Universität Zürich[UZH]

SUAQ

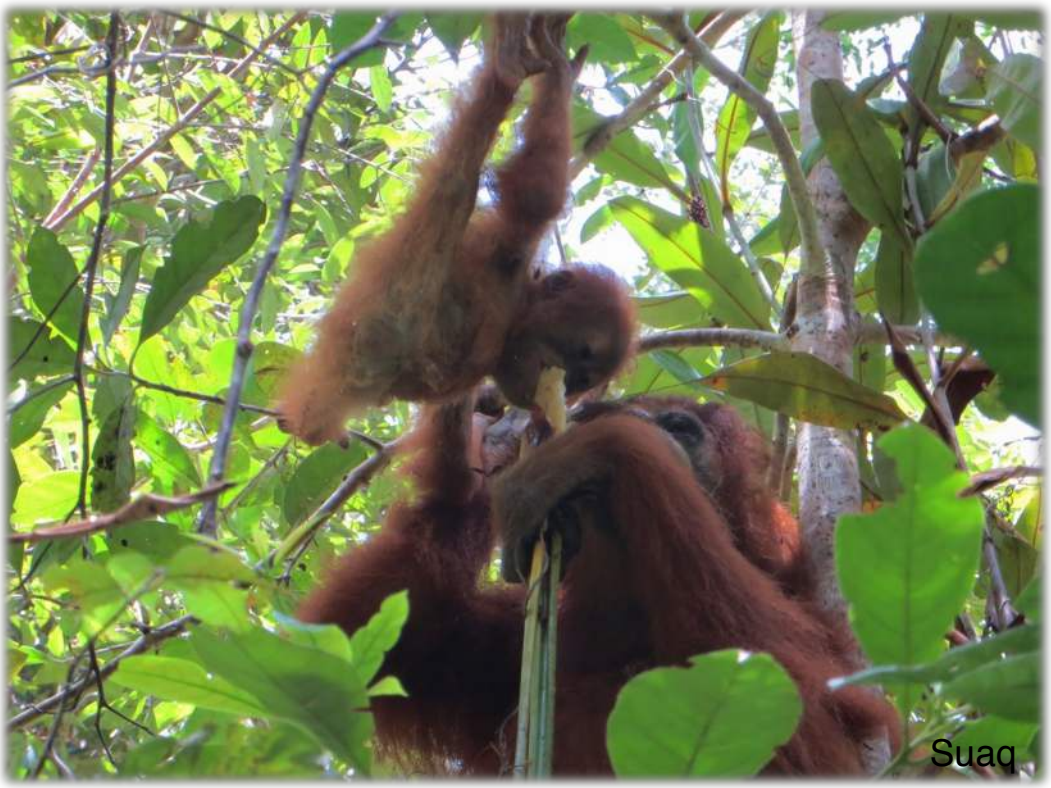
Master Thesis

Begging for and sharing information – Orangutan infant begging behaviour and maternal response in feeding skill acquisition

An observational field study on wild immature Sumatran orangutans (*Pongo abelii*) at Suaq Balimbing in the Gunung Leuser National Park, Aceh Selatan, Indonesia

Belinda Kunz, Master student

Supervised by Dr. Caroline Schuppli & Dr. Maria van Noordwijk
Department of Anthropology, University of Zurich



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I. Abstract

Sumatran orangutans (*Pongo abelii*) have exceptionally slow life histories: with an age of weaning at 7 - 8 years and age at first reproduction of 15 – 16 years, they develop slower than any other non-human primate. It has been suggested that orangutans are slow in their development because of their need to acquire complex and manifold skills during the immature phase. Orangutans indeed live in complex foraging niches and have to acquire cognitively demanding foraging skills, which takes time and thus may have an effect on the timing of their developmental milestones. Previous studies have shown that orangutans rely on social learning to acquire their foraging skills. But so far, the role of the mother in the process of skill acquisition remained unclear. In my master thesis, I investigated begging behaviour in infants, defined as all attempts of orangutans to obtain a food item or a part of a food item from another orangutan by obvious gestures. I also looked at the mothers' responses to these begging events, as a possible means to guide the infants' learning process. Based on the findings of previous studies I predicted that begging is an important means of gaining knowledge for infant orangutans during their development. I also investigated feeding rates of infant and juvenile orangutans as a direct measure of feeding competence. My data consist of 744 begging events recorded from 14 infants during the time from January 2011 until January 2019 and of 1526 feeding rates recorded from 17 immatures and their mothers between February 2008 and January 2019 at the research station Suaq Balimbing in South Aceh, Sumatra, Indonesia. I looked into effects of age and sex of the immatures, as well as the effects of complexity and frequency of the food item on immatures' begging behaviour and feeding rates. I found a significant age effect on the begging rate, showing that older infants beg less than younger infants. Infants also beg more for rare food items than for more common ones, but not for more complex food items than for easier-to process ones. On the other hand, mothers are more tolerant when their infants are begging for more complex food items, but not when they are begging for rarer food. Age did not have an effect on the success of infants' begging events. Age was the only factor that had a significant effect on feeding rates, suggesting that with increasing age infants approach their mother's speed of ingesting food items. Throughout all the analyses, I did not find any evidence for sex differences. The age effect on the begging rate probably reflects older infants' higher feeding competence as I found that with increasing age immatures increase their feeding rates.
All in all, I found some indication that begging behaviour is a means of skill learning during the developmental phase of wild Sumatran orangutans. The findings that infants do not beg more for complex food items but are more successful in obtaining them suggest that infants are not able to assess complexity to the full extent while mothers are, indicating a more active role of mothers in skill learning of their infants than previously thought. Because of the clear effects of frequency and complexity of the food items and age of the infants on begging behaviour the findings from my study point into the direction that intense skill learning during the developmental phase might be important in setting the pace of life history in Sumatran orangutans.

II. Statement of authorship

I declare that I have only used the sources stated in the references and no others. All passages contained in other publications or from other sources are indicated as such, i.e. cited and/or attributed. I did not submit this thesis for another degree or diploma at any other university or at any institute of tertiary education.

Zürich, 17.12.2019 Belinda Kunz

III. Table of contents

I. Abstract 1
II. Statement of authorship 2
III. Table of contents 3
1. Introduction 5
1.1 Great ape life history 5
1.2 Skill learning (time) vs. growth and differentiation (energy) and life history 5
1.3 Complexity of the foraging niche and life history 6
1.4 Food availability and differences in orangutans and chimpanzees 6
1.5 Hypotheses to explain the orangutan's exceptionally slow life history 7
1.5.1 Arboreality 7
1.5.2 Semi-solitary lifestyle 7
1.5.3 Skill learning 7
1.5.4 Combination of skill learning and growth 8
1.5.5 Female reproduction 8
1.6 Social learning 9
2. Questions and predictions 10
2.1 Part 1: Begging behaviour – Infant's perspective 10
2.2 Part 2: Begging behaviour – Mother's perspective 11
2.3 Part 3: Feeding rates 11
2.4 Part 4: Combination of begging and feeding 11
3. Material and Methods 12
3.1 Study period and study site 12
3.2 Study subjects 12
3.3 Data collection 13
3.3.1 Activity Data 13
3.3.2 Begging Data 13
3.3.3 Feeding Data 14
3.4 Variables 14
3.4.1 Response variables 14
3.4.2 Explanatory variables 15
3.5 Statistical analysis 15
3.5.1 Model selection 16
3.5.2 Simple correlation analyses 16
3.5.3 Visualisations 16
4. Results 18
4.1 Descriptive statistics 18
4.1.1 Part 1 and 2: Begging behaviour 18
4.1.2 Part 3: Feeding rates 19
4.2 Part 1: Begging behaviour - Infant's perspective 19
4.3 Part 2: Begging behaviour - Mother's perspective 22
4.4 Part 3: Feeding rates 24
4.5 Part 4: Combination of begging and feeding 26
4.5.1 Infant's perspective 26
4.5.2 Mother's perspective 27
5. Discussion 29
5.1 The effects of age and feeding competence on infants' begging behaviour and their mothers' tolerance 29
5.2 The effect of food item frequency on infants' begging behaviour and their mothers' tolerance 29

5.3 The effect of food item complexity on infants' begging behaviour and their mothers' tolerance ……..…...30
5.4 The effect of sex on infants' begging behaviour and their mothers' tolerance……...32
5.5 Effects on feeding rates ……..……32
5.6 Conclusion ……..…….33
6. Acknowledgments ……..……..34
7. References ……..……35
8. Appendix ……..……...39

1. Introduction

1.1 Great ape life history

According to the classic life history theory, animals should reach the reproductive phase as early as possible to maximize reproductive outcome (Charnov, 2004). But at the same time, they need to grow and acquire skills during the developmental phase to be able to survive and reproduce as adults. Primates, in general, have slow life histories (Harvey & Clutton-Brock, 1985) with great apes, including humans (van Schaik & Isler, 2012), being the slowest. Because of the slow pace of development and longevity of great apes, they are suitable study species to investigate under what conditions slow life histories, including long periods of immaturity, evolved and what factors they are correlated with.

When looking at life histories among great apes (Table 1) it seems that in terms of longevity chimpanzees (*Pan*) and orangutans (*Pongo*) are the slowest with orangutans probably being a bit slower. The current data suggest life expectancy to be similar (around 50 years), but the lower mortality of orangutans (adult mortality and infant survival: van Noordwijk et al., 2018; mortality throughout their lifespan: Wich et al., 2014) suggests higher longevity in orangutans. Wich et al. (2004) showed that orangutans have longer interbirth intervals and a later age at first reproduction than chimpanzees and gorillas. Gorillas (*Gorilla*), in general, are faster in their development than chimpanzees and orangutans (Watts & Pusey, 1993; Watts, 1991).

Table 1: **Life history parameters concerning the reproduction of great ape species**.
[1] In gorillas, Watts (1991) found that suckling bout frequency seemed to be the most important influence on interbirth interval length.
[2] Measured as not sharing the same night nest anymore.

	Age at weaning (years)	**Female age at first reproduction (years)**	**Interbirth interval (years)**
Gorillas	**3–4** (Watts & Pusey, 1993)	**10–12** (Watts & Pusey, 1993, Watts, 1991)	**3–5** (Watts, 1991[1])
Chimpanzees	**Around 5** (Bray et al., 2017; Watts & Pusey, 1993)	**14–15** (Watts & Pusey, 1993)	–
Orangutans	**6–9** (van Noordwijk & van Schaik, 2005[2]; van Noordwijk et al., 2009; van Noordwijk et al., 2018)	**Around 15** (Watts & Pusey, 1993; Knott, 2001; Knott et al., 2009 (range: 13–16); van Noordwijk et al., 2018)	**Around 8** (van Noordwijk & van Schaik, 2005; Knott et al., 2009; van Noordwijk et al., 2018)
Bonobos	–	**Approx. 13–15** (Watts & Pusey, 1993)	_

1.2 Skill learning (time) vs. growth and differentiation (energy) and life history

Schuppli et al. (2012) investigated in mammals and birds whether it is the time needed to learn skills ('needing-to-learn hypothesis') or the energy to grow and differentiate the brain ('expensive brain hypothesis') that generally limit the duration of the immature phase and thus the timing of age at first reproduction. The 'needing-to-learn hypothesis' suggests that large-brained animals are limited by the need to acquire adult-level skills before they start to reproduce (Ross & Jones, 2001). It implies that adult skill competence is reached around the age at first reproduction and as such limits the onset of

reproduction. The 'expensive brain hypothesis' on the other hand suggests that high investment into brain tissue among large-brained species like primates (Shea, 1973) during immaturity limits body growth (Isler & van Schaik, 2009; Barrickman et al., 2008). Brain tissue needs exceptionally high energy supplies (Rolfe & Brown, 1997) which cannot be reduced temporarily as for other organs (Karasov et al., 2004; Bauchinger et al., 2005) because brain starvation will lead to irreparable damage of the brain tissue. Thus, the implication of the 'expensive brain hypothesis' is that species with large brains must have strategies to ensure that these high energy costs can be met at all times. These strategies can include a reduced total energy turnover or reduced energy allocation to other expensive functions like digestion, locomotion or production (growth and reproduction) (Isler & van Schaik, 2009). In terms of developmental schedule in comparison to the 'needing-to-learn hypothesis' the 'expensive brain hypothesis' claims that body growth is only completed around the age at first reproduction and as such limits the onset of reproduction.

Schuppli et al. (2012) found that for birds, adult-level skill competence and not growth is limiting the age at first reproduction, whereas in mammals, adult-level skill competence is reached before the age at first reproduction. Thus, the acquisition of skills is not limiting the onset of reproduction in mammals. Usually, mammals reach adult-level skill competence around the timing of weaning. It may, therefore, be that skill acquisition does limit the developmental pace in mammals too, just not via the age at first reproduction (like in birds) but via the age at weaning. This is plausible because most mammals don't have post-weaning provisioning and hence must be self- supporting after weaning, for which enough skills are necessary.

Orangutans and chimpanzees seem to roughly fit the mammalian pattern in terms of acquisition of skill competence before the age at first reproduction, seemingly around the time of weaning (chimpanzees: Bray et al., 2017; orangutans: van Noordwijk & van Schaik, 2005; Schuppli et al., 2016b). However, detailed data on the timing of the acquisition of different skills and the involved skill acquisition processes are still lacking.

1.3 Complexity of the foraging niche and life history

Schuppli et al. (2012) also found that there is variation among mammals when adult skill competence in relation to the age at first reproduction is reached. This variation is related to the complexity of the foraging niche of a species: with increasing complexity of the foraging niche, the time span until adult skill competence is reached increases. The same concept has been suggested by Ross (1998): Species feeding on food which is easy to find and process, as for example leaves in unseasonal habitats, should show faster growth rates than species which feed on more difficult to find and process food, as for example insects and fruits (with fruits being seasonal in certain habitats and thus not always available). Species experiencing periods of unstable food availability need to ensure that their brains do not starve during these periods. The argument of the 'expensive-brain-hypothesis' is that the development becomes slower, thus the body does not need too much energy at once for growth and development, which acts as a buffer for periods with low energy availability.

Leigh (1994) found this correlation within certain primate species, including gorillas, comparing folivorous with non-folivorous primate species. Gorillas are more folivorous and hence experience a more stable food availability. Because of this, they have a lower risk of starvation or malnutrition during immaturity (Janson & van Schaik, 1993) which speeds up the pace of development.

1.4 Food availability and differences in life history in orangutans and chimpanzees

A comparison of orangutans with chimpanzees shows that their development is similar in general (van Noordwijk & van Schaik, 2005). The most obvious difference is that chimpanzee immatures get weaned

earlier, even though they stay in proximity (within 10 meters) to their mother after weaning longer (van Noordwijk & van Schaik, 2005). Accordingly, in line with Ross' (1998) prediction, orangutans have a higher variation in energy intake than chimpanzees (Conklin-Brittain et al., 2006). It could thus be argued that this higher variation may account for the longer interbirth intervals in orangutans compared to chimpanzees. Looking at this higher variation from the infant's perspective, it may be that the variability of food availability of orangutan habitats combined with the need to keep the energy input for growth and maintenance constant, slow down the pace of development. When growth and development are slowed down, the body does not need as much energy at the same time compared to when growth and development are faster. The periods of food scarcity are thus softened („buffered"). Looking at the higher variation in energy intake from the mother's perspective, it may be that species, such as orangutans, showing multi-year lactation which need to keep providing milk to their offspring through peaks and troughs of food availability (van Noordwijk et al., 2013), need to increase the time period before weaning and slowing down the growth rate of the offspring to buffer the low points in food availability.

1.5 Hypotheses to explain the orangutan's exceptionally slow life history

To answer the question why orangutans have this exceptionally late age of weaning (Wich et al., 2004; van Noordwijk et al., 2018) and the longest interbirth intervals of any primate species (van Noordwijk et al., 2018; van Noordwijk & van Schaik, 2005; Knott et al., 2009), several hypotheses have been proposed. These are not mutually exclusive.

1.5.1 Arboreality: Because in general arboreal mammals have slower life histories than terrestrial mammals (van Schaik & Deaner, 2003), Wich et al. (2004) suggested that the difference between orangutans and chimpanzees in life history pace might be linked to the higher degree of arboreality in orangutans. Climbing up and down in a three-dimensional habitat is energetically more costly than walking on the ground (Thorpe et al., 2007; Halsey et al., 2016). This might slow down the pace of life history, because, with a higher energetic need for locomotion, periods of starvation are more likely. This would mean that as a consequence of arboreality, many different life history parameters are all altered. Accordingly, we would expect orangutans to get weaned later, have longer interbirth intervals, reach age at first reproduction later and live longer. So far, when comparing chimpanzees and orangutans, the data suggest that in orangutans, only the timing of weaning is significantly later (van Noordwijk & van Schaik, 2005), although Wich et al. (2004) consider from their data (estimated ages) that orangutans might live longer than chimpanzees. It might also be that the timing of weaning is more flexible than age at first reproduction and longevity and thus experiences the greatest effect from a higher degree of arboreality.

1.5.2 Semi-solitary lifestyle: Another hypothesis for the exceptionally late weaning in orangutans is the 'semi-solitary lifestyle hypothesis' proposed by van Noordwijk & van Schaik (2005). This hypothesis suggests that orangutans have a later weaning than the other great apes because of their semi-solitary lifestyle. The East Asian rainforests have a low productivity (van Schaik & Pfannes, 2005), forcing the orangutans to forage alone for most of the time (van Schaik, 1999). Because of the generally low food availability, in most populations, orangutan mothers cannot let their weaned offspring stay in close association for extended periods after the next offspring is born. In the more gregarious chimpanzees, on the other hand, weaned immatures still range with their mother and often two younger siblings and thus may continue to learn from their mother after weaning. Because of the lack of a close association with the mother after weaning, weaned orangutan immatures need to have acquired enough skills to survive. This view implies that orangutan immatures master essential skills earlier (in terms of life history events) to a greater extent than chimpanzee immatures do.

1.5.3 Skill learning: Orangutans have a broad diet including many difficult-to-process food items (Schuppli et al., 2016b). Thus, during the immature period, they need to acquire cognitively demanding

foraging skills. Moreover, orangutans are a large-brained species, thus, intense skill learning and growth and differentiation of the brain possibly lead to a prolonged developmental phase (see 'needing-to-learn hypothesis' and 'expensive brain hypothesis' described above). The Sumatran orangutan (*Pongo abelii*) population at Suaq (where the data for this thesis will be collected) additionally uses tools as an extractive foraging technique (van Schaik & Fox, 1996; van Schaik, 2004; van Schaik & Knott, 2001; Meulmann & van Schaik, 2013): They use sticks to extract insects and honey from holes in tree trunks and branches. Likewise, they use sticks to get rid of the very thin and sharp hair protecting the seeds of the Neesia fruit (*Neesia aquatica*) and (in a second step) to extract the seeds afterward from the hard shell of the fruits (van Schaik & Knott, 2001).

Schuppli et al. (2016b) investigated foraging skills in Sumatran orangutans at Suaq. The results from this study show that immatures eat an increasing number of food items with increasing age and around the time of weaning immatures reached 80 to 99% of their mother's diet, thus roughly speaking, adult-like diet repertoires (whereby diet repertoire size served as a measure of food selection competence). The results from that study suggest that female immatures seem to reach a higher diet repertoire size earlier than male immatures. Adult-like ramble ratios (a measure of food locating competence) are reached at the start of ranging independence, around the age of 10, 11 years (also van Noordwijk & van Schaik, 2005). The results from Schuppli et al. (2016b) also show that feeding rates (a measure of food processing competence) for easier-to-process food items are reached earlier than feeding rates for more difficult-to-process food items. Immatures start feeding on difficult-to-process food items later in their development than on easier-to-process food items. Adult-like feeding rates are reached after weaning but before the age at first reproduction. Male immatures reach faster feeding rates earlier than female immatures.

1.5.4. Combination of skill learning and growth: Schuppli et al. (2016b) suggested that the timing of weaning and the age at first reproduction might be set by a combination of the 'needing-to-learn' and 'expensive brain frameworks' (described above). Energetic investment into learning might reduce the energetic investment into body growth and vice versa. Thus, during immaturity before weaning energy is needed for the brain and thus limits body growth, but energy might also be used intensely for skill learning during infancy where most skills seem to be acquired and thus also limit body growth. After weaning the body can catch up to reach adult body size to start to reproduce.

1.5.5. Female reproduction: Most hypotheses I present focus on the development of the immature orangutans. But very important too for the slow life history of orangutans, including late age of weaning and long inter-birth intervals, are female reproductive characteristics since females invest a lot of energy in their offspring (van Noordwijk, 2012). In this section, I will, therefore, describe some important characteristics following van Noordwijk et al. (2013). Orangutans, along with other species with slow life histories, show patterns of multi-year lactation, meaning that mothers provide their offspring with milk over multiple years. These species cannot predict and time the periods of highest energy need with the periods of highest food availability. Instead, they experience several fluctuations in food availability during their extended periods of lactation. Orangutan females are limited in storing excess energy from periods of high food availability for periods of low food availability since they bear a large cost of weight because of the arboreal lifestyle (Pontzer et al., 2010). On a daily basis, female orangutans can adjust their energetic demands by adjusting food intake, mobilizing energy reserves or adjusting their activity levels. These adjustments can be effective because the cost of daily lactation is not that high (maximally 25% above the baseline). The low productivity of the Southeast Asian rainforests (van Schaik & Pfannes, 2005) has resulted in metabolic adaptations in orangutans (Pontzer et al., 2010). According to van Noordwijk et a. (2013), this might have led to an exaggeration of the conservative nature of lactation in orangutans. They also describe that infants have to supplement their milk intake from an early age onwards (around 1.25 years) because mothers are not able to provide enough energy through lactation over several years to their growing offspring.

1.6 Social learning

To master the complex foraging skills needed for adult survival orangutans rely on social learning (Borneo: Jaeggi et al., 2010; Sumatra: Schuppli et al., 2016a). For species like orangutans that have to learn cognitively demanding foraging skills, simple social learning forms like enhancement (Galef & Giraldeau, 2001) might not be enough. They rely on observational forms of learning in which individuals observe actions of other individuals and then practice what they observed themselves (reviewed in Hoppitt & Laland, 2013). Bastian et al. (2010) suggested that Bornean orangutans show local diet traditions, meaning that diet repertoires are socially learned. In addition to diet traditions, there are other behaviours being described as cultural differences between locations in orangutan populations at different sites, including Sumatra and Borneo (van Schaik, 2004, p137-166; van Schaik et al., 2003; van Schaik et al., 2009; Schuppli & van Schaik, 2019). Social learning is an important means of the transmission of culture (van Schaik & Burkart, 2011).

Studies on orangutan social learning have so far mainly focused on peering behaviour, defined as attentive close range watching of a conspecific's actions (Schuppli et al., 2016a; Ehmann, 2019). These studies have found that orangutan infants undergo so-called peering-practicing cycles where they observe an action and then try to execute the same action. These studies found that infant orangutans peer more and extensively for more complex (difficult-to-process) food items and more for rarer food items than for more common food items (items the mother feeds on more frequently). They also found that juvenile orangutans peer more for rarer food items but not for more complex food items. This is probably the case because juveniles already had more time to perfect their foraging skills, also for difficult-to-process food items. Thus, they are most interested in rare food items they do not encounter often.

However, infant orangutans might also learn about difficult-to-process food items via food transfer from their mothers (Brown et al., 2004). Jaeggi et al. (2008) investigated food transfers in Bornean orangutan (*Pongo pygmaeus wurmbii*) infants. They looked into begging behaviour, defined as the attempts of an orangutan to obtain a food item or a part of it which another orangutan is holding, by obvious gestures (such as reaching for the food or holding an outstretched hand at the food owner's mouth). When the orangutan was able to take some food, the solicitation was considered successful and when the begging orangutan stopped and started doing another activity, it was considered unsuccessful.

Jaeggi et al. (2008) found a high negative correlation between the infants' ages and the number of solicitations, meaning older infants beg less than younger infants. They also found that all four offspring in their study begged more for difficult-to-process food items than for easier-to process food items (they divided the complexity of the food items into two categories: easy and difficult). Younger infants begged for a wider variety of food items than older infants. They expected the begging rate to correlate negatively with the number of feeding bouts of the mother on a particular food item (a measure of frequency of the food items), but surprisingly, they found the opposite pattern. Studies on feeding competences show that age is positively correlated with feeding competence (Schuppli et al., 2016a). But age and competence might still hold different information, thus this distinction is important. Jaeggi et al. (2008) also investigated ecological competence of the infants and found that ecologically more competent offspring solicited less food from the mother. When looking into success they found that infants were more successful when they begged for more complex food items than for easier food items.

2. Questions and predictions

The aim of this thesis is to investigate the development of feeding skills during the developmental phase in Sumatran orangutans (*Pongo abelii*). The main focus hereby lies on i) begging behaviour, a potentially important means of gaining knowledge and acquiring skills for immature orangutans, and ii) on feeding rates, a direct measure of food processing skills. These topics are highly important for understanding the long developmental phase in Sumatran orangutans. In most of the presented hypotheses on why orangutans show such late weaning and long inter-birth intervals (described in the introduction above), skill learning plays a crucial role. Even though previous studies have found suggestive patterns, there is still more research needed to understand the development of skill acquisition and the effect it has on the life history of orangutans.

In a first step, I will look into infants' begging behaviour and how its occurrence and outcome might be affected by the factors age and sex of the infant orangutans, and the complexity and frequency of the food items. I will look into the begging behaviour from the infant's perspective, thus investigating the number of solicitations and I will look into the begging behaviour from the mother's perspective, thus investigating the success of the solicitations.

In a second step, I will focus on feeding rates, as a measure of food processing competence, which is an important aspect of feeding competence to acquire for orangutan immatures. In this part, I will also look into the factors age and sex of the immatures, and complexity and frequency of the food items.

In a third step, I will add the parts on begging and feeding together because another important factor possibly having an influence on begging behaviour is actual feeding competence.

2.1 Part 1: Begging behaviour - Infant's perspective

How do the factors complexity and frequency of the food items influence the begging rate of infants?
Predictions:
Under the assumption that begging is a means of gaining knowledge about food items and their required processing, infants should beg more frequently for complex food items, because it takes several years to perfect feeding techniques for difficult-to-process food items. Infants should also beg more frequently for rare food items because it is important to use every provided learning opportunity. Previous studies on peering behaviour of infants (Schuppli et al., 2016a; Ehmann, 2019) could show that item complexity and rarity affect peering behaviour. A previous study on begging behaviour (Jaeggi et al., 2008) showed that infants indeed beg more for complex food items, but also that infants beg more for more common food items, contradicting my prediction.

How do the factors age and sex of the infants influence the begging rate of infants?
Predictions:
Under the assumption that begging is means of gaining knowledge about food items and their required processing, age should be negatively correlated with solicitation frequency, because as infants get older, they become more competent (Schuppli et al., 2016b). The study conducted by Jaeggi et a. (2008) found this effect. Observations on chimpanzees show that females are faster in acquiring nut-cracking skills than males (Boesch & Boesch-Achermann, 2000), maybe because females are more interested in learning complex foraging techniques like nut-cracking or termite fishing. Based on these findings, I predict that female orangutan infants will beg less than male orangutan infants.

2.2 Part 2: Begging behaviour - Mother's perspective

How do the factors complexity and frequency of the food items influence the success of begging events?
Predictions:
Under the assumption that begging is a means of gaining knowledge about food items and their required processing and that mothers adjust their behaviour to support their infants' learning process infants begging for more complex and for rarer food items should be more successful. Jaeggi et al. (2008) found that infants begging for more complex food items indeed were more successful.

How do the factors age and sex of the infants influence the success of begging events?
Predictions:
Under the assumption that begging is a means of gaining knowledge about food items and their required processing and that mothers adjust their behaviour to support their infants' learning process, success rates should decrease with increasing age of the infants, because older infants will have reached higher skill levels (Schuppli et al., 2016b). Findings from studies on chimpanzees show that sons receive a larger number of nuts from their mothers than daughters do (Boesch & Boesch-Achermann, 2000; Estienne et al., 2019a) and mothers are more likely to refuse sharing of nuts with daughters than with sons (Estienne et al., 2019a). This behaviour of the mothers could be linked to the observations that females acquire nut-cracking skills earlier than males (Boesch & Boesch-Achermann, 2000), maybe because females are be more interested in learning complex foraging techniques like nut-cracking or termite fishing. Based on these findings, I predict that male orangutan infants will have more success with their solicitations than females,

2.3 Part 3: Feeding rates

How do the factors complexity and rarity of the food items influence feeding rates?
Predictions:
Immatures should reach adult-like feeding rates faster for easier-to process food items (showed in Schuppli et al., 2016b) and for more frequent food items because for the latter they have more opportunities to practice their skills.

How do the factors age and sex of the infants influence feeding rates?
Predictions:
Under the assumption that immatures acquire their foraging skills throughout their developmental phase and based on previous studies (Schuppli et al., 2016b), I predict that age has a positive effect on feeding rates, meaning that with increasing age immatures approach adult-like feeding rates. Schuppli et al. (2016b) showed that males reach faster feeding rates earlier than females. However, the data of this study are heavily biased since all feeding rates from young infants are by males and all feeding rates by juveniles are by females. Contradicting the findings from Schuppli et al. (2016b), studies on chimpanzees show that females reach complex foraging skills like nut-cracking earlier than males (Boesch &Boesch-Achermann, 2000). Therefore, I predict that females reach faster feeding rates earlier than males, at least for difficult-to-process food items.

2.4 Part 4: Combination of begging and feeding

By combining the parts on begging with the part on feeding I gain the factor feeding competence from the part on feeding rates for the analyses on begging behaviour. Age and feeding competence are thought to be highly correlated (Schuppli et al., 2016b) but might still hold different information, meaning that feeding competence is thought to be the more accurate measure than age.

How does the factor feeding competence of the infants influence the begging rate of infants?
Predictions:
Under the assumption that begging is a means of gaining knowledge about food items and their required processing, I predict that more competent infants will beg less than less competent infants. This effect was already shown in the study done by Jaeggi et al. (2008).

How does the factor feeding competence of the infants influence the success rate of infants?
Predictions:
Under the assumption that begging is a means of gaining knowledge about food items and their required processing and that mothers adjust their behaviour to support their infants' learning process, I predict that more competent infants will have less success during their begging events than less competent infants.

3. Material and Methods

3.1 Study period and study site

Data were collected between March and July 2018 at the study site Suaq Balimbing (3°42′ N, 97°26′ E), located in the Gunung Leuser National Park in Aceh Selatan, Sumatra, Indonesia (see Figure 13 in the appendix). Between 1992 and 1997, as well as since 2007 standardised behavioural data have been and are since being collected at this site on wild Sumatran orangutans. The study site mainly consists of peat swamp forest. It offers a higher fruit availability compared to other sites with wild orangutan populations (Marshall et al., 2009), which ultimately results in the currently highest density of wild orangutans with seven individuals per square kilometres (Husson et al., 2009; van Schaik, 2004).

3.2 Study subjects

The main focus of my thesis were orangutan infants, hence the study subjects were mainly infants between the ages zero and nine years (Table 2 and Table 3). Sumatran orangutans reach age at first reproduction between 14-16 years of age (van Noordwijk et al., 2018; Knott et al., 2009; van Noordwijk et al., 2009; Watts & Pusey, 1993). Before becoming adults, they are referred to as immatures. Weaning takes place between 7 to 9 years of age in Sumatran orangutans (van Noordwijk et al., 2018; van Noordwijk & van Schaik, 2005; van Noordwijk et al., 2009), which is later than in any other primate species. In my thesis, I refer to unweaned immatures as infants whereas weaned immatures are referred to as juveniles. Depending on the dataset for the different parts of the thesis, all infants or a part of the infants were represented (Table 2 and Table 3).

Table 2: **Infants observed for begging behaviour.** The infant focal animals, their mothers, sex, estimated Date of Birth (DoB), half-yearly age categories during which data on their begging behaviour were available, total observation hours and total number of begging events recorded.

Infant	Mother	Sex	DoB	Observed ages	Observation hours	Begging events
Amor	Alice	male	01.09.14	2.5	33	3
Cinnamon	Cissy	female	01.04.12	1.5 - 3, 5 - 6.5	919	85
Dalia	Dodi	female	01.10.12	2	63	6

Diddy	Dodi	male	01.01.06	5, 8	44	4
Eden	Ellie	female	01.11.14	0.5, 2 - 4	1271	120
Frankie	Friska	male	01.08.12	1-2, 4.5 - 5.5, 6.5	2681	264
Fredy	Friska	male	01.01.05	6, 8.5 - 9	74	6
Lois	Lisa	male	01.07.10	0.5, 3 - 4.5, 6.5 - 7, 8 - 8.5	1507	144
Luther	Lilly	male	01.02.16	1.5, 3	93	13
Pepito	Piniata	male	01.01.13	4.5, 5.5	128	12
Rendang	Raffi	male	01.04.13	1	258	26
Ronaldo	Raffi	male	01.01.06	5	7	1
Simba	Sarabi	male	01.04.13	0.5 - 1	734	62
Tornado	Tiara	male	01.06.14	3	24	2

Table 3: **Infants and juveniles observed for feeding rates**. Infant and juvenile focal animals, their mothers, sex, estimated Date of Birth (DoB), half-yearly age categories during which feeding rates were available, total number of feeding rates per infant/juvenile, total number of feeding rates per mother.

Infant/ Juvenile	Mother	Sex	DoB	Observed ages	Nr Feeding rates	Nr Feeding rates mother
Chindy	Cissy	female	01.01.03	11	18	82
Cinnamon	Cissy	female	01.04.12	1.5, 6.5	31	82
Eden	Ellie	female	01.11.14	3.5	6	45
Frankie	Friska	male	01.08.12	1	5	55
Fredy	Friska	male	01.01.05	8.5, 9	38	55
Lois	Lisa	male	01.07.10	3, 3.5, 7.5, 8, 8.5	93	132
Luther	Lilly	male	01.02.16	3	2	15
Ronaldo	Raffi	male	01.01.06	8	5	5
Tornado	Tiara	male	01.06.14	4	2	15
–	Dodi	–	–	–	–	1

3.3 Data collection

3.3.1 Activity Data

Data were collected by following the focal animals from their morning to their evening nest whenever possible. Standardized methods of focal animal sampling including instantaneous scan sampling at two-minute intervals and ad libitum focal animal sampling were applied for behavioural observations (detailed description on https://www.aim.uzh.ch/de/orangutannetwork/sfm.html). This method has been used since 2007, thus providing this study with long-term data on most focal animals.

As part of the scan sampling, every two minutes the activity of the focal was recorded. If the activity was feeding, details about what the focal animal was feeding on were recorded: the species of food and which part of the species was fed on (fruit, flower, leaf, vegetation, pith or bark). The combination of the species and the plant part was referred to as "food item". A two-minute interval which consisted of feeding was considered a feeding event.

3.3.2 Begging Data

Special focus was put on begging behaviour. All attempts of orangutans to obtain a food item or a part of a food item which another orangutan is holding, by obvious gestures (such as reaching by hand or by mouth for food items in the mother's hands or mouth, trying to grab food items in the mother's hand or mouth) and all food transfers were classified as begging. This behaviour is mostly observed in orangutan infants begging for food items their mothers are holding. Begging behaviour was recorded ad libitum and described in detail: for every begging event, the identity of the begging individual, the age, the sex and the mother of the begging individual, the food item and the complexity and frequency of the food item (more details in the section variables) was noted. Aside from the begging events which I collected in the field, I had access to begging events collected by previous observers, which resulted in

a total of 744 begging events by 14 infants during the time from January 2011 until January 2019. Only selected observers that were trained in infant behaviour collection were taken into account.

3.3.3 Feeding Data

The second special focus of this thesis were feeding rates which refer to the observed length of ingestion of a food item. Feeding rates were either taken in the field with the help of a stopwatch or by video recordings which were taken when the focal animal was feeding and visible in the canopy. The feeding videos were analysed after the same criteria as the rates which were taken in the field. Depending on the food item type, the processing technique used by the orangutan and on the visibility in the videos and in the field, the used start and endpoint of the ingestion differed. Different starting points included "pick by hand", "pick by mouth", "pick within a bundle of food items", "start to ingest/chew" and different ending points included "drop", "drop within a bundle of food items", "last chew", and "next pick".

The final feeding rate data set included 1526 feeding rates recorded from 17 immatures and their mothers between February 2008 and January 2019. 1005 of these feeding rates were taken directly in the field and 521 were coded from videos. For the mother's speed, I used the average speed per food item.

I also used the feeding rates to measure feeding competence of the immature orangutans. For every immature, its average speed per food item at the age when the rate was taken was calculated and expressed in percentage of the mother's speed for that food item. For 196 of the 1004 feeding rates on infants, there were no feeding rates from the mother available, and so the average over all mothers was taken.

3.4 Variables

I divided my thesis into four parts. The first part focuses on begging behaviour from the infant's perspective where I investigated which factors might affect the number of begging events conducted by the infants, thus the begging rate. In the second part, I looked into the mother's perspective. I tried to find out which factors could influence the success of a begging event, thus which factors are important for a mother to allow her infant to take food from her or not. In the third part, I focused on feeding rates being a part of the competences immature orangutans learn throughout their developmental phase. In the fourth part, I combined the first two parts with the third part to obtain a measure of feeding competence for the analyses on begging behaviour. Details on the four parts and their analyses can be found in Table 4.

3.4.1 Response variables

Depending on the analysis, the response variable differed while the explanatory variables stayed the same or very similar (Table 4). In the first and the fourth part of the thesis, begging rate was the response variable. Begging rate was corrected for the opportunity to beg, meaning the number of begging events per infant, per half-yearly age category and per food item within this infant was divided by the number of feeding events that were recorded of the mother on this particular food item during that time (i.e. while the infant was within this half-yearly age category). With this correction, I took into account the time the mother was feeding on a specific food item while the infant was in a specific half-yearly age category, and thus the opportunity the infant had to beg for this food item. In the second part of the thesis, the success of a begging event was the response variable, which was coded as a binary variable, whereby yes referred to begging events where the infant got the begged for food or a part of it and no referred to begging events where the infant did not get the begged for food or a part of it. In the third part of the thesis, the feeding rate was the response variable, expressed as the percentage of the mother's speed per food item (see section above on data collection). The feeding rate became an explanatory variable in the fourth part of the thesis (see section below on explanatory variables). In the fourth part begging rate was the response variable (see above in this section, but with the change from half-yearly to three-

yearly age categories, see below) when looking into the infant's perspective. When looking into the mother's perspective, success rate per infant, per three-yearly age category and per food item within this infant was the response variable. I calculated this rate by dividing the number of successful begging events per infant, per three-yearly age category and per food item within this infant by the total number of begging events (from which I knew if they turned out to be successful or not) per three-yearly age category and per food item within this infant.

3.4.2 Explanatory variables

For each food item occurring in a begging event or in a feeding event from which the feeding rate was taken, I approximated its complexity via the number of processing steps orangutans have to apply before ingesting the food item (following the description in Schuppli et al., 2016b). The number of the feeding events recorded per food item across all mothers in the population (population frequency) was used to calculate a measure of frequency of the food item in the population by calculating its percentage share of all recorded feeding events.

In addition to complexity and frequency, the age and the sex of the immatures were other explanatory variables. Depending on the analysis and dataset used in the analysis, age was measured as half-yearly age category, three-yearly age category or the exact age was used (Table 4). The immatures' ages were estimated in the field based on the state of their physical development when the birth date was unknown. In the fourth part of the thesis, begging behaviour and feeding rates were combined into the extra explanatory variable feeding competence, which was computed by the immatures' feeding rates in percentage of the mother's speed for this particular food item (see section above on data collection).

3.5 Statistical analysis

I used the R programming language, version 3.6.1 (R Core Team, 2019) for all analyses and plots. To analyse the data, I used general linear mixed models (GLMM), specifically the glmer function which is part of the "lme4" (Bates et al, 2015) package. For the plots, I applied the ggplot function, part of the "ggplot2" package (Wickham, 2016). In the general mixed models, I exerted the Gaussian or the binomial distribution (details in Table 4 and below). I used the cftest function from the "multcomp" package (Hothorn et al., 2008) to obtain p-values in the analyses using Gaussian distribution because Gaussian GLMM's do not automatically give p-values. I used different datasets for the different analyses (Table 4).

The models used to analyse the infant's perspective of the begging behaviour (part one) used a condensed dataset of the four infants observed the most (two females, Cinnamon and Eden, and two males, Frankie and Lois). The data was based on a combination of infant, half-yearly age category and food item. Because the response variable was the infants' begging rate, the Gaussian family distribution was used for the analysis.

The models used to analyse the mother's perspective of the begging behaviour (part two) used the dataset based on the individual begging events. For these analyses, the binomial family distribution was used in the models because the response variable 'success' is either 'yes' or 'no'.

The models used for the analyses of the feeding rates (part three) were based on the dataset where individual feeding rates across infants and mothers were recorded. Gaussian distribution was used for the analysis of the feeding rates.

The models used to analyse the infant's feeding competence and its effect on the begging rate and on begging success (part four) used a condensed dataset based on a combination of three-yearly age category across all infants and food item. In order to obtain enough data points comprising information on begging behaviour (begging rate and success rate respectively) and feeding rates at the same time, the data was lumped across the different immatures and the age category had to be increased from half-yearly to three-yearly. I created two datasets, one containing the infants' begging rates (infants'

perspective) and one containing success rate (mother's perspective). Besides three-yearly age category as explanatory variable, both datasets contain the explanatory variables complexity and frequency as well as feeding competence represented as feeding rates measured as the percentage of the mother's speed. For both analyses, I used models with a Gaussian family distribution.

To account for the fact that several individuals occur multiple times within the dataset (e.g. at different developmental time points), I added the individual as a random effect to the models, whenever this was the case. I did the same for food items in the datasets where the same food items occurred more than once within the same individuals. Specifically, for part two of the thesis on the success of begging behaviour, I added the mother as a random effect as well, because the mother is an important factor for the outcome of a begging event as successful or not.

3.5.1 Model selection

I applied backward model selection based on the Akaike Information Criterion using the AIC and the anova function, both from the "stats" package (R Core Team, 2012). Projects investigating similar relations (Ehmann, 2019; Jaeggi et al., 2010; Schuppli et al., 2016a) noticed that certain variables being investigated can have strong effects on the response variable and thus influence the effect other variables have on the response variable. With backward model selection, it is possible to find out which variables have strong effects. This is important because if a variable has a strong effect, I might need to correct for it to find effects of other variables. I used almost the same order of removing explanatory variables in the model selection process throughout all parts of the analyses to ensure a standardized procedure. I removed the variables in the following order: age, frequency, complexity, sex; unless I noticed that it might be better to remove them in a different way. Before the model selection process, I determined if certain variables need to be log-transformed to ensure a normal residual distribution. I did this by visual inspection of the residual distribution of the full mode.

3.5.2 Simple correlation analyses

For the fourth part of the thesis on the combination of begging behaviour and feeding, I used simple correlation analyses because the samples were small. I needed a feeding rate and a begging/success rate per three-yearly age category and per food item to obtain the information I need for the fourth part. The datasets are small because this overlap was small. The dataset containing begging rate as response variable has 13 datapoints while the dataset containing success rate as response variable has 17 datapoints. Because of these small sample sizes ($N < 30$) and because of an assessment of normality I decided to use Kendall's tau as correlation coefficient. The checks of normality with numbers as well as diagnostic plots (histograms and qq-plots) revealed that in both datasets the response variable is not normally distributed (details and plots in the results section below). I used the function cor.test from the "stats" package (R Core Team, 2012) and specified the method as 'Kendall'.

3.5.3 Visualisations

For some visualisations of the results from the analyses, I used residual plots (indicated in Figure description), because of the strong effects certain variables can have on the response variable as described above. In these cases, when showing the relation of an explanatory variable and the response variable, I corrected the response variable for the effects of all other explanatory variables to get a visualisation of the pure relationship of the response variable and the explanatory variable visible in the plot. I only used residuals for the plots to achieve a clear visualisation, but not for any analyses.

Table 4: **Summary of the statistical analyses** of the four parts of the thesis containing information on the datasets, response variables, distribution used in the models, random effects and explanatory variables.

Thesis part	**Analysis**	**Dataset**	**Response variable**	**Random effect 'Individual'**	**Random effect 'Food item'**
1	Infant's perspective	condensed (per infant, half-yearly and food item)	begging rate	yes	no
2	Mother's perspective	event-based	success	yes	yes
3	Feeding rates	event-based	feeding rate	yes	yes
4a	Infant's perspective (begging + feeding)	condensed (per three-yearly and food item)	begging rate	no	no
4b	Mother's perspective begging + feeding)	condensed (per three-yearly and food item)	success rate	no	no

Thesis part	**Explanatory variables**					**Distribution**	**Random effect 'Mother'**
	Age	**Complexity**	**Frequency**	**Sex**	**Feeding competence**		
1	half-yearly	yes	yes	no	no	Gaussian	no
2	exact	yes	yes	no	no	Binomial	yes
3	exact	yes	yes	yes	no	Gaussian	no
4a	three-yearly	yes	yes	no	yes	Simple correlation with Kendall's tau	no
4b	three-yearly	yes	yes	no	yes	Simple correlation with Kendall's tau	no

4. Results

The results section is divided into four parts based on the four parts of the thesis described in the methods above. Before the first part, there is a chapter on descriptive statistics to visualise the data used in this thesis.

4.1 Descriptive statistics

4.1.1 Part 1 and 2: Begging behaviour

Most begging events in my datasets are from young infants and then from age seven onwards, there are very few begging events available (Figure 1). It is evident that there is a bias towards begging events from males in my data (Figure 1 right). All begging events from individuals aged seven or older are by males. Almost all begging events are directed at the mother and only very few at other individuals (Figure 2). Because all observers were recording all begging events of their infant focal animals, this descriptive result is not a bias but depicts the real pattern. Figure 3 shows the percentage of the begging events which were successful, not successful and from which the outcome was not available, per half-yearly age category.

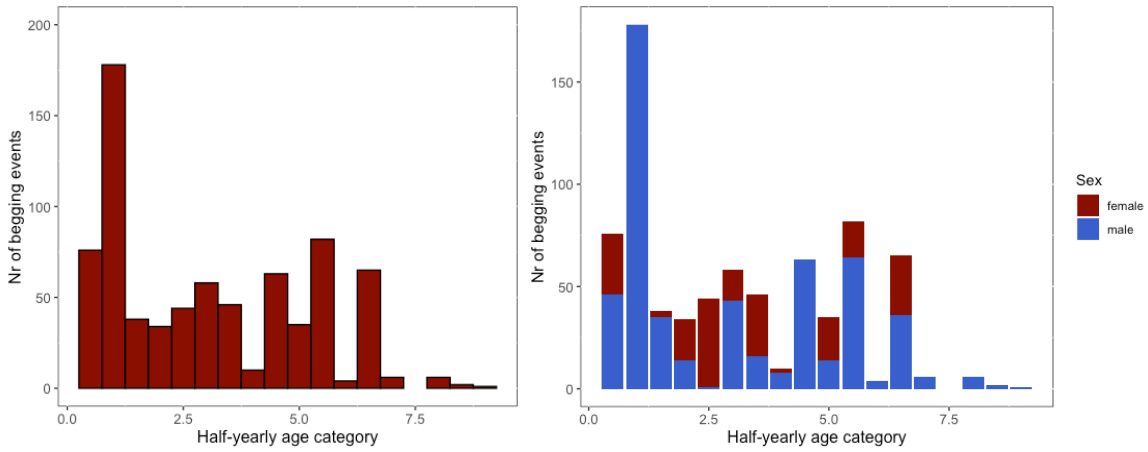

Figure 1: **Begging events available, grouped by sex.** Number of begging events per half-yearly age category (left), grouped by sex (right).

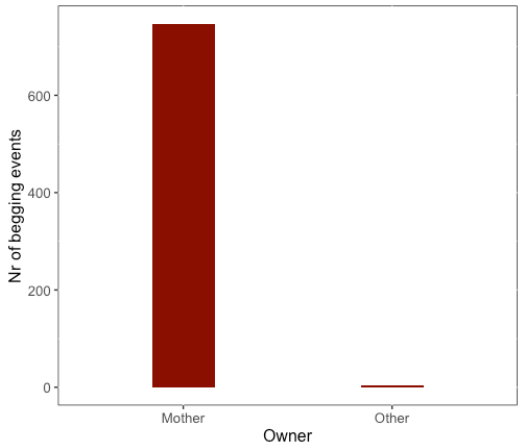

Figure 2: **Identity of the owner**. The number of begging events directed at the mother vs. at other individuals (owner of the begged for food items).

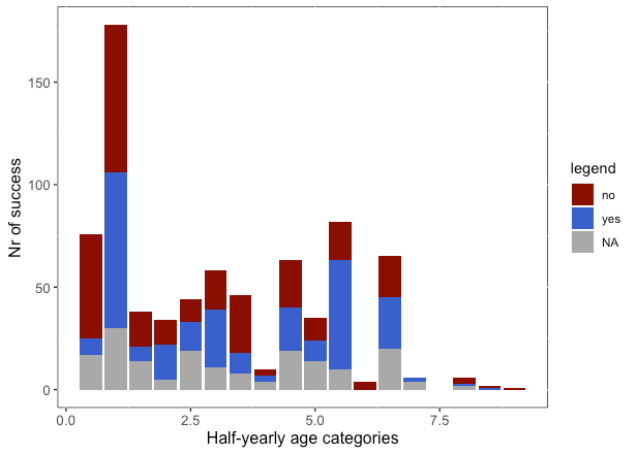

Figure 3: **Begging over age grouped by success**. Number of begging events per half-yearly age category grouped by if they were successful or not or the outcome was not available.

4.1.2 Part 3: Feeding rates

In Figure 4 it is visible that, even though there are feeding rates from all ages, I have more feeding rate measures available from older infants and juveniles than from younger infants. In Figure 4 (right) it is visible that there is a bias in the data when it comes to the two sexes: All feeding rates from juveniles are by females while most of the feeding rates from infants are by males.

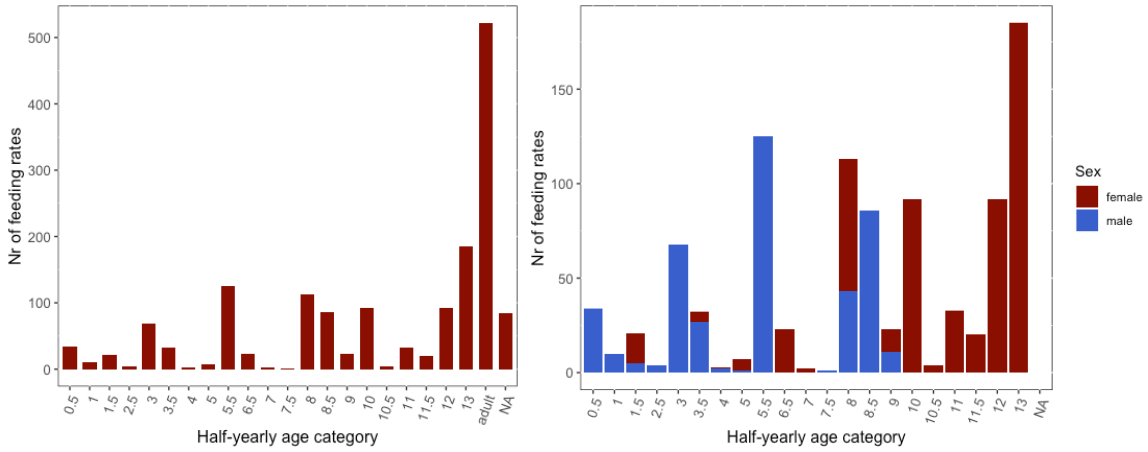

Figure 4: **Feeding rates available across age, grouped by sex**. Number of recorded feeding rates per half-yearly age category including the feeding rates recorded from mothers (adult category) (left). Number of recorded feeding rates on immatures grouped by sex (right).

4.2 Part 1: Begging behaviour - Infant's perspective

The first of the four main parts of this thesis is to analyse the effects of different factors on infants' begging behaviour. For these analyses, the begging rate (corrected for the opportunity to beg, see methods) is the response variable. Age and sex of the infants, complexity, and frequency of the food items are the explanatory variables. Begging rate and frequency are log-transformed in order to achieve normally distributed model residuals. See 'Material and Methods', specifically Table 4 for more information on the analyses.

The full model contains all four explanatory variables; age and sex of the infants, complexity and frequency of the food items. According to the AIC values, no other model performs better than the full

model (AIC(full model) < AIC(other models) or deltaAIC < 2). The effects of the factors sex and complexity did not reach statistical significance (Table 5). Likewise, when repeating the model selection process with Anova comparisons of the different models, the inclusions of the factors sex and complexity was not warranted (see Table 11 in the appendix). Because of these contradictions, I will present the full model and the model containing age and frequency.

In the full model age and frequency both have a negative significant effect on the begging rate (p-value < .05 and p-value < .001 respectively), whereas sex and complexity do not have a significant effect on the begging rate (p-value > .05) (Table 5). Likewise, in the model containing age and frequency but not sex and complexity, age and frequency both have a negative significant effect on the begging rate (p-value < .001 for both variables) (Table 6).

The AIC model selection shows that the full model performs better than the null model (the AIC of the full model is lower than the AIC of the null model by 104.29 points). This is confirmed by an Anova comparison (see Table 12 in the appendix). When assessing the proportion of the total variation explained by the full model, R^2c shows that 41.24% of the variation within the data is explained by the fixed and random effects of the model. R^2m shows that 36.10% of the variation within the data is explained purely by the fixed effects, thus the explanatory variables.

The AIC comparison between the model containing age and frequency but not sex and complexity and the null model shows that the AIC of the model containing age and frequency is lower than the AIC of the null model by 47.14 points. This is confirmed by an Anova comparison (see Table 13 in the appendix). When assessing the proportion of the total variation explained by the model containing only age and frequency, R^2c shows that 38.65% of the variation within the data is explained by the fixed and random effects. R^2m shows that 34.60% of the variation within the data is explained purely by the fixed effects, thus the explanatory variables.

All in all, the results of the first part of the thesis coherently show that i) older infants beg less than younger infants (Figure 5), ii) that infants beg more for food items which are rare than for more common food items (Figure 6), iii) the complexity of the food item does not affect begging rates and that iv) there is no difference in begging rates between male and female infants.

Table 5: **Effects on begging behaviour**. Full GLMM with begging rate (corrected for the opportunity to beg) per food item and per half-yearly age category as the response variable. Estimates, standard errors, z-values and p-values of the explanatory variables age, sex, frequency and complexity, and individual as a random effect. N gives the number of observations and the number of levels in a categorical variable.

Effect	**Effect type**	**Estimate**	**Std. Error**	**z**	**p-value**	**N** (116)	**95% CI**
Intercept	-	-4.95	0.61	-	-	-	-
AgeCat1/2Y	Fixed	-0.19	0.07	-2.50	**< .05**	Cont.	-0.32 to -0.04
Sex	Fixed	0.40	0.52	0.78	> .05	2	-0.52 to 1.33
Complexity	Fixed	-0.56	0.11	-0.53	> .05	Cont.	-0.27 to 0.14
Frequency (log)	Fixed	-0.63	0.08	-7.55	**< .001**	Cont.	-0.79 to -0.46
Individual	Random	-	-	-	-	4	-

Table 6: **Effects on begging behaviour**. GLMM with the begging rate (corrected for the opportunity to beg) per food item and per half-yearly age category as the response variable. Estimates, standard errors, z-values and p-values of the explanatory variables age and frequency, and a random effect of the individual. N gives the number of observations and the number of levels in a categorical variable.

Effect	**Effect type**	**Estimate**	**Std. Error**	**z**	**p-value**	**N** (132)	**95% CI**
Intercept	-	-4.67	0.49	-	-	-	-
AgeCat1/2Y	Fixed	-0.22	0.07	-3.33	**< .001**	Cont.	-0.35 to 0.09
Frequency (log)	Fixed	-0.63	0.08	-7.89	**< .001**	Cont.	-0.78 to -0.47
Individual	Random	-	-	-	-	4	-

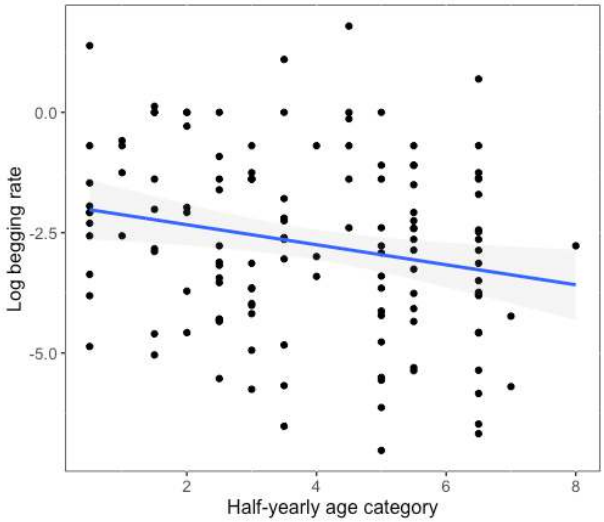

Figure 5: **The effect of age on the begging rate**. Age (measured in half-yearly age categories) has a significant negative effect on the begging rate (log-transformed) (p-value < .05 in the full model and p-value < .001 in the model containing age and frequency but not sex and complexity) visible by the linear regression line and its surrounding 95% confidence interval, showing that with increasing age infants beg less.

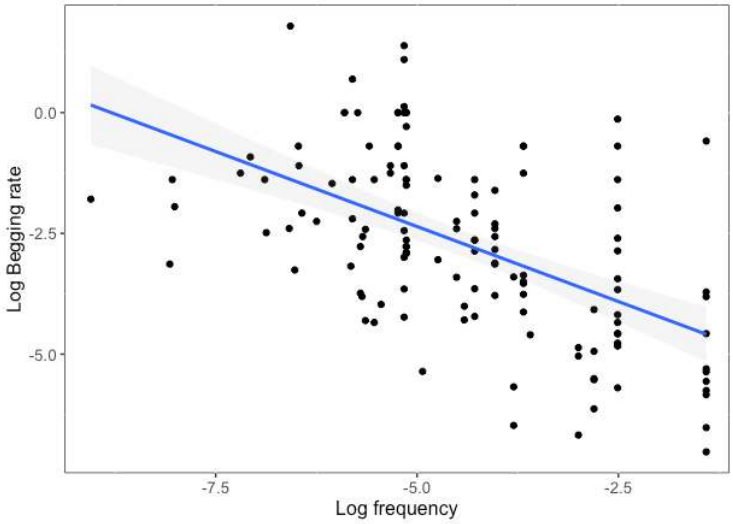

Figure 6: **The effect of frequency on the begging rate**. Frequency (log-transformed) has a negative significant effect on the begging rate (log-transformed) (p-value < .001) visible by the linear regression line and its surrounding 95% confidence interval, showing that infants beg more for rare than for more common food items.

4.3 Part 2: Begging behaviour - Mother's perspective

The second question was which factors influence the success of begging behaviour. Success per begging event, coded binomially as 'yes' or 'no', is the response variable. The explanatory variables are the same as in part one: age and sex of the infants, complexity and frequency of the food items. See 'Material and Methods', specifically Table 4 for more information on the analyses.

The full model contains all four explanatory variables, age and sex of the infants, complexity and frequency of the food items. The model selection process was not quite clear in this analysis (see Table 17 in the appendix for an overview). According to the AIC values, the full model performs better than all other models (AIC(full model) < AIC(other models) or deltaAIC < 2), but according to the Anova comparisons the full model does not perform significantly better than most other models (Anova comparison between the full model and the model containing complexity can be found in Table 14 in the appendix) while there are some trends showing that the full model seems to perform better than some models (see Table 17 in the appendix). Complexity reaches statistical significance in all models containing this variable while all other variables did not reach statistical significance in any models. In the model selection process with Anova comparisons excluding complexity was not warranted. Because of that and the contradictions between the AIC values and the Anova comparisons, I will present the full model and the model containing only the variable complexity, being one of the lean models.

In the full model and the model containing complexity the variable complexity has a positive significant effect on the success of a begging event (Table 7 and Table 8). Infants are more successful when begging for more complex food items than when begging for easier-to-process food items, showing that mothers might be more tolerant when infants beg for complex food items (Figure 7).

The AIC model selection shows that the full model performs better than the null model with a difference of 123.03 points. The Anova comparison of these two models contradicts this result (see Table 15 in the appendix). When assessing the proportion of the total variation explained by the full model, R^2c shows that 21.46% of the variation within the data is explained by the fixed and random effects. R^2m shows that 4.22% of the variation within the data is explained purely by the fixed effects, thus the explanatory variables. Thus, a lot of the variation the full model explains is due to the random effects,

individual differences, food item differences and differences between the mothers, rather than the fixed effects.
The AIC comparison between the model containing complexity and the null model shows that the model containing complexity performs better than the null model by 92.98 points. The Anova comparison of these two models confirms this finding (see Table 16 in the appendix). When assessing the proportion of the total variation explained by the full model, R^2c shows that 20.58% of the variation within the data is explained by the fixed and random effects. R^2m shows that 3.87% of the variation within the data is explained purely by the fixed effects, thus the explanatory variables. As with the full model, a lot of the variation the full model explains is due to the random effects, individual differences, food item differences and differences between the mothers, rather than the fixed effects.

All in all, the results of the second part show that i) infants are more successful when begging for more complex food items (Figure 7), ii) age of the infants does not have an effect on the success of begging events, iii) the frequency of the food items does not affect the success of begging rate and that iv) there is no difference in success per begging event between male and female infants.

Table 7: **Effects on the success of begging events**. Full GLMM with success of begging events as the response variable. Estimates, standard errors, z-values and p-values of the explanatory variables age, sex, frequency and complexity, and a random effect of the individual and the food item. N gives the number of observations and the number of levels in a categorical variable.

Effect	**Effect type**	**Estimate**	**Std. Error**	**z**	**p-value**	**N** (486)	**95% CI**
Intercept	-	-1.25	0.54	-	-	-	-
Age	Fixed	0.04	0.06	0.70	> .05	Cont.	-0.08 to 0.17
Frequency	Fixed	0.93	2.81	0.33	> .05	Cont.	-5.20 to 6.75
Complexity	Fixed	0.26	0.11	2.36	**< .05**	Cont.	0.04 to 0.48
Sex (male = 0)	Fixed	0.14	0.53	0.27	> .05	2	-1.07 to 1.29
Individual	Random	-	-	-	-	15	-
Food item	Random	-	-	-	-	60	-

Table 8: **Effects on the success of begging events**. GLMM with success of begging events as the response variable. Estimates, standard errors, z-values and p-values of the explanatory variable complexity, and a random effect of the individual and the food item. N gives the number of observations and the number of levels in a categorical variable.

Effect	**Effect type**	**Estimate**	**Std. Error**	**z**	**p-value**	**N** (511)	**95% CI**
Intercept	-	-1.02	0.34	-	-	-	-
Complexity	Fixed	0.28	0.10	2.86	**< .05**	Cont.	0.08 to 0.48
Individual	Random	-	-	-	-	15	-

Food item	Random	-	-	-	-	72	-

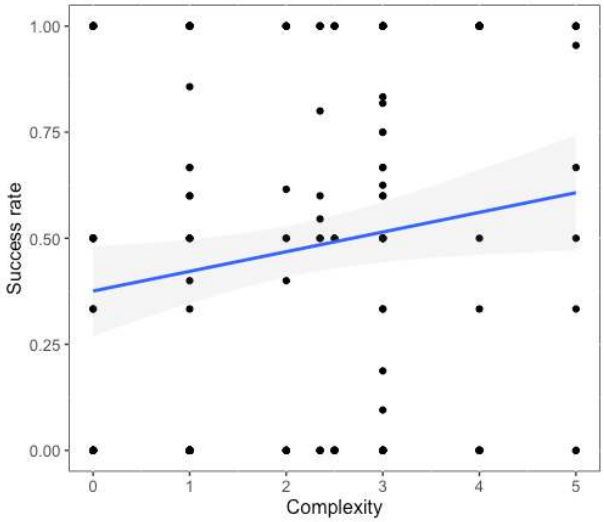

Figure 7: **The effect of complexity on the success of begging events**. Complexity has a positive significant effect on the success of begging events (p-value < .05) visible by the linear regression line and its surrounding 95% confidence interval, showing that infants are more successful when they beg for more complex food items. I used a condensed dataset for better visualisation (success rate per individual, per half-yearly age category and per food item within the individual and the half-yearly age category) in contrast to the analysis where I used the event-based dataset.

4.4 Part 3: Feeding rates

The third question was which factors affect feeding rates. The response variable is feeding rate while the explanatory variables are the same as in the two preceding parts: age and sex of the immatures, complexity and frequency of the food items. See 'Material and Methods', specifically Table 4 for more information on the analyses.

The full model contains all four explanatory variables; age and sex of the infants, complexity and frequency of the food items. According to the AIC values, the model containing only the variable age performs better than any other model, including the full model (deltaAIC = 11.55). This is confirmed by an Anova comparison (see Table 18 in the appendix). The variable age reached statistical significance in all models it was contained while all other variables did not reach statistical significance in any model. Additionally, in the model selection process with Anova comparisons excluding age was not warranted. I will present the full model and the best model according to AIC values and Anova comparisons, thus the model containing age.

In the best model as well as in the full model age has a positive significant effect on the feeding rate (p-value < .001) (Table 9 and Table 10), meaning immatures become more competent when they get older, approaching their mother's speed of ingesting food items (Figure 8).

The AIC model selection shows that the full model performs better than the null model by 100.57 points. The Anova comparison of these two models indicates that the full model does not perform significantly better than the null model, contradicting the AIC values (see Table 19 in the appendix). When assessing the proportion of the total variation explained by the best model, R^2c shows that 50.88% of the variation within the data is explained by the fixed and random effects. R^2m shows that 25.82 % of the variation within the data is explained purely by the fixed effects, thus the explanatory variables.

The AIC comparison between the best model containing age and the null model shows that the AIC of the model containing age is lower than the AIC of the null model by 112.11 points. The Anova comparison reveals that the best model does not perform significantly better than the null model (see Table 20 in the appendix), contradicting the AIC values. When assessing the proportion of the total variation explained by the best model, R^2c shows that 50.00% of the variation within the data is explained by the fixed and random effects. R^2m shows that 26.03% of the variation within the data is explained purely by the fixed effects, thus the explanatory variables.
All in all, the results of the third part of the thesis show that i) with increasing age immatures become more competent in their feeding skills, approaching their mothers' speed of ingesting food items, ii) frequency of the food items does not have an effect on the feeding rate, iii) complexity of the food items does not affect the feeding rates and iv) there is no difference in feeding rates between male and female immatures.

Table 9: **Effects on feeding rate**. GLMM with the feeding rate as the response variable. Estimates, standard errors, z-values and p-values of the explanatory variable age, and a random effect of the individual and the food item. N gives the number of observations and the number of levels in a categorical variable.

Effect	**Effect type**	**Estimate**	**Std. Error**	**z**	**p-value**	**N** (880)	**95% CI**
Intercept	-	-1.51	0.15	-	-	-	-
Age	Fixed	0.11	0.01	9.98	**< .001**	Cont.	0.09 to 0.14
Individual	Random	-	-	-	-	14	-
Food item	Random	-	-	-	-	16	-

Table 10: **Effects on feeding rate**. Full GLMM with the feeding rate as the response variable. Estimates, standard errors, z-values and p-values of the explanatory variables age, complexity, frequency and sex, and a random effect of the individual and the food item. N gives the number of observations and the number of levels in a categorical variable.

Effect	**Effect type**	**Estimate**	**Std. Error**	**z**	**p-value**	**N** (879)	**95% CI**
Intercept	-	-1.55	0.34	-	-	-	-
Age	Fixed	0.11	0.01	9.60	**< .001**	Cont.	0.09 to 0.14
Complexity	Fixed	0.08	0.08	1.01	> .05	Cont.	-0.07 to 0.24
Frequency (log)	Fixed	0.04	0.05	0.76	> .05	Cont.	-0.06 to 0.13
Sex (male = 0)	Fixed	0.05	0.21	0.24	> .05	2	-0.36 to 0.47
Individual	Random	-	-	-	-	14	-
Food item	Random	-	-	-	-	15	-

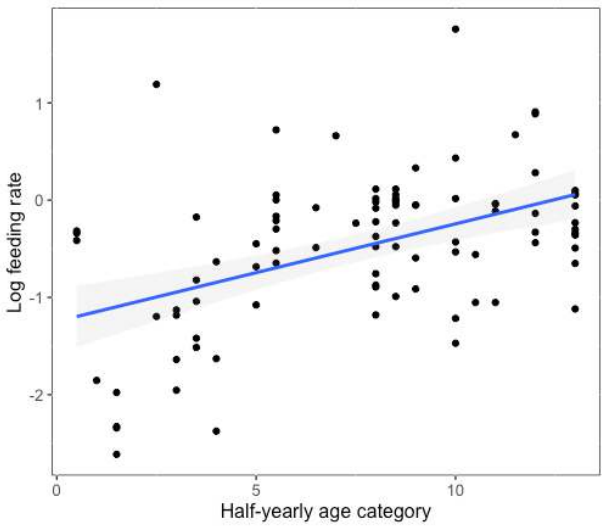

Figure 8: **The effect of age on the feeding rate**. Age has a positive significant effect on the feeding rate (log-transformed) (p-value < .001) visible by the linear regression line and its surrounding 95% confidence interval, showing that with increasing age infants become more competent and approach their mother's speed. I used a condensed dataset for better visualisation (average feeding rate per individual, per half-yearly age category and per food item within the individual and the half-yearly age category) in contrast to the analysis where I used the event-based dataset.

4.5 Part 4: Combination of begging and feeding

In the fourth part of the thesis, I bring together part one and two on begging behaviour and part three on feeding. With these merged datasets I gain feeding competence from part three as an explanatory variable for the analysis of begging behaviour (details in the methods above). I have a dataset with begging behaviour as response variable (infant's perspective) and one with success rate as response variable (mother's perspective). The explanatory variables are three-yearly age category, frequency, complexity and feeding competence. As mentioned in the methods I perform simple correlation analyses of the response variable and one explanatory variable at a time. See 'Material and Methods', specifically Table 4 for more information on the analyses.

4.5.1 Infant's perspective

The assessment of normality revealed that the response variable begging rate is not normally distributed (Shapiro-Wilk test: W = 5.47, p-value < .001). This is confirmed by a visual assessment with the help of a histogram and a qq-plot (Figure 10). Because of that and because of the small dataset (N < 30) I will use Kendall's tau as correlation coefficient for the correlation analysis.

The aim of this part of the thesis is to make a distinction between the factors age and feeding competence even though from part three on feeding rates and from earlier studies (Schuppli et al., 2016b) it becomes evident that these two seem to be linked. Age and feeding competence might hold different information even though they are correlated. It is visible in Figure 9 that feeding competence might have a positive effect on the begging rate (given that the data point at feeding competence equals 2 is not an outlier), in contrast to the variable age which has a negative significant effect on the begging rate, as seen in the results in part one (Table 5 and Table 6 and Figure 5). This would mean even though age and feeding competence seem to be correlated that they have opposite effects on the begging rate. The correlation analysis reveals that feeding competence and begging rate are not correlated (T = 46, p-value > .05). More information on the other variables can be found in Figure 14 in the appendix.

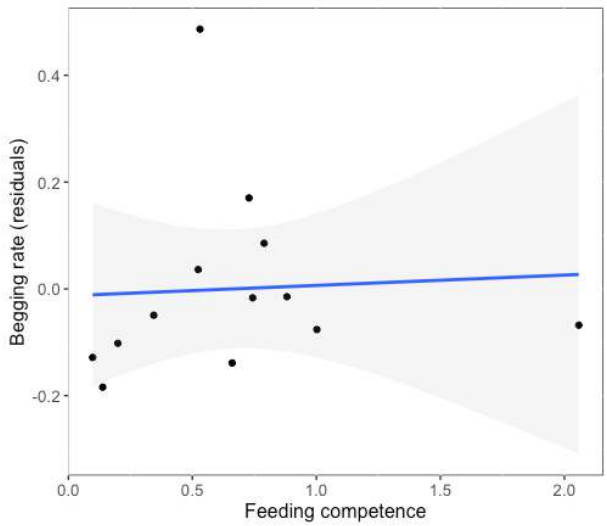

Figure 9: **Relationships of the begging rate with feeding competence**. Even though it looks like the feeding competence might have a positive significant effect on the begging rate, the simple correlation analyses with Kendall's tau reveals they are not significantly correlated (p-value > .05). I used residual plots for this Figure because they represented the individual relationships of the explanatory variables with the response variable clearer.

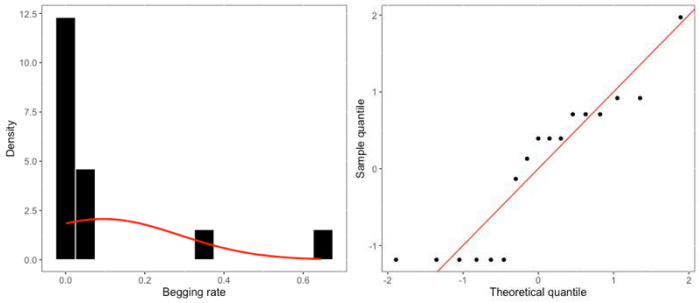

Figure 10: **Histogram (left) and qq-plot (right) of the distribution of the response variable begging rate**. Both plots confirm the Shapiro-Wilk test (p-value < .001) that begging rate is not normally distributed.

4.5.2 Mother's perspective

As in the section above on the infant's perspective, the assessment of normality revealed that the response variable success rate is not normally distributed (Shapiro-Wilk test: W = 0.86, p-value < .05). This is confirmed by a visual assessment with the help of a histogram and a qq-plot (Figure 12). Because of that and because of the small dataset (N < 30) I will use Kendall's tau as correlation coefficient for the correlation analysis.

In Figure 11 it is visible that feeding competence could be positively correlated with the success rate of begging events (given that the data point at feeding competence equals 2 is not an outlier). The same trend was visible with the begging rate in the section above (Figure 9). The correlation analysis reveals that feeding competence and success rate are not correlated (z = 0.68, p-value > .05). More information on the other variables can be found in Figure 15 in the appendix.

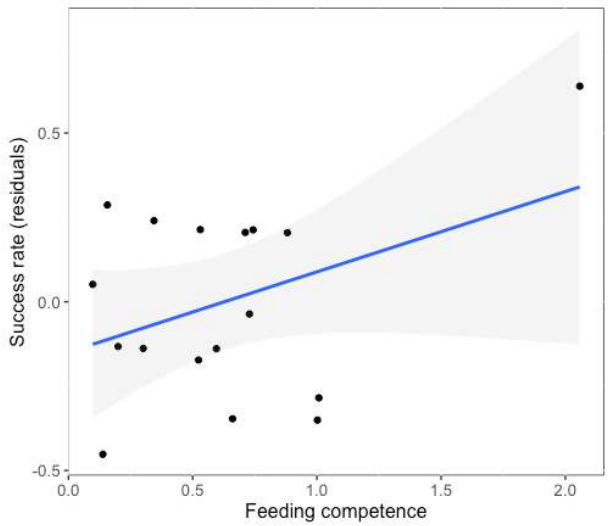

Figure 11: **Relationships of the success rate with feeding competence**. Even though it looks like the feeding competence might have a positive significant effect on the success rate, the simple correlation analyses with Kendall's tau reveals they are not significantly correlated (p-value > .05). I used residual plots for this Figure because they represented the individual relationships of the explanatory variables with the response variable clearer.

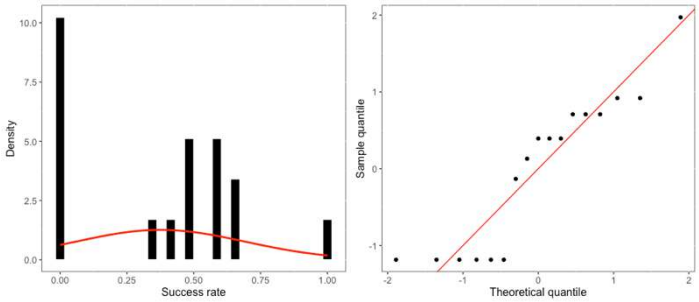

Figure 12: **Histogram (left) and qq-plot (right) of the distribution of the response variable success rate**. Both plots confirm the Shapiro-Wilk test (p-value < .05) that begging rate is not normally distributed.

All in all, the pilot results from the fourth part of the thesis show that competence does not have an effect on the begging as well as the success rate even though in the plots (Figure 9 and Figure 11) it looks like feeding competence might have a positive effect (given that the data point at feeding competence equals 2 is not an outlier), in contrast to the age having a negative effect on the begging rate (results part one).

5. Discussion

The aim of my thesis was to investigate immatures' begging behaviour and the development of feeding competence in Sumatran orangutans (*Pongo abelii*). The ultimate goal was to gain a better understanding of the connection between the orangutans' slow life history and their skill acquisition. I looked at begging behaviour from the infant's perspective as well as from the mother's perspective to find out which factors affect the begging behaviour of the infants and the success of their begging behaviour. Additionally, I looked into feeding rates, the speed with which orangutans ingest food items. In a last step, I combined the parts on feeding and begging to gain the extra factor feeding competence which might have an effect on begging behaviour.

5.1 The effects of age and feeding competence on infants' begging behaviour and their mothers' tolerance

The analyses on begging behaviour revealed that the number of begging events decreases with increasing age of the infants, thus infants beg more when they are younger. This finding is in line with my prediction and confirms the results from Jaeggi et al. (2008) on Bornean orangutans which also found that the number of solicitations decrease when infants become older. It is likely that older infants have already gained enough knowledge and skills and thus do not rely on their mothers to obtain most food items anymore. However, the pilot results on the connection between feeding competence and begging rates from part four of this thesis do not find a correlation between skill level and begging behaviour, and thus as such contradict the results from Jaeggi et al. (2008). However, the data set used in the fourth part of my thesis was very small. Similarly, the study done by Jaeggi et al. (2008) only comprises four infants at one specific age between the range of two to six years. Therefore, to draw more founded conclusions about the competence of the infants and how it is reflected in their begging behaviour, a bigger dataset is needed.

When looking into the success of the begging behaviour (i.e. proportion of begging events that resulted in a food transfer by the mother) the results reveal that the infants' age does not have an effect on their success, contradicting my prediction. Older infants are equally successful as younger infants, which could mean different things. As just described above, older infants beg less, thus either older infants are more persistent when begging or more skilled in taking food from their mothers when they decide to beg. The results could also imply that the mothers do not take the age of their infants into account when they decide to grant success to a solicitation. Like with the analysis of the effect of feeding competence on begging rate, the pilot results from the analysis of feeding competence on success rate showed that there is no correlation between these two factors. Since age does not have a significant effect on the success of begging events, it is therefore well possible that feeding competence also does not. However, this preliminary finding has to be confirmed with a bigger dataset.

5.2 The effect of food item frequency on infants' begging behaviour and their mothers' tolerance

As predicted, I found an effect of the frequency of a food item on the begging rate: Infants beg more for rarer food items than for more common food items. This finding supports the hypothesis that begging serves as a means to social learning through which the infants are able to get to know food items which are difficult to find (Galef & Giraldeau, 2001). It makes sense that infants beg more for rarer food items, which they do not encounter often because they have limited learning opportunities for these items. These results contradict what Jaeggi et al. (2008) found in Bornean orangutans. They did not find a negative correlation, on the contrary, they found some positive correlations. Notably, the sample size of my study and the one of Jaeggi et al. (2008) differ: even though both data sets comprise of four infants, contrarily to Jaeggi et al.'s study, the data set of my thesis contains data on these infants at several

different points in their development, collected over several years per. The higher resolution of my data set allowed for more detailed analyses (see below).

Jaeggi et al. (2008) argue that increased food interest in a new food item might only be detectable when the infant first encounters this food item, but this detection was not possible with their sampling schedule. My data does not support this prediction. Interestingly, in the correlation analyses they did for the four infants separately, Jaeggi et al. found that within two of them the frequency of a food item and the begging rate were significantly positively correlated. This is probably the case, because they were not able to correct for the opportunity to beg, meaning the number of solicitations need to be corrected for the time the mother was actually feeding on a specific food item enabling the offspring to beg for it. The positive correlations of begging rate and frequency might also be individual differences between the four infants in their study. Jaeggi et al. (2008) did valuable groundwork in this area even though their sample size was very small. With my thesis, I was able to add more resolution to several aspects of the analyses. Among other things, I corrected for the individuals and for the opportunity to beg. Since the GLMM of this analysis in my thesis explains over 30% of the variation within the data, I feel confident to draw conclusions based on my results.
Contrary to my prediction that the success of the begging behaviour would increase with decreasing frequency of the food items, I found that there is no effect of the frequency of the food items on the success of begging events. A possible explanation of this would be that the mothers do not want to give up rare food items themselves. This could be the case because these rare food items might hold important nutrients, which females rely on since they have to provide milk to their offspring over multiple years which demands an energy effort of up to 25% higher than the baseline throughout the period of lactation (van Noordwijk et al., 2013). Another possibility why success rate is not higher when infants beg for rarer food items is that it might be enough for the infants to see the mother feed on these rare food items since most of them are easy-to-process (e.g. lianas and leaves).

When summarizing the effect of frequency of the food items on begging behaviour it becomes evident that infants beg more for rare food items than for more common ones, but they are not more successful in obtaining them, possibly because the mothers are reluctant to share rare food items.

5.3 The effect of food item complexity on the infants' begging behaviour and their mothers' tolerance

Against my prediction and the results from Jaeggi et al. (2008) that infants beg more for complex food items, I found that there is no significant effect of the complexity of the food items on the begging rate. Interestingly however, there is a positive significant effect of complexity on the success of begging events: When begging for more complex food items, infants are more successful than when begging for easier-to process food items. This suggests that infants are not able to assess complexity of food items while mothers are. But infants must have some idea that complex food items are important because studies on peering behaviour in Sumatran orangutans show that infants peer more for complex than for easier-to process food items (Ehmann, 2019; Schuppli et al., 2016a). Thus, even though infants seem to be more interested in complex foods compared to rare foods, they do not try to solicit them more often.

So far, great ape mothers have mainly been found to be passive without any support for a more active role, although socially highly tolerant (van Schaik, 2008), while the immatures were found to be the main drivers for skill acquisition (noue-Nakamura & Matsuzawa, 1997; Lonsdorf, 2006; Thornton & Raihini, 2008. My findings show that orangutan mothers might have a more active role than previously thought. This is in line with other current findings on chimpanzees: Estienne et al. (2019a) investigated maternal influences on skill acquisition of nut-cracking in chimpanzee immatures. They found that mothers allow

tool transfer by leaving their tools available for their offspring. Importantly, adult females rarely leave their tools unattended, except when infants are present or no other adult is around (Boesch, 1991). This study shows how maternal behaviour, even though potentially unintentional, can positively influence the skill acquisition in chimpanzees. Another study in chimpanzees, conducted by Estienne et al. (2019b) found that mothers seemed to change their behaviour to promote their infant's learning process. They did this by changing the time spent being inactive depending on their offspring's age and sex while being at foraging sites to extract bee nests under the ground. Musgrave at al. (2016) conducted a study on tool transfer in chimpanzees which they may be seen as a teaching-like behaviour. They found that immatures receiving tools for termite extraction from their mothers have an immediate benefit because of the opportunity to manipulate and use an appropriate tool. This resulted in an increased tool use and increased termite consumption of these immatures. Additionally, this study found that mothers anticipated tool transfers to their offspring and found strategies to buffer associated costs of losing a tool through transfer. These mothers either brought several tools to the foraging site or divided their fishing tool lengthwise to be able to transfer one part but still keep the other part. There is also anecdotal evidence for teaching-like behaviour in chimpanzees described in detail in Boesch (1991). There are two mothers in this study who noticed their infant's difficulties in nut-cracking, and who made a clear demonstration to improve their infant's performance. Thus, with more studies elaborating on the role of the mothers, we may find even more evidence pointing into the direction that great ape mothers engage in a more active role in skill acquisition of their offspring. The possibility of teaching-like behaviour in great apes would have implications for the cognitive abilities of the apes enabling these behaviours. Additionally, there might be mechanisms that humans share with the non-human primates that make these complex interactions possible.

The contradiction to the study conducted by Jaeggi et al. (2008) might be a resolution issue because Jaeggi et al. (2008) divided the food items in two categories (difficult-to process and easy-to-process) while I used categories between one and five. In summary, infants do not beg more for complex food items, but they are more successful in obtaining them when they beg for them indicating that infants are not able to interpret complexity as a reason to beg more whereas their mothers are.

The contradiction to Jaeggi et al. (2008) could also reflect differences between the two sites Suaq Balimbing in Sumatra and Tuanan in Borneo. An important difference between these two sites is that the habitat where Suaq lies is more productive than the one where Tuanan lies (Marhsall et al., 2009). In Suaq, fruit is always a major part of the diet whereas in Bornean populations there can be months where fruit is only a minor part of the diet due to the lack of availability (Morrogh-Bernard et al., 2009). Bornean orangutans also have a higher proportion of bark in their diet (Wich et al., 2006 and greater variation in time spent feeding on leaves (Morrogh-Bernard et al., 2009). Because of these differences, the orangutan density in Suaq is higher (Husson et al., 2009; van Schaik, 2004). This gives the orangutans of the Suaq population more opportunities for associations and social learning from other individuals than the mother (Ehmann, 2019: Schuppli et al., 2016a). The higher food availability in Suaq also leads to a slower life history with a longer developmental phase, because a more stable energy input reduces mortality (times of starvation and malnutrition decrease) which in turn leads to slow life histories (Wich et al. (2004)'s 'ecological life history hypothesis'). Thus, infants from the orangutan population in Suaq have more time to learn their skills than their Bornean peers. Additionally, the higher sociability levels (mentioned above) of infants in Suaq seem to positively influence independent exploratory tendencies, lasting into adulthood (Schuppli et al., 2017). Schuppli et al. (2017) found that this is connected to a higher innovation frequency and hence also to the larger and more complex skill repertoire of this population. Thus, infants from the Suaq population need to master a larger number of and more complex skills during their immaturity than Bornean orangutan infants. This could explain why infants from my study were not able to assess complexity in a way that they would beg more for these foods, while the infants from Jaeggi et al.'s study were found to beg more for complex food items.

5.4 The effect of sex on the infants' begging behaviour and their mothers' tolerance

I did not find any evidence for an effect of the sex of the infants on begging behaviour in any analyses of my study, contradicting my predictions that males would beg more for food items and be more successful than females. These predictions were based on findings in chimpanzees showing that females reach skills on nut-cracking earlier than males (Boesch & Boesch-Achermann, 2000) and mothers share a greater number of nuts with their sons than with their daughters (Estienne et al., 2019a). It might be worthwhile to look into one complex foraging technique of orangutans in a future study and investigate the sex difference within this restricted frame to have a more equal comparison with the studies on chimpanzees. Since I also did not find sex differences in feeding rates (see below), it might be that in orangutans there is no sex difference in begging behaviour or only a very slight one which has not been detected so far. According to Ehmann (2019), there are sex differences in peering behaviour of infant orangutans from the Suaq population. This study found that with increasing age males become gradually more interested in other individuals as role models than their mothers, whereas females also gradually become more interested in other individuals until the age of 3.5 years and then this interest decreases, and they focus more on the mother again. Since begging behaviour is almost exclusively directed towards the mother, I cannot draw a direct comparison to the study conducted by Ehmann (2019). But it becomes evident that the different strategies and lifestyles of females and males (maturing females usually settle close to their mothers while males disperse (van Schaik & van Hooff, 1996)) are a reason for sex differences in certain behaviours already during immaturity.

5.5 Effects on feeding rates

As predicted and showed by Schuppli et al. (2016b) age has a positive significant effect on the feeding rates, meaning that with increasing age immatures approach their mother's speed of ingesting food items. This makes sense since immatures should become more competent in their feeding skills throughout their development. In chimpanzees, the same pattern is found (Bray et al., 2017). This confirms the correlation of age and feeding competence.

Complexity of the food items did not have a significant effect on the feeding rates contradicting the findings from Schuppli et al. (2016b) which show that feeding rates for easier-to-process food items are reached earlier than for difficult-to-process food items. Frequency of the food items also did not have a significant effect on feeding rates. Hence, immatures reach adult-like feeding rates independently of the characteristics frequency and complexity of the food items. I also did not find a sex difference contradicting Schuppli et al. (2016b) who found preliminary evidence that male immatures might reach faster feeding rates earlier than females. But just as the data from Schuppli et al. (2016b), the data in this study are biased because all feeding rates from young orangutans are by males while all feeding rates from juveniles are by females. In my dataset, this sex bias is less pronounced, especially during infancy. Additionally to the sex bias, there are very few infants between the ages of 4 and 8 in the study conducted by Schuppli et al. (2016b), which might also influence the results of complexity and frequency. My current dataset includes several data points for these age classes which softened this bias. In summary, whereas I could not confirm the effects of complexity or sex, I could confirm that age significantly affects feeding competence.

5.6 Conclusion

In sum, I could show that infants do have preferences for rare food items when begging, and at the same time, their mothers are more ready to share complex food items with their infants. Both of these results strongly support the hypothesis that begging behaviour by infants and the maternal response are a means of gaining knowledge about food items and acquire processing knowledge. Interestingly, whereas infants seem to be aware of the frequency of food items, they do not seem to be able to assess their processing complexity, but their mothers do. This suggests that the mother is part of the learning process of the infants. Age does not seem to be an important factor for mothers when they decide to share food after a begging event, but age is important for the infants: they beg less when they get older, possibly because they became more competent and do not rely on their mothers that much anymore to obtain and learn about food items. This possible explanation is supported by the findings that feeding rates are affected by the age of the infants, showing that with increasing age the infants approach their mother's speed of ingesting food items, thus age and feeding competence are correlated. But to confirm that feeding competence is a potential reason that infants beg less when they become older more data are needed.

All in all, this study added resolution to the topic of skill development in Sumatran orangutans, underlining the importance of skill learning for adult survival. As investigated and proposed by Schuppli et al. (2012) and Schuppli et al. (2016b) the energetic investment into learning during the learning-intense developmental phase might limit body growth before the timing of weaning and vice versa. They suggest that this combination could set the timing of weaning and age at first reproduction. The data on begging behaviour from this study illustrating effects of frequency and complexity of the food items and age of the infants show why infants need several years to acquire complex feeding skills. Therefore, my results point into the direction that skill acquisition could be an important factor in setting the pace of life history in Sumatran orangutans.

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8. Appendix

Material and Methods

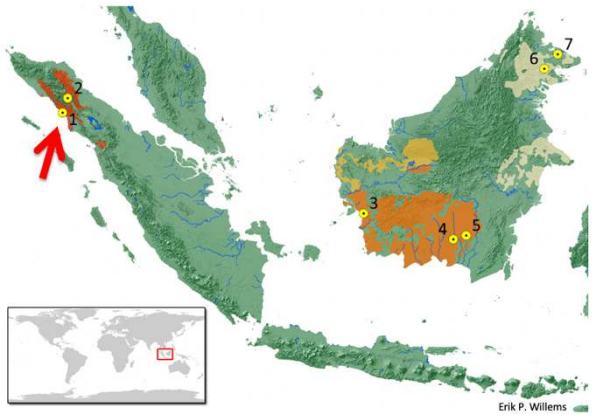

Figure 13: **Location study site**. The research site Suaq Balimbing is located in South Aceh, Sumatra, Indonesia, indicated with the red arrow. The other numbered sites are orangutan research sites as well.

Results - Part 1: Begging behaviour - Infant's perspective

Table 11: The Anova comparison between the full model and the model containing age and frequency reveals that the full model does not perform better than the model containing age and frequency, contradicting the AIC values of the two models.

χ^2_1	p-value	Delta df	Df(full model)	Df(model containing age & frequency)
1.36	> .05	2	7	5

Table 12: The Anova comparison between the full model and the null model confirms the AIC values indicating that the full model performs significantly better than the null model.

χ^2_1	p-value	Delta df	Df(full model)	Df(null model))
53.90	**< .001**	4	7	3

Table 13: The Anova comparison between the model containing age and frequency and the null model confirms the AIC values indicating that the full model performs significantly better than the null model.

χ^2_1	p-value	Delta df	Df(model containing age & frequency)	Df(null model)
52.54	**< .001**	4	5	3

Results - Part 2: Begging behaviour - Mother's perspective

Table 14: The Anova comparison between the full model and the model containing complexity reveals that the full model does not perform significantly better than the model containing complexity, contradicting the AIC values of the two models.

χ^2_1	p-value	Delta df	Df(full model)	Df(model containing complexity)
0.56	> .05	3	8	5

Table 15: The Anova comparison between the full model and the null model reveals that the full model does not perform significantly better than the null model, contradicting the AIC values indicating that the full model performs significantly better than the null model.

χ^2_1	p-value	Delta df	Df(full model)	Df(null model))
6.56	> .05	4	8	4

Table 16: The Anova comparison between the model containing complexity and the null model reveals that the model containing complexity performs significantly better than the null model, confirming the AIC values.

χ^2_1	p-value	Delta df	Df(model containing complexity)	Df(null model))
6.00	**< .05**	1	5	4

Table 17: **Overview of the model selection process in part two.** All models from part two of the thesis on success of begging events, because the model selection process was not that clear. The table contains AIC values of all models, detlaAIC of all models to the full model, p-values from the Anova comparison of all models to the full model.

Model	AIC	DeltaAIC to full model	p-value anova comparison with full model
Full: age, frequency, complexity, sex	628.78	-	-
frequency, complexity, sex	627.27	< 2	> .05
complexity, sex	660.76	-	> .05
sex	753.78	-	**= 0.90**
complexity	658.83	-	> .05
age, complexity, sex	662.50	-	> .05
age, complexity	660.61	-	> .05
age, sex	755.09	-	**= 0.065**
age, frequency	714.56	-	**= 0.067**
age	753.17	-	> .05
frequency	713.41	-	**= 0.092**
null	751.81	-	> .05

Results - Part 3: Feeding rates

Table 18: The Anova comparison between the full model and the best model containing age reveals that the full model does not perform significantly better than the best model containing age, confirming the AIC values of the two models.

χ^2_1	p-value	Delta df	Df(full model)	Df(model containing age)
1.97	> .05	3	8	5

Table 19: The Anova comparison between the full model and the null model reveals that the full model does not perform significantly better than the null model, contradicting the AIC values indicating that the full model performs significantly better than the null model.

χ^2_1	p-value	Delta df	Df(full model)	Df(null model))
13.27	**< .05**	4	8	4

Table 20: The Anova comparison between the best model containing age and the null model reveals that the best model containing age does not perform significantly better than the null model, contradicting the AIC values indicating that the best model performs significantly better than the null model.

χ^2_1	p-value	Delta df	Df(model containing age)	Df(null model))
11.30	**< .01**	1	5	4

Results - Part 4: Combination of begging and feeding

Infant's perspective

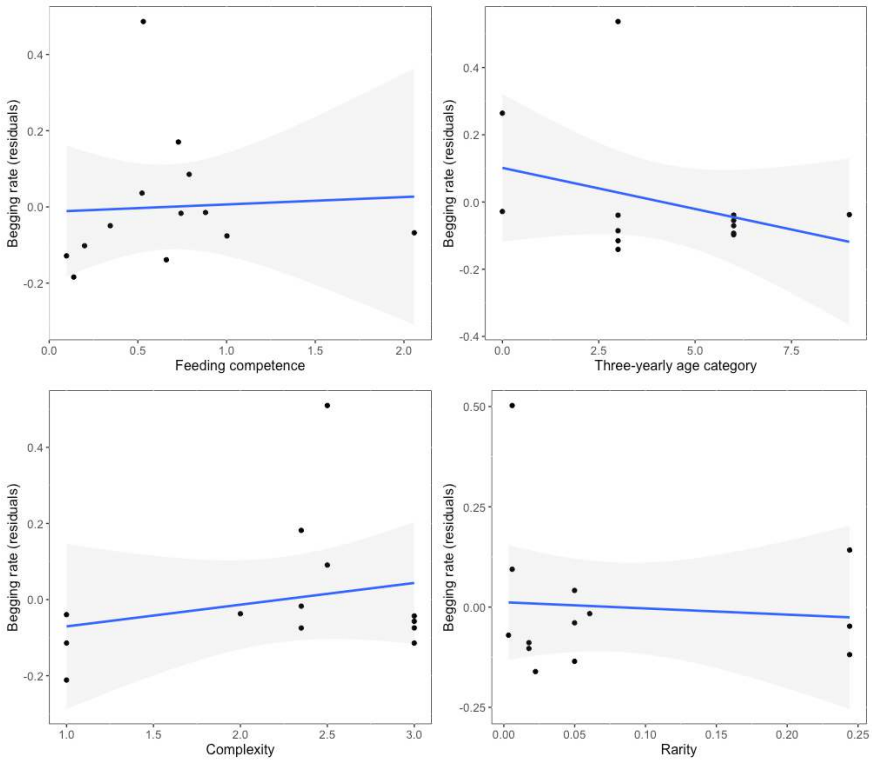

Figure 14: **Relationships of the begging rate with feeding competence (left up), age (right up), complexity (left down) and frequency (right down)**. Even though it looks like age and frequency might have an effect on the begging rate, the simple correlation analyses with Kendall's tau reveal that all four explanatory variables are not significantly correlated with the begging rate (three-yearly age category: z = -0.33, p-value > .05; frequency: z = -1.37, p-value > .05; complexity: z = 1.20, p-value > .05; feeding competence: T = 46, p-value > .05). I used residual plots for this Figure because they represented the individual relationships of the explanatory variables with the response variable clearer.

Mother's perspective

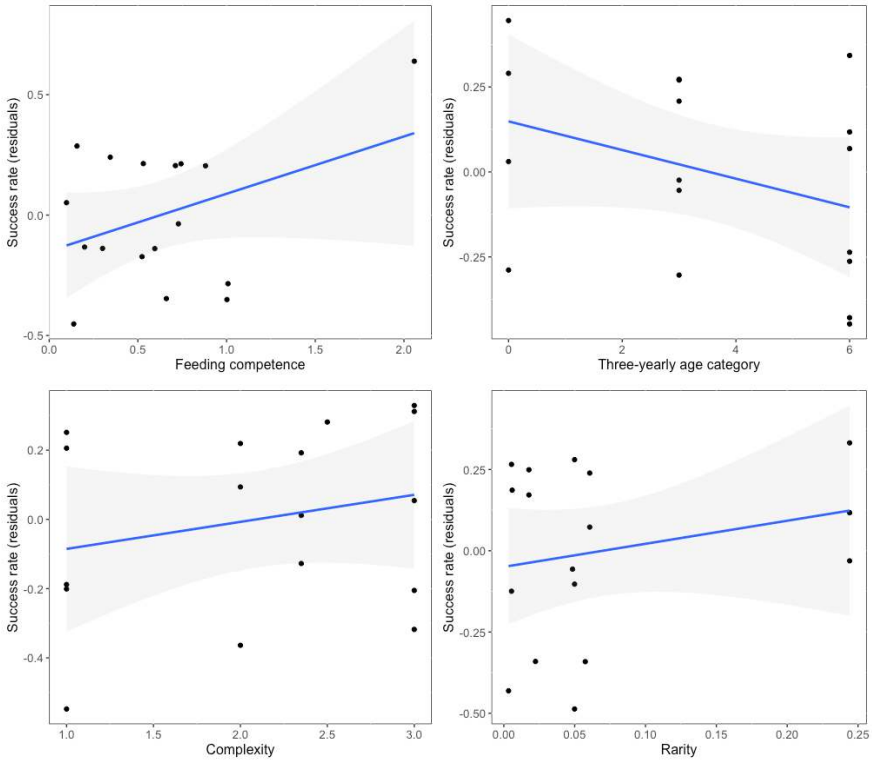

Figure 15: **Relationships of the success rate with feeding competence (left up), age (right up), complexity (left down) and frequency (right down)**. Even though it looks like all factors might have an effect on the begging rate, the simple correlation analyses with Kendall's tau reveal that they are not significantly correlated with the begging rate (three-yearly age category: z = -1.10, p-value > .05; frequency: z = 0.86, p-value > .05; complexity: z = 0.62, p-value > .05; feeding competence: z = 0.68, p-value > .05). I used residual plots for this Figure because they represented the individual relationships of the explanatory variables with the response variable clearer.