzees is allowed due to gregariousness.

Though the results of this study provide important insights on orangutan ecological competence acquisition it is difficult to make firm statements on their significance with respect to human origins. Perhaps in humans some aspects of foraging competences are achieved as with orangutans before weaning, but it is also known that humans actively provide subsidies to their weaned immatures. In humans we find a lot of tolerance among kin. Another point is that if humans are weaned they don't have to be ready to digest adult's food since much food is cooked or chewed by other members of a population first and provided in a form that can be digested by infants.

Kennedy (2005) proposed that natural selection targets the child's intellectual development rather than its survival. Furthermore, he suggested that brain growth needs a lot of energy provided by adult's food, also if processed first, and energy is not provided by human milk solely.

Nevertheless I allow myself to say that the trend seems to lead towards supporting the Needing-to-Learn hypothesis, thus to the hypothesis that

human life history is in some aspects slowed down due to prolonged ecological incompetence as result of the complexity of the human foraging niche (Kaplan et al. 2000).

4.5. Summary of the objectives and results:

Hypothesis 1: Lack of strength rather than lack of skill is the reason that immatures don't forage at adult levels. If there is a strength effect concerning foraging in immature orangutans, we expect:

- Hard foods are not eaten by young infants but by older individuals.
Even hard foods were eaten by all infants.

- If young immatures eat some hard foods, then, they feed less long on hard foods than on soft foods.
No differences in feeding time were observed for hard or soft foods

- While feeding independently, infants select soft foods rather than hard foods.
No tendency was seen for selecting rather soft than hard food when independently feeding

- **No strength effect was detected**

Therefore the following hypothesis is only tested for the Needing-to-learn hypothesis:

Hypothesis 2: The food selection competence is fully acquired around the age of first reproduction, thus we expect:

- The similarity of diet for mother-infant pairs increases with age.
A high similarity in diet was already reached at the age of 2 yrs and fully reached at the age of weaning

- The number of events, where the infant feeds independently or before mother increases with age.
Independent feeding behaviour increases with age.

- **The results indicate that food selection competence is fully acquired at the age of weaning.**

Hypothesis 3: The foraging efficiency can only be estimated for the Needing-to-learn hypothesis and is fully acquired around the age of first reproduction, we expect:

- The similarity of feeding techniques between mother and infant increases with the infant's age and is fully acquired at the age of first reproduction.
Observations show that the same feeding techniques the mothers use are acquired as soon as infants forage by themselves on a certain food item.

- Feeding rates increase with age and reach stable adult value at the age of first reproduction.
Feeding rates increase with age but do not reach adult values at the age of weaning. At age of weaning and early independent immaturity, individuals' feeding rates are still below that of the average adult values.

- **The knowledge how to eat seems to be acquired at the age of weaning. But the efficiency to eat didn't reach adult value yet.**

5. Conclusion

The hardness of foods doesn't cause any delayed acquisition of feeding competences. It seems that feeding on hard food isn't related to the tradeoff between growth and reproduction - as big body size correlates with strength– but it might be the case for other size dependent skills, like moving efficiently in the canopy.

It seems that the food selection competence is based exclusively on social learning, through vertical transmission from mother to offspring during dependency. A reason could be the importance to avoid noxious foods because weaned immature orangutans have to cope with their own life. Correspondingly, the youngest infants' diet overlaps largely with that of their mothers' diet and overlap fully at the age of weaning. Moreover, the knowledge of feeding techniques seems to be fully developed for all food items included in the infants' diet at the age of weaning. This knowledge is probably acquired through observations made by the infant, thus socially learned (Tomasello et al. 1987, Adrian Jaeggi Diploma thesis 2006). Only the efficiency of the techniques needs further improvement during independent immaturity based on individual learning/training or maturation. Furthermore, it is possible that the range-use competence will develop mostly after weaning through individual experimentation combined with social learning from kin or conspecifics. Such a mixture of social and individual learning is expected at intermediate rates of environmental change, which is the case in tropical forests (Galef & Giraldeau 2001).

The long dependency period of orangutans seems to be necessary to learn what foods can be eaten and how and basically where to find them based on social learning. Orangutans' late weaning, by contrast to gregarious apes or humans, seems related to their solitary lifestyle enforced by ecological conditions and arboreal lifestyle (van Noordwijk & van Schaik 2005, van Adrichem et al. subm.), thus weaning is delayed until the immature is ready to leave its mother as soon as her next infant starts to demand a lot of her energy.
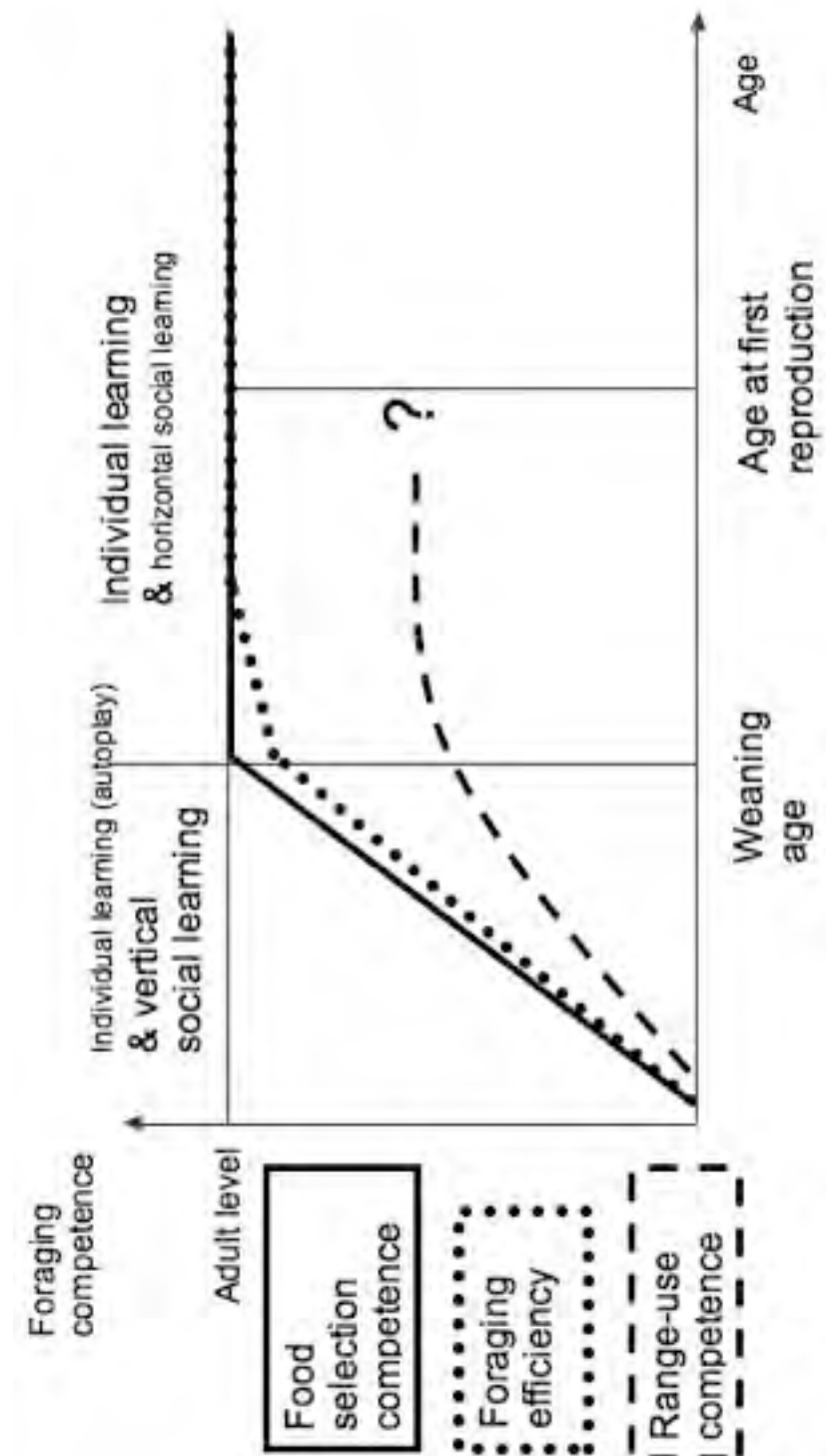
Other aspects may also play a role, like temperature regulation, which is provided by the mother at night through body contact or protection from predation and the transportation help in the canopy (see appendix 7.5).

Fig. 20 represents a brief overview of the consequence for the Needing-to-learn hypothesis. The results for both components of the foraging competence, which are food selection competence and foraging efficiency would lead to the rejection of the Needing-to-learn hypothesis as these are acquired well before age at first reproduction. Only the range-use competence could still lead to its support, this competence couldn't be estimated through observations on dependent immatures, as they remain in close association to their mothers, thus a lot clinging to her body and always in close proximity to her (small distances) (see appendix 7.5.).

The long period before weaning allows immature orangutans to learn a lot of skills from their mothers. However, in contrast to the other apes and humans, orangutans leave the permanent close association with their mother shortly after weaning (van Noordwijk & van Schaik 2005, van Noordwijk et al. in prep.). During the long post-weaning pre-reproductive period (in this population at least 5 years) the immature still needs to grow a lot (see appendix 7.6. photo 12) and may have the opportunity to learn from occasional contact with conspecifics.

Fig. 20: Needing-to-learn. Competence in function of age. When are the competences at adult level acquired?

Acknowledgements

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7. Appendix

7.1. Age Estimations

(From Kuze et al. 2005)
Kuze N et al. looked at facial morphology in Bornean orangutans. They found:

Marks: colour of skin around eyes, mouth, head hair, whiskers, beard.

Females:

Eyes: 0-7 years very light coloured
Big differences for ≤ 10 years and ≥ 11 years
> 20 years: dark

Eyelid: ≤ 20 years light coloured eyelid

Mouth: light 0-3 years; ≥ 9 dark

Head hair: infant hair ≤ 7; adult hair ≥ 9

Whiskers: all ≥ 21

Males:

Eyes 0-7 very light coloured
10 years dark

Eyelid: ≤ 10 years very light coloured

Mouth: light 0-3 years; ≥7 years dark

Head hair: infant hair all 0-3; adult hair ≥ 7

Whiskers: all ≥ 7 whiskers

The animals of the Kuze study were all rehabilitant orangutans or from zoos all with estimated ages.
It is known that those animals, which have a non-stop good food availability develop much faster in any aspect than their wild cousins in the forest.

I compared pictures and video of the 4 infants and Juni in Tuanan ranging from August 2003 until July 2005 (Photo 9).

| Jerry | Susi | Milo | Kondor |

Photo 9: Facial morphology changes in 4 immatures from August 2003 until July 2005

For Juni:

Photo 10: Facial morphology changes for an independent immature female.

In August her light eyelids are still visible, as well as some pink spots around her mouth. In July 2005 her face is much more black. On the 10th of February 2006 she got her first infant at the estimated age of 12 (born 1994). After judging these pictures I would say that in August 2003 Juni was around 11 years old (cf. Kuze et al. 2005) (big difference for eyes coloration around 11) At this picture she doesn't show any coloration around the eyes. The eyelid can stay pink until the age of 20. Mouth will be dark at the age of 9 years. In 2003 she doesn't show the typical infant hair (scattered, upstanding hair), but adult hair (dense thicker hair lying down on the head) (Photo 10)

Photo 11. (Left) Kondor with Kerry in December 2003, (right) Mindy with Milo in July 2005.

Kondor is slightly bigger compared to her mother than Milo is on these pictures. As one and a half years separate these pictures, an estimated difference of two years was made for Kondor and Milo (Photo 11).

Based on the photo and video comparisons I have used the following estimates of date of birth:
- Jerry: first half of 2003
- Susi: second half of 2002
- Milo: second half of 2001
- Kondor: second half of 1999
- Juni: second half of 1994
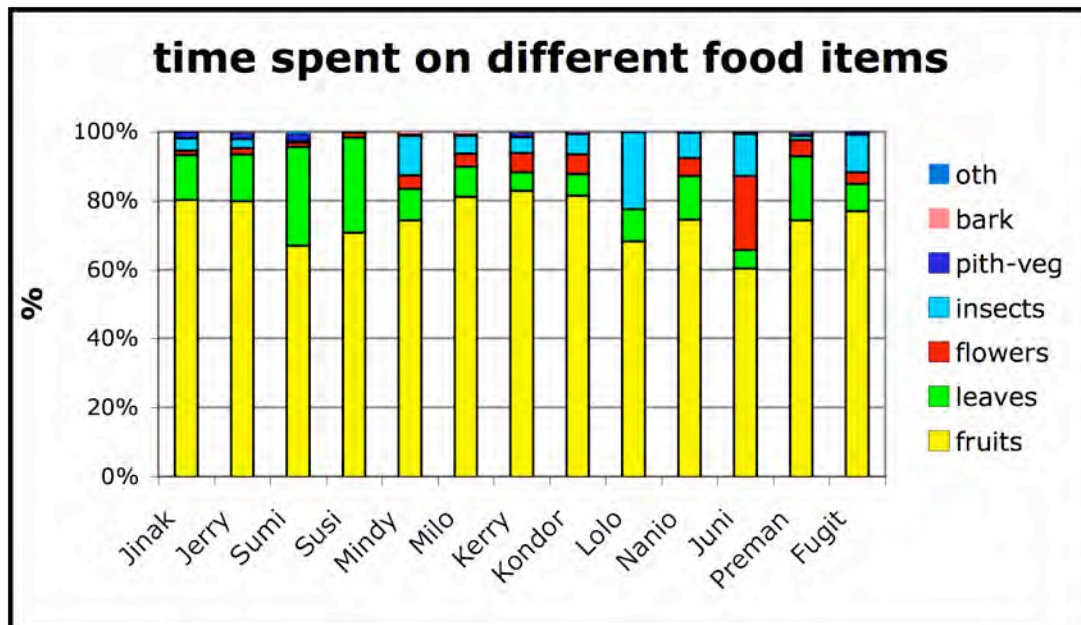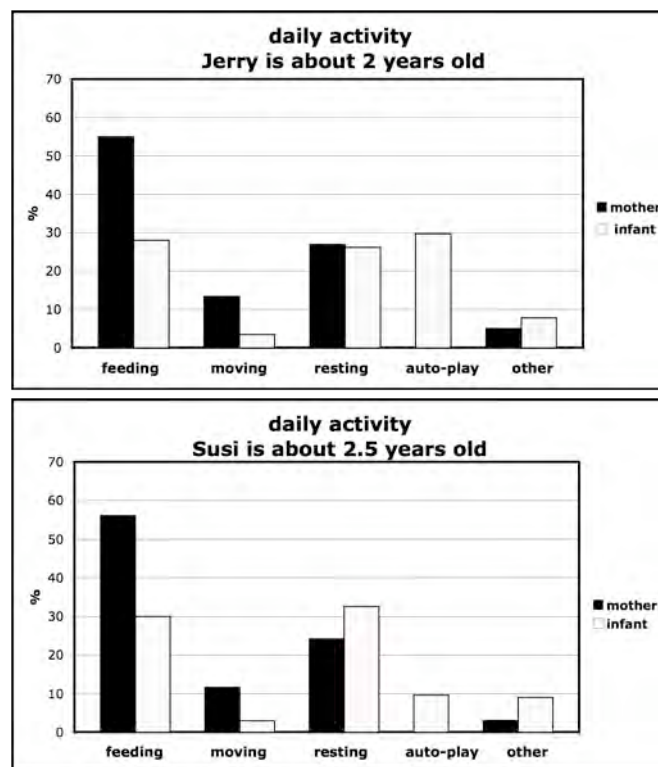
7.3 Similarity of diet

Fig 21: Time spent on different food items for mother infant pairs as well as independent immatures: Lolo, Nanio and Juni. I included an unflanged male, Preman and a flanged male, Fugit for comparison.

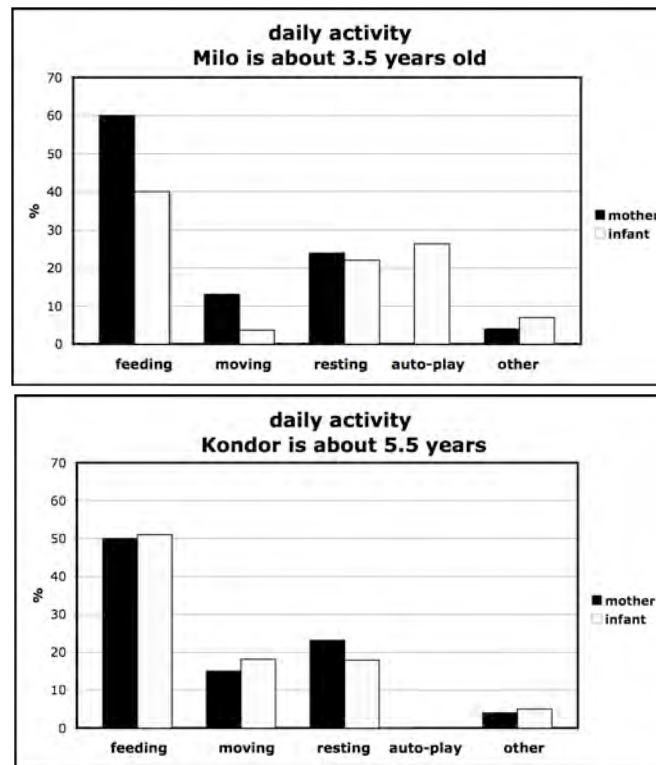## 7.4. Daily activity of all four infants and their mothers

Fig. 22. "other" means for example social activites, nest building and auto-play for the mother. For better overview the y-axis only reach until 70%.

Kondor's activity is similar to that of her mother. The younger infants spent a lot of time on auto-play and less time on feeding. Resting for infants includes the clinging behaviour when the infants are not feeding or playing while clinging.

7.5. Clinging behaviour and distances between mother-offspring

A first step, which explains why range-use competence can't be estimated by observations on mother-infant pairs.

As mentioned in the introduction, we focused mainly on mother-infant pairs for this study, thus no clear estimations could be made for the range-use competence. Here some results concerning the clinging behaviour of dependent infants, as well as the distances between mother-infant pairs, which both show that dependent immatures still remain in close proximity to their mothers and thus don't explore a lot around on their own yet.

For the range-use competence it is important to mention that it is estimated by the knowledge where to find good food patches. A lot of food is constantly distributed throughout the whole forest, whereas, some large trees, like *Ficus sp.* or *Campnosperma coriaceum* aren't that common. If their fruits are ripe, they are often visited by many individuals. This leads to the conclusion that orangutans know where to find these trees (Bard 1995, Rijksen 1978, MacKinnon 1974). Actually we can only test for this hypothesis, if infants already feed on their own, which presuppose them to travel on their own.

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7.5.1. Locomotion competence

An analysis of time spent by infants clinging to their mothers shows that it significantly decreases with age for almost all of the infants but not Susi (Fig.23). She remained more time cling than the others (Spearman's rho rank correlation p=0.158). Jerry (p<0.05) reduced his clinging behaviour more quickly than the other infants, with respect to his young age. Clinging decreased with age. (Milo: p<0.05, Kondor: p=0.036). The clinging behaviour for all infants, but not Susi, correlated significantly negative with age.
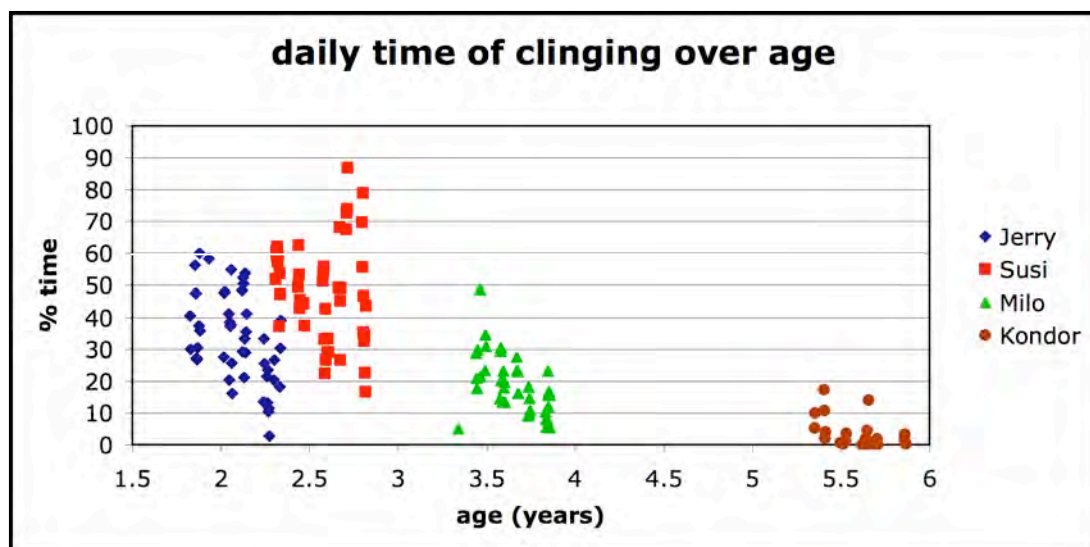

Fig.23: Total clinging behaviour per day in function of age.

At the end of this study Kondor was almost never cling anymore. Fig. 23 represents the infants' clinging behaviour during the whole day, including resting and feeding behaviour of the mother's.

Yet, we had to check for seasonal effects. The data collection started during the wet season, when heavy rains made the branches very slippery, which could be problematic for infants. If so, their clinging behaviour decreased over this period only, because of weather changes. Fig. 24. shows that all infants presented a significant decrease in their daily clinging behaviour over the last two years.
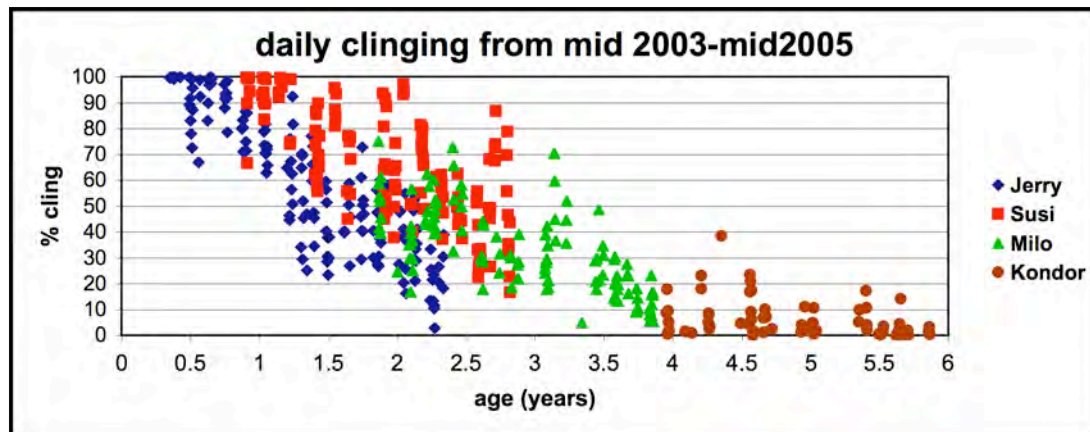
Fig 24. Daily clinging behaviour since 2003.

Thus it might be that Susi stayed more cling because of seasonal effect during my stay in Tuanan. It also often happened that Sumi stayed in a very bad, burned area where she moved a lot at the ground, therefore Susi had to stay more cling.

Right after birth, the offspring are 100 % of their time clinging (Bard 1995). As soon as their locomotion is coordinated, they start to play around during resting or feeding periods (Fig. 22) and than also start to explore feeding trees. Soon they only cling when the mother travels or during lactation and sleeping.

Clinging during travelling

The clinging behaviour of the infants when their mothers are moving shows an even steeper decrease for all of the infants, but not Susi (spearman's rho rank correlation p=0.505) (Fig. 25). Kondor (p<0.05) stopped clinging around March 2005, concerning clinging when mother is moving. Jerry (p<0.05) and Milo (p<0.05) show a very steep decrease in clinging.
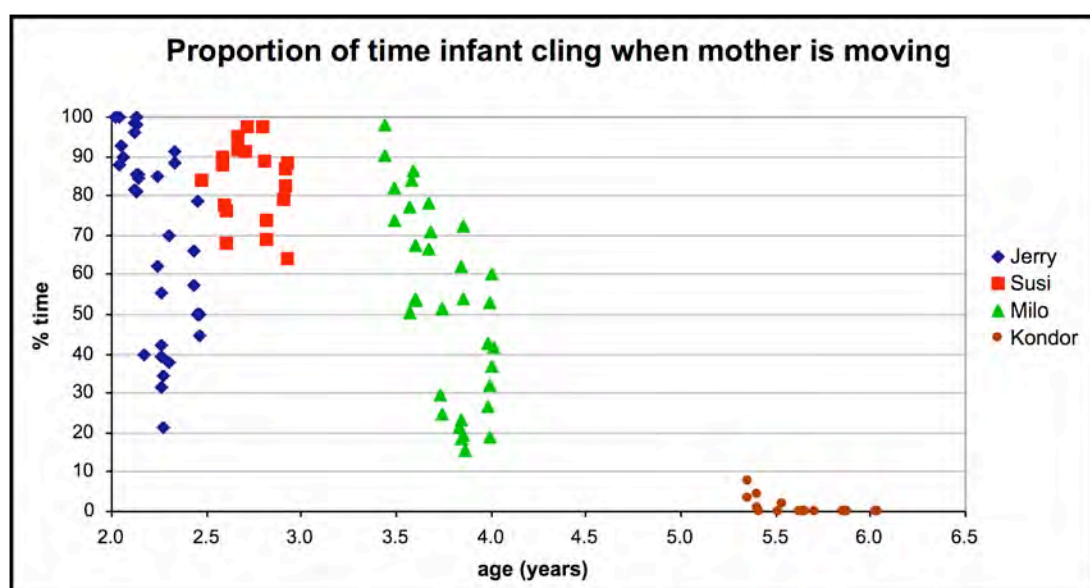

Fig 25: infants clinging behaviour when their mothers are moving over age.

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Fig. 25 shows that all infants but not Susi's clinging time during travelling correlate significantly negative with age. Thus 2-4 years old infants take care of most of their own transportation.

The clinging behaviour, during the mother's moving activity starts at a higher percentage than the overall daily clinging. Moving in the canopy of a forest can pose problems for small infants. They are often not able to cross trees due to limited weight or size. The large branches don't bend under their body weight. If a mother walks further, infants who can't cross a gap in the canopy, starts whining until the mother comes back to make a bridge with her long arms so that the infant can just pass over her body (Galdikas 1979, MacKinnon 1974, Rijksen 1978). Older infants cross gaps away from their mother's body but make use of her bended tree to reach the next one (Bard 1995). By the age of weaning the immature Kondor had stopped clinging for travelling. Yet, she still was in body contact for rare social contact with her mother, as well as to sleep.

Susi was still around 80% of the mother's moving activity cling, which could be explained by the fact that her mother often roamed about in her old home range, a burned area close to an inhabited village. There she moved a lot on the ground or a bit above the ground in small trees and bushes. That might be the reason why her offspring is most of the time clinging, whereas the other infant, with estimated half a year younger, moved a lot on its own. The clinging behaviour decreases, as the infants grow older.

7.5.2. Distances away from mother

This result represents the infants' distance away from their mothers. As the infants grow older they stay more often and further away from their mothers.
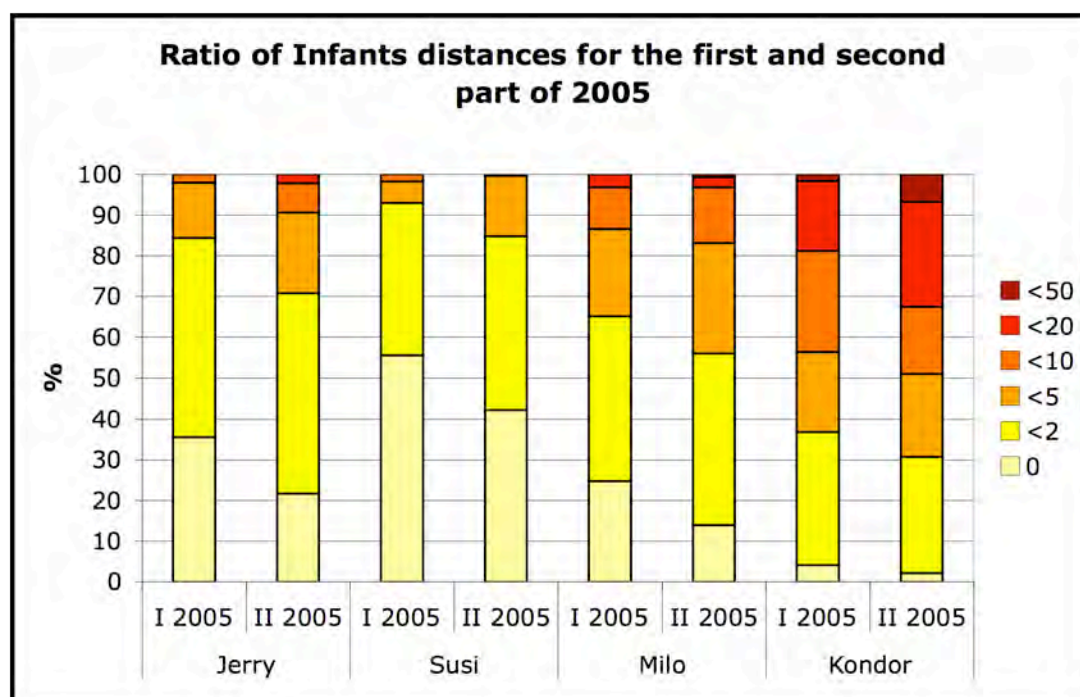

Fig.26: The graph shows the distances and time ratio of the infants spent away from the mothers. The measurements were made taking half hour scans. I 2005 means first part of 2005, II 2005 means second part of 2005.

The distances and time spent away from their mothers increased with age, which seems to be closely correlated with the infants' independent moving efficiency. As long as the infants need their mothers for travelling in the canopy, whether for clinging or for bridging, infants don't move too far away from their mothers. They remained mostly within a 10 m range to their mothers. Further, around the age of weaning they stop clinging for travelling and begin to spend more time away from their mothers within a range of 20-50 m. Kondor travelled mostly a parallel route of her mother. So she was still in earshot to Kerry. Younger infants will at most move farther in the canopy of large feeding trees and maybe to neighbouring trees, but not much further away. Milo for instance shows a high tendency to explore away from her mother, but still within 10 m, rarely up to 20 m. The youngest infant Jerry seemed to have been the most explorative of all infants observed, as he showed a faster decrease in clinging as well a faster increase in distances and time spent away from mother, compared to the others. This could be a sex effect. Of course, to test this suggestion, a bigger sample size is needed, as Jerry was the only male infant in this study.

But it is important to mention, that it has been interfered that independent female orangutans remain in a home range adjacent to that of their mothers' home range, whereas males move away (Galdikas 1995, Singleton and van Schaik 2002) or at least highly expand. Since adult females inhabit smaller home ranges than males do, females are more likely to revisit more often food patches, therefore they know where these patches are located and when food is available. Whereas males, who inhabit large home ranges, seem to be more likely not to revisit the same food patches within short intervals, but the rather only need to know when the commonly distributed food is abundant. This doesn't conclude that males don't know where to eat!

A special case, the immature Lolo, born in the second half of 2003, didn't reach adult size yet, but lived on her own. Unfortunately it could not be established whether she was an orphan or whether she was truly independent of her mother since her relatedness to other individuals in the area is still unknown (future DNA analyses by N.Arora / M. Krützen will hopefully clarify this). Unfortunately she wasn't followed often enough to include her data to the analyses. However, she didn't seem to know where to go, as the maps taken on her daily moving way showed an unoriented behaviour. Adult orangutans may manifest mental mapping skills when they travel over long distance to a specific goal (Bard 1995, Rijksen 1978, MacKinnon 1974). Their daily travel route mostly doesn't cross itself again. Whereas Lolo's route crosses itself several times a day. (not formally tested due to limited data).

For better understanding how and when immatures know where and when to eat, more research has to be done on weaned individuals.

7.6. Size difference Kerry-Kondor, October 2005

Photo by Anne van der Sluis

Photo 12: on the left Kerry the mother and on the right Kondor the weaned infant.

After weaning there is still a size difference seen between mother and infant.