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**Master of Science**

**Early Childhood Research**

Title of the thesis

The Role of the Mother in Feeding Skill Acquisition in Immature Sumatran Orangutans *(Pongo abelii)*

Master’s thesis to obtain the academic degree

Master of Science (M.Sc.)



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List of abbreviations

IBI: interbirth interval

POC: Parent-Offspring Conflict theory

PI: Parental investment

PC: Parental cost

OC: Offspring’s cost

GLMM(s): general linear mixed model(s)

Summary

Unlike humans or other non-human primates, orangutan mothers have been believed to be passive and even uninvolved in skill acquisition of their offspring, while one could not rule out the possibility that this attributes to the exceptionally long time it prepares orangutans for their adulthood. To make sure the survival of the offspring, orangutan mothers invest their maternal effort the most among the great apes and therefore, they should have an important influence on the competence gain of their young ones. The aim of this project was to investigate how Sumatran orangutan mothers are involved in the acquisition of the feeding skills of their offspring. For this purpose, I looked at the reaction of the mother during the offspring’s begging (i.e. one of the most acknowledged learning technique of non-human primates). I put special focus on the tolerance of the mother (i.e. letting the offspring have the food or refuses the begging call. Data on wild Sumatran orangutans (N=19) at different age categories were collected for 13 years to be able to manifest the developmental trend with the targeted phenomenon, data on captive Sumatran orangutans (N=3) were gathered at a different research period for two months. I hypothesized five variables that might impact the mother’s tolerance when begging occurs. From the mother’s perspective, I found … (summary of my results). My results suggest that orangutan mothers do change their behavior at their cost to contribute to skill obtaining of their offspring. Hereby, I conclude that although not easily detectable and hence more subtle, orangutan mothers so show subtle maternal scaffolding in skill acquisition of their young, and this may bring an important clue on why orangutans have an exceptionally slow life history with their prolonged immaturity and thereby provides an important message about the evolution of social-cognitive development with social learning of humans.

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Introduction

* 1. Research background and objective

Great apes, including humans, are known for their longer lifespan but much slower developmental pace compared to other mammals (Harvey et al.,1987; Janson & van Schaik 1993; Ross, 1998; Ross & Jones 1999; van Adrichem, Utami, Wich, van Hooff, & Sterck, 2006; Dunkel, 2006; Schuppli, 2012). Several hypotheses have tried to explain primates’ slow life history schedule. The energy-consumption hypothesis postulates that the slow life history schedule in primates is a result of their slower metabolism compared other mammals (figure1.1, (Pontzer et al., 2014)). Among all primates, Bornean orangutans (*Pongo pygmaeus*) show the lowest total energy expenditure per body weight on a daily base (figure1.2, (Pontzer et al., 2014)). Similarly, free-living Sumatran orangutans (*Pongo abelii*) spend much less metabolic energy per day than expected for their body weight (Pontzer, Raichlen, Shumaker, Ocobock, & Wich, 2010). It was suggested that reducing energy throughput is an evolved strategy of orangutans to decrease the risk of starvation via attenuating hunger during times of low food availability, which can be unpredictable. This “stingy strategy” of orangutans’ by staying solitary rather than spending much energy for foraging in a big group may explain their prolonged lifespan.

Along the same line, the expensive-brain hypothesis infers that it takes longer time for large-brained specie to reach adult brain and body size compared to small-brained species. This is because brain tissue is energetically more expensive to develop and maintain than other tissues, what’s more, the energy flow to the brain should be constant to avoid brain damage which means that energy flow goes into two parts: maintaining the brain and developing it. Yet, it’s already expensive to maintain existing brain tissue developing new brain tissue takes even more energy (Isler and van Schaik, 2009; Barrickman et al., 2008, as cited in Schuppli, 2012). These hypotheses predict the reason why orangutans have the most prolonged developmental stages among primates from a physiological perspective.

Life history pace can be measured in the timing of the following three ontogenetic events: weaning, first reproduction, and interbirth interval (IBI). Harvey and Clutton‐Brock (1985) gathered 14 life events and traits of 135 species including chimpanzees (*Pan troglodytes*), Bornean orangutans, gorillas (*Gorilla gorilla*), and humans (*Homo sapiens*), disentangling that, among those groups, humans give their first birth at the latest age but wean at the earliest age (figure1.3, (Harvey & Clutton‐Brock, 1985)). Their results also expounded that all those traits vary among taxa. Regarding weaning, Sumatran orangutans wean at an age of 7-8 (table 1.1) years which is 2-3 years later than chimps, bonobos, and gorillas. Weaning, meaning “the act or process of causing a baby or young animal to stop feeding on its mother's milk and to start eating other food” (Cambridge Dictionary, n.d.), is a significant life event which prepares the infant for surviving more independently and the step into the juvenile phase (Pereira and Altmann, 1985; van Noordwijk and van Schaik, 2005). In terms of IBI, Wich and colleagues (2004) found that Sumatran orangutans have the longest IBI (M= 9 years) in comparison to Bornean orangutans (M=7 years), chimpanzees (M= 6 years), bonobos (*Pan paniscus*) (M= 6 years), and gorillas (M= 4 years) (figure1.4), which is compatible with findings in Singleton and van Schaik (2002), van Noordwijk and van Schaik (2005), Tilson et al. (1993), and Watts (1991). However, van Noordwijk and colleagues (2018) argued the difference between Bornean and Sumatran orangutans in IBI is rather minor.

|  |  |
| --- | --- |
| Figure 1.1: **Mean daily energy consumption per body weight (kcal/kg/d) between primates and non-primates.** Primates spend nearly ten times less energy than non-primates do on a daily base on average (data extracted and modified from Pontzer et al. 2014, p.1434). | Figure 1.2: **Daily energy consumption per body weight (kcal/kg/d) among eight species**. Bornean orangutans show the lowest ratio among these species, indicating that they save their metabolic energy the most (data extracted and modified from Pontzer et al. 2014, p.1434). |

Table 1.1: **Age at weaning, age at first reproduction, and the IBI of Bornean and Sumatran orangutans.** Data on weaning extracted from Dunkel 2006, p. 15; data on first reproduction from Schuppli 2012, p. 13; data on IBI from Wich et al. 2004, p. 393.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Weaning age in years | First reproduction in years | IBI in years |
| Bornean orangutan | 5-6 | 12-14 | 7-8 |
| Sumatran orangutan | 7-8 | 15-16 | 8-9 |

|  |  |
| --- | --- |
| Figure 1.3: **Comparison of life history in four domains among four primate species.** Humans show the longest lifespan, the latest breeding age, and wean the earliest is this group (data extracted and modified from Harvey and Clutton‐Brock 1985, p. 566). | Figure 1.4: **Comparison of the mean age of interbirth interval (IBI) among five great ape species**. Sumatran orangutans have the highest IBI among these species (data extracted and modified from Wich et al. 2004, p. 393). |

One important factor for trying to understand the slow life history pace of orangutans (i.e. a much later age at weaning of immatures than that of other great apes & longest IBI among all the primates) is their lifestyle, which ranges from semi-solitary to fission fusion (van Schaik, 1999). Orangutans from birth to the first birthday have body contact with their mothers almost all the time but it declines to 50% when they are about two years old (van Noordwijk et al., 2009). After weaning, not only do their mothers significantly reduce their investment in them especially once the mothers give birth to the next offspring, but they also end the permanent association with the weaned offspring soon thereafter (van Schaik CP, 2016). Orangutan mothers do this because they may want to make sure that there is enough food to afford the younger one and ensure its survival (van Schaik, 1999). What’s more, due to a low birth rate among orangutans, mothers mostly only have one child that they closely associated with, while most other primate species at the same age are more sociable because they have siblings who can reduce the maternal effort by being other model models (van Noordwijk & van Schaik, 2005). This semi-solitary lifestyle of orangutans means that weaned orangutans need to leave their mothers and thereafter rely on their own skills and knowledge for large amounts of time (Dunkel, 2006).

To be able to survive on their own without resorting to their mothers, juvenile orangutans have to have their skills sufficiently in place. Ultimately, this may result in a slow life trajectory from the immaturity to the independency of orangutans because they need to learn various subsistence skills and acquire lots of knowledge to survive (i.e. the needing-to-learn hypothesis). This hypothesis predicts that the knowledge and skills that at least hold the survival of an animal is crucial for its development, therefore, the amount of knowledge that needs to be learned can estimate the length of immaturity. In mammals, for instance, essential skills like foraging competences are normally well acquired a few years before the age at first reproduction (Ross and Jones, as cited in Schuppli et al, 2016). Yet, with a drastic decline in maternal support and perhaps still so much left to learn after weaning, compared to young chimpanzees, juvenile orangutans are under more pressure to be master of various skills on its own.

Immature orangutans get their mothers’ full maternal investment until they reach their juvenile period which includes that they are intensively taken care by their mothers and spend most of their time in proximity. Van Noordwijk and colleagues (2005) observed that Sumatran orangutans (at Suaq Balimbing forest in Indonesia) spend almost one hundred percent of the time within 10 meters of their mothers from birth till the age of 10. This proximity allows for many social interactions during feeding, travelling (with mother carrying the 0-2-year-olds), nesting, resting, and playing together (van Noordwijk & van Schaik, 2005). The close proximity to their mothers also provides the immatures with opportunities to obtain skills through social learning from their mothers. This leads to an important question: how is knowledge transferred from the orangutan mother to her offspring?

* + 1. Knowledge transfer

To extend the concept of learning to other species besides humans, learning is commonly defined “a set of complex ontogenetic processes that allows animals to acquire, store, and subsequently use information about their environment.” (Galef and Laland, 2005, p. 495). Broadly speaking, there are two types of learning: social learning and individual leaning (also referred to as asocial or independent learning). Asocial learning is defined as the exploratory experience of naïve conspecifics such as trial-and-error learning (Rendell et al., 2011). In social learning, the learning process is based on observations of the activities of or interaction with a conspecific or its products (Heyes, 2012). To be more precise, there are two mediums in social learning: social information and social interaction. With the present of mere social information, there is non-observational social learning (i.e. social facilitation and stimulus enhancement) and observational social learning (i.e. observational conditioning and emulation). When adding social interaction to the social learning process, there is interactive conditioning and teaching (Hoppitt and Laland, 2013; van Schaik, 2016; Rapaport and Brown, 2008). As many scholars have claimed so far, neither do non-human primates show the full episode of joint attention nor they imitate (e.g. Tennie, Call, & Tomasello, 2006; Rosati et al., 2014). With the vast majority of the time orangutan mothers have body contact or at least stay close with their immature offspring, there should be not only social information on various skills involved but lots of social interaction between them can be assumed.

For human learning, teaching wildly exists and is an important element (e.g. Kline, 2015; Strauss and Ziv, 2012), but do non-human great apes also teach? Musgrave and colleagues found that more skilled wild chimpanzees helped less skilled individuals with utilizing tool during feeding by transferring the tool to them which ultimately reduced their chances to get fed while it increased the conspecifics’ tool using skills, and this falls within the framework of teaching (2016). What’s more, wild chimpanzee mothers showed a great level of simulation, facilitation, and some signs of active teaching during nut-cracking with their offspring (Boesh, 1991). There are several definitions of teaching but for this thesis I will focus on the definition is introduced by Caro and Hauser (1992, p. 153): “an individual actor A can be said to teach if it modifies its behavior only in the presence of a naïve observer, B, at some cost or at least without obtaining an immediate benefit for itself. A’s behavior thereby encourages or pushes B’s behavior, or provides B with experience, or sets an example for B. As a result, B acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all”.

An increasing number of studies suggests that social inputs are crucial for primates’ development. The cultural intelligence hypothesis predicts that, on the developmental level, opportunities for social learning during early ontogeny are key to cognitive development and skill acquisition later in development (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007, as cited in Rosati et al., 2014). Schuppli, vanNoordwijk, Atmoko, and van Schaik (2020) explored that the more social experiences the wild orangutans had at the earlier stage, the more frequently they explored (i.e. a common way of social learning among the wild animals). On the evolutionary level, the hypothesis also assumes that evolved learning mechanisms allow species learn both socially and individually to a great extent but more social individuals show more advanced cognitive skills (van Schaik and Burkart, 2011; Forss, Willems, Call, and van Schaik, 2016). Overall, these learning mechanisms prepare young orangutans for being able to survive in their natural habitat where there are many challenges regarding different tasks.

Immature orangutans must acquire a large number of skills before being able to survive without their mothers. Broadly speaking, those skills can be grouped into three categories (figure 1.5, (van Noordwijk et al., 2009). The acquisition of these skills might set the age at which immature orangutans can be weaned (Schuppli et al. 2016). The focus of this thesis is on the feeding techniques of the young orangutans.

Figure 1.5: **Skills immature orangutans must acquire before reaching independence.** Feeding techniques are about foraging skills with information of food items involved; nest building technique is one of the social skills learned by observing orangutan mothers which includes organizing branch and leaves; locomotion includes swinging, swaying, and twirling (summarized from van Noordwijk et al. 2009).

* + 1. Feeding techniques

Wild orangutans eat more than 200 different food items, many of which require multiple steps of processing before ingestion (Schuppli et a. 2019 and Schuppli et al. 2016). It has been shown that it takes immature orangutans up to 12 years to acquire certain feeding skills (Schuppli et al. 2016). Feeding skills include recognizing distinct food items and differentiating the edible ones from those that are not, knowing when and where to obtain them, and how to process them before digestion (figure 1.6, (Galef and Giraldeau, 2001)). The different food items in the orangutans’ diet differ in terms of their required processing techniques and their availability in orangutan populations’ habitat (Schuppli et al., 2016; Jäggi, Van Noordwijk, & Van Schaik, 2008).

Figure 1.6: **Feeding skills immature orangutans must acquire before maturation.** Knowing what, when, and where is easier than knowing how for the immatures (summarized from Galef and Giraldeau, 2001).

There are two major types of feeding skills that have been researched with young orangutans (table 1.2): peering and begging. Immature orangutans in nature seem to obtain substance skills by peering, which is free-willingly watching other individuals in proximity (Schuppli et al., 2019). Some findings suggest that peering manifests an approach to learning and it happens mostly during infancy, therefore, the infant orangutans peer at their mothers the most and the focus gradually switches to other individuals as they age (Schuppli et al., 2016; Schuppli et al., 2019). In terms of what may impact such learning strategy, Schuppli and colleagues found that the behavior with an item that a young orangutan peered at increased in frequency of its occurrence with the same individual after the peering took place. In the feeding context with the mother, the more steps it takes to process a food item, the more often the young orangutan peers at her feeding on it than feeding on less complex food item; the mother feeds on a food item that is less often seen by the offspring, the more time it spends on peering at her feeding on the rare food item (2016).

Being another approach of young orangutans to learn feeding skills, begging, meaning young orangutans soliciting food from their mothers by reaching its hand or mouth to its mother’s hand or mouth, varies among very similar attributes of food items (e.g. Jäggi et al., 2008). When begging occurs, orangutan mothers either accept the begging of the offspring (i.e. being tolerant by letting their offspring take a food item and showing no objection) or reject it (i.e. being not tolerant by showing aggression towards the begging offspring or keeping the food on her own) (Jäggi et al., 2008). For this thesis, I emphasized the begging behavior as the target behavior.

* + 1. Why Begging? What may impact begging behavior?

Brown, Almond, and Bergen (2004) introduced two hypotheses to explain begging behavior in non-human primates. The *nutritional hypotheses* assume food has to sole role of supplying energy. This means that in the begging context, the immature individual will only solicit food when its hungry and will show very little interest in feeding once it doesn’t need it anymore. This hypothesis implies that immatures don’t beg to acquire any knowledge about when, where, and how to eat a certain food item. The *informational hypotheses* states that there is a higher level of the role of the begged for food: it brings not only short-term energy but also in the long-term because through begging the immature obtains information which increase its own feeding skills (Brown et al., 2004).

Among immature Bornean orangutans, more complex food items (i.e. more than one processing step required) were begged more frequently from their mothers than the easier-manipulating ones. This finding suggests that the motivation behind the begging is probably to get information about the food (as predicted by the informational hypothesis) and not just to fill the empty stomach (as suggested by the nutritional hypothesis) (Jaeggi et al., 2008). Moreover, in the same study it was found that the more skillful (i.e. higher percentage of an offspring’s feeding bouts that initiated by itself without any triggers from its mother) the immature was the less frequently it was found begging, once again supporting the informational hypothesis. However, one could argue that older offspring naturally more competent in their feeding skills and consequently, age should be a main factor in the increasing feeding competence.

If begging were means to acquire feeding skills, we would expect that the processing complexity of the food item and the rarity of the food item have positive effects on begging rates. Aside from the negative correlation between the begging rate of the immature focal and its age, a negative correlation between the feeding competence of the immature orangutan and the occurrence of the begging can be assumed. Jäggi and colleagues (2008) indeed also discovered that there is a and positive correlations of the complexity and the availability of the food item in the given season and the begging behavior of the immature orangutan. These results suggest that through begging, orangutans learn socially from the mother as and that this might be an important way for them to acquire their adult like feeing-skills (e.g. Rapaport and Brown, 2008). Whereas the main focus of Jäggi et al. (2008) study was on the behavior of the immatures, they also found some results on the mothers’ reaction to the immatures begging which was sharing the food to the offspring in response to its initiative food solicitation (i.e. begging). Nonetheless, to date, very little is known about the orangutan mother’s role in the foraging technique learning of the immature, which underlines the originality of this study.

The results on peering and begging nicely demonstrate that there is a strong social component in orangutan learning. However, these results have only focused on the learners’ side of skill acquisition. How are the role model (i.e. orangutan mothers) involved into this learning process? Previous studies have stated that unlike human mothers, orangutan mothers usually play an inactive role in the acquisition of the offspring’s feeding skills in that they rarely actively provision the young with food or intentionally offer their offspring with any learning opportunity (Jäggi et al., 2008; Rapaport and Brown, 2008; Jäggi, van Schaik, Fischer, & Burkart, 2010). Since orangutan mothers don’t conceive until the current infant reaches the weaning age (i.e. nutritional independence), they are expected to maximize (which suggests that peering is used for learning) the speed at which their current offspring reaches nutritional independence while maximizing its survival probability. Therefore, orangutan mothers are expected to invest into their offspring’s skill acquisition so that the immatures can reach independence faster.

Table 1.2: **Food-related social interactions between orangutan mother-infant pairs.** Data extracted from *Instructions for collection of behavioral data on orangutans during focal follows (orangutan project Tuanan and Suaq Balimbing)* in Schuppi 2016, p. 9.

|  |  |
| --- | --- |
| Food related social behavior: peering and begging | |
| Interaction | Definition |
| Begging | Trying to obtain food from conspecific.  By reaching with hand, stretching hand  out towards mouth or hand of target  or brining mouth close to mouth or  hand of the target. |
| Peering | Directly looking at the action of  another individual sustained over at  least 5 seconds, and at a close enough  range that enables the peering  individual to observe the details of the  technique used by the other. |

Yet, unlike humans, according to the published literature, orangutan mothers seem surprisingly uninvolved in their offspring’s skill acquisition. While this phenomenon might contribute to answering the question why it takes immature orangutans longer than any non-human great apes to reach adulthood it also raises the question if orangutan mothers are indeed as uninvolved as the current studies suggest. Although some argue that teaching is not exclusively anthropomorphic and it does exist in some animals such as meerkats and ants, the “teacher-learner” dyads in their studies are not mother-offspring pairs (Thornton & McAuliffe, 2006). Moreover, the authors discussed a profound point about how the future research should outstretch the framework of teaching to dig out a behavior that is unambiguously teaching in the animal kingdom rather than end conversation with no-teaching-exists conclusion. In orangutan mothers, the way of facilitating the feeding technique of their offspring may be to alter their tolerance during the begging, which is much of an indirect way of coaching.

The aim of this project was to investigate how Sumatran orangutan mothers are involved in the acquisition of the feeding skills of their offspring. For this purpose, I looked at the reaction of the mother when the young one is begging from her which occurs regularly during feeding events of 0-5-year-olds (van Noordwijk & van Schaik, 2005). Because reactions can have multiple ways to be measured here, I put special focus on the tolerance of the mother (i.e. letting the offspring have the food or refusing the begging call. Data on wild Sumatran orangutans at different age categories (e.g. per 0.5 year as a category) were collected for 13 years to be able to manifest the developmental trend with the targeted phenomenon (i.e. mother-offspring dynamic during the offspring’s begging), data on captive Sumatran orangutans were gathered at a different research period for two months. I investigated what elements could impact the mother’s tolerance when begging occurs to capture some presentation of regulation of the orangutan mother towards the feeding skill acquisition of her immature. This may bring an important clue on why orangutans have an exceptionally slow life history with their prolonged immaturity and thereby provides an important message about the evolution of social-cognitive development with social learning of humans.

* 1. Novelty of this study: what impacts the mother’s tolerance during the begging?

From the standpoint of the immature orangutan, age and the complexity of processing a food item showed effects on its begging (Jäggi et al., 2008), as one would predict under the assumption that begging is means to information acquisition. Notably, the effect of age found in the study by Jäggi and colleagues could be preliminary as the age range of their subjects was much smaller than this thesis, the age effects I found from this study could be more pronounced. From the mother’s perspective, however, besides the seemingly passive role, to what extent do orangutan mothers adjust their tolerance during begging and what factors affect the mother’s tolerance during the begging behavior? Thus, the novelty of this study is to discover the orangutan mother’s role in the acquisition of their offspring’s feeding skills. The following part presents what may affect the mother’s tolerance based on existent research with free-ranging chimpanzees and a theory that elaborates various mother-offspring conflicts with a special focus on nutrition supply.

* 1. What could influence the orangutan mother’s tolerance towards begging?
     1. Role of the mother in feeding skill acquisition in immature wild chimpanzees

Like orangutans, young chimpanzees also need to reach an adult-level foraging skill by the time they reach their independency through learning, mainly from their mothers. However, contrary to orangutans, young chimpanzees have more role models than their mothers not only because they are more gregarious than orangutans but also because the weaned individuals don’t leave their mothers so they can be role models for their younger siblings (e.g. van Noordwijk and van Schaik, 2005). Yet, due to the species close relatedness and their shared extended dependence on their mothers, we might gain important insight about the role of the mother in foraging technique acquisition by looking at results on chimpanzees. Lonsdorf (2006) investigated the role of the mother by looking at mother-infant interactions during termite fishing, which requires tool usage. Results suggest that wild chimpanzee mothers spend significantly more time accompanying their offspring when they are fishing termites than during other events and are tolerant to the young when the offspring takes the tool or the termite from them (i.e. begging).

Interestingly, further research on termite fishing in wild chimps discovered that female immature chimps acquire fishing technique earlier than the male offspring and show more overlap of feeding technique with that of their mothers than the male ones do, implying that female youngsters may rely more on observing their mothers in feeding acquisition than the male immatures do (Lonsdorf, 2005). Since learning approaches of immatures of different sexes seem to differ, one could argue that different attitudes of the primate mother toward the skill acquisition of offspring of different sexes attribute to such sex difference of skill acquisition of the young in pace? In a nut-cracking task, chimpanzee mothers (N=8) were more tolerant to their immature sons’ begging calls than to their immature daughters’ and generally shared more nuts with their sons (Estienne et al., 2019a). However, in a complex honey extraction task, chimpanzee mothers (N=9) provided more learning opportunities to their daughters but it decreased as daughters aged while the opposite pattern was found for sons (Estienne et al., 2019b).

Besides sex, what else may alter the orangutan mother’s tolerance to the begging? Since the first three years of their lives, orangutans spend almost 100% of time within 10m from 0-8y with their mothers (van Noordwijk & van Schaik, 2005), and immatures and mothers might not always have the same interests, conflicts between the infant and the mother could occur, also during begging events. But, is there a pattern of conflicts at the different age of the offspring? In the following session, I will introduce a theory that states many types of mother-offspring conflicts from an evolutionary angle (Trivers, 1974).

* + 1. Parent-Offspring Conflict theory (POC)

Trivers (1974) describes that parent-offspring conflicts (POC) are virtually caused by unbalanced demand and supply of parental investment (PI) in mother-infant pairs among all mammals. He defines PI as “anything done by the parent for the offspring that increases the offspring's chance of surviving while decreasing the parent's ability to invest in other offspring” (Trivers, 1974, p. 249). In this concept, there are two other very important terms: parental cost (PC) and offspring’s cost (OC). Since a POC is a dynamic phenomenon between the young and the parent with one’s cost benefiting the other in its reproductive success, there should be a balance point of the cost and the benefit (i.e. the benefit/cost ratio: B/C) where peace could be remained. With the Sumatran orangutan population, the balanced point where this ratio shows one, meaning that B equals to C, may occur at around the offspring’s age at weaning (Mean=7.5 years).

Before weaning of the offspring, the orangutan mother is naturally conditioned to invest in nursing even though it requires more parental input effort when the immature is younger to heighten the chances of survival of the young. However, as soon as this offspring reaches its juvenile age, it is in the mothers interest to get ready for producing the next offspring and therefore saves its maternal effort for when the next young is born and the circle of the B/C with the age of the offspring continues (figure 1.7, (Trivers, 1974)).

1

W: 7.5 yo

0.5

0

the benefit/cost ratio: B/C

Figure 1.7: **The B/C of the PI toward an offspring as it grows**. W= weaning, the shaded area in purple represents the period when there are mother-offspring conflicts (adapted for the Sumatran orangutan population from Trivers 1974, p. 251).

* 1. Research question, hypotheses, and predictions

The main question of the presented study was what is the role of the mother in feeding skill acquisition in immature Sumatran orangutans? I aimed to investigate this question by researching what factors affect the mother’s tolerance during the begging of her offspring. Before I present different sections of my predictions, there are **four universal independent variables (i.e. age and sex of the offspring & complexity and rarity of the food item)** that were researched repeatably with different outcome measures. All my predictions can be divided into three parts.

**Part 1: begging success (i.e. the mother’s tolerance to the begging) ~ four universal independent variables**.

*Prediction one: I hypothesize that as the immature orangutan grows older, the mother shows less tolerance during begging.* This prediction is based on the POC theory by Trivers (1974) in which he argues that the older the offspring is, the more competent it will be, and thus it needs less parental support. Meanwhile, the more sense it makes for the mother to reduce her investment, so that she can get energetically ready for having the next baby. Hence, I expect more conflicts when older immatures beg for food from their mothers as the mother will be more likely to reject the elder offspring’s begging call than the younger ones’.

*Prediction two: I assume that there is a sex difference in mother’s tolerance towards begging behavior and there is an interaction between the age and the sex variables*. While the difference of sex in the performance of peering or begging in young orangutan population is under-research, this prediction is based on the findings from the two tasks (i.e. nut-cracking and complex honey extraction) where, although the measurements of the chimpanzee mothers’ invest in their offspring’s feeding skill gaining in those two contexts differed, sex difference was found in both tasks with sex and age interacting in the honey extraction task (Estienne et al., 2019a; Estienne et al., 2019b).

*Prediction three: I expect that the more effort (in terms of processing intensity) it takes the immature orangutan to acquire a certain food item, the more tolerant the mother is when the offspring solicitates the food item from her*. In a previous study it was shown that more complex food items require higher skill level and that competence is reached with enough exposure of mother’s manipulating complex foods (Schuppli et al., 2016). Noteworthily, the measure of complexity of a food is derived from the number of steps it takes a subject to process the food item, which is also adapted from the measure from Schuppli et al., (2016).

*Prediction four: I predict that the more uncommon the food item is in the habitat, the higher the tolerance of the orangutan mother.* In terms of the measurement of the rarity of a food item, if the occurrence of a food item A is lower than a food item B in the whole observed food population, then I consider the rarity of the food item A is higher than that of the food item B. Therefore, the rarity is always a relative value in my measure. In the peering data, Schuppli and colleagues (2016) found that the immature orangutans spent more time peering at a less common food item its mother fed on. This can imply that rarer items mean that the immatures have less opportunities to learn them. Hence, if orangutan mothers want to facilitate the learning process of their offspring, they should be more tolerant for rarer item their immatures beg for.

**Part 2: begging success ~ site (i.e. wild vs zoo)**

2a) I look at the comparison of the mother’s tolerance in a begging event between the wild and the captive orangutans;

2b) besides the universal four independent variables, within the captive orangutan sample, I also look at how the desirability of the food item (i.e. a food item is favored by how many orangutans from the same group) influences the success of a begging event.

*Prediction five: I predict that the general tolerance of the orangutan mothers in the zoo is higher than that of the mothers in the wild. I* base this prediction on the fact that there are more food resources with smaller variety and more even occurrences in the zoo than there are in the wild. Therefore, the captive orangutan mother can afford to be more tolerant once the offspring begs the food from her.

**Part 3: begging frequency & begging rate ~ four universal independent variables + Site**

3a) begging frequency and 3b) begging rate. Begging frequency was calculated by dividing the total number of begging events of each focal animal by the total observation hours spent on this focal during the observation period of this study, begging rate was based on each observed food item throughout all begging events, it’s a ratio of the total number of begging events with a certain food item of each focal animal to the number of bouts its mother fed on this food item during the observation period of this study. I’m interested in how all the universal independent variables affect begging frequency and begging rate to discover how the results correlate with those on the tolerance of the mother separately in the zoo and the wild samples.

*Prediction six: I assume that begging frequency and begging rate decrease with age of the immature but increase with complexity and rarity of the food item.* I base these assumptions on the informational hypothesis and the results on the peering behavior found by Schuppli et al. (2016).

*Prediction seven: I expect to see sex differences in begging frequency and begging rate in wild orangutan population.* This prediction is inspired by the study with wild chimpanzees in the nut-cracking task whereby the sex difference was revealed significant in begging of immatures (Estienne et al., 2019a). Additionally, in field study about a very specific feeding skill termite-fishing in wild chimpanzees, immature female chimps acquired this technique earlier and outperformed the young male ones with higher occurrence of replication of the strategies their mothers used, suggesting that there is sex differences in terms of observational learning and practicing in young wild chimpanzees (Lonsdorf, 2005). In this thesis, also being a very important observational learning approach, begging may differ between sexes in young orangutans as well.

*Prediction eight: I look for the begging frequency manifesting differently from the wild subjects to the zoo subjects (i.e. higher in the wild than it is in the zoo).* I assume this difference because regarding the food, there are generally more food resources with overall lower complexity and more even availability among distinct food items in the zoo than in the wild; regarding the life style, there are more role models available in proximity for the young orangutans in the zoo than in the wild so compared to this in the wild, the reliance on the mother to learn skills is lighter in the zoo.

Material and methods

* 1. Study sites and study periods

This study was based on behavioral observations on wild and captive Sumatran orangutans. The data on wild orangutans (i.e. wild data) was collected at the Suaq Balimbing research station (3°42′N, 97°26′E, Aceh Selatan, Indonesia, figure 2.1) by students, researchers and field assistants of the Department of Anthropology of the University of Zürich from June 2007 till January 2020. The data on captive orangutans (i.e. zoo data) was collected by me at the Leipzig Zoo (51.349°N 12.369°E, Leipzig, Germany) from January 2020 to March 2020. Among the subjects in this thesis, individuals that weaned were called juveniles.

Begging was defined as attempts by the focal individual to solicit food from another individual through gestures (i.e. by reaching for the food). The collection of begging events followed a standardized protocol (https://www.aim.uzh.ch/de/orangutannetwork/sfm.html). Between two begging events there must be a pause of at least ten seconds where the focal is on a different activity than begging, otherwise it’s still considered as one begging event.

A close up of a map

Description automatically generated

Figure 2.1: **Former and current orangutan study sites**. By van Schaik and van Hooff 1999; taken from Delgado and van Schaik 2000, p. 202.

* 1. Focal orangutans
     1. Wild Sumatran orangutans

The data set from the wild included 19 immatures and 12 mothers (figure 2.2).

|  |  |
| --- | --- |
| A monkey sitting on a branch  Description automatically generated  Name: Chindy; Age: 14.5; juvenile  Taken by Guilhem on 26 July 2017 | A close up of an animal  Description automatically generated  Name: Cinnamon; Age: 5; infant  Taken by Caroline on 14 February 2017 |
| A monkey sitting on a branch  Description automatically generated  Name: Frankie; Age: 1; infant  Taken by Mukhlis on 20 August 2013 | A picture containing animal, mammal, outdoor, priest  Description automatically generated  Name: Lois; Age: 6.5; infant  Taken by Armas on 10 February 2017 |
| A monkey sitting on a branch  Description automatically generated  Name: Eden; Age: 2; infant  Taken by Sofia on 02 November 2016 | A fox standing in forest  Description automatically generated  Name: Ellie; Age: 11.5; juvenile  Taken by Caroline in December 2010 |
| A close up of a monkey  Description automatically generated  Name: Lilly; Age: 10; juvenile  Taken by Caroline on 19 February 2011 | A monkey sitting on a branch  Description automatically generated  Name: Luther; Age: 2; infant  Taken by Saidi on 11 June 2018 |
| A monkey sitting on a branch  Description automatically generated  Name: Tornado; Age: 4; infant  Taken by Natasha on 25 July 2018 | A monkey sitting on a branch  Description automatically generated  Name: Albin; Age: 4.5; infant  Taken by Caroline on 25 December 2010 |
| A monkey sitting on a branch  Description automatically generated  Name: Amor; Age: 0.5; infant  Taken by Eric on 21 Feburary 2015 | A monkey sitting on a branch  Description automatically generated  Name: Chuck (left); Age: 1; infant  Taken by Iz on 19 Junary 2008 |
| A monkey sitting on a branch  Description automatically generated  Name: Rendang (left); Age: 1; infant  Taken by Caroline on 21 March 2014 | A monkey sitting on a branch  Description automatically generated  Name: Dalia; Age: 2; infant  Taken by Eric on 13 October 2014 |
| A monkey sitting on a branch  Description automatically generated  Name: Fredy; Age: 6; infant  Taken by Caroline on 16 December 2010 | A monkey sitting on a branch  Description automatically generated  Name: Simba (left); Age:1; infant  Taken by Zia on 28 Junary 2014 |
| A monkey sitting on a branch  Description automatically generated  Name: Pepito; Age: 5; infant  Taken by Rizal on April 15 2018A monkey sitting on a branch  Description automatically generated  Name: Diddy; Age: 12.5; juvenile  Taken by Natasha on 16 September 2018 | A monkey sitting on a branch  Description automatically generated  Name: Ronaldo; Age: 5.5; infant  Taken by Basri on 09 August 2011 |

Figure 2.2: **Wild Sumatran Orangutan population of this study**. All these pictures were retrieved from https://suaq.org/orangutan/.

During the study period (June 2007 – January 2020), a total amount of 8303 observation hours was collected on the focal individuals. The overall information (i.e. name, estimated date of birth, age range [from their first available to the last available begging event during the study period] (rounded to the nearest half-year interval), sex, mother, observation hours [follow hours]) of all wild and captive immature focal animals of this study is listed below (table 2.1). Notably, because the exact date of birth of the free-ranging orangutans is often unknown, their birth dates were roughly estimated to month based on their developmental characteristics when they were first found.

Table 2.1: **general information on all subjects of this study**: name, estimated date of birth (DOB), age range (in years) from their first available to the last available begging event during the study period, mother of the focal, sex, from which site the focal is from (Site: wild=Suaq Balimbing; zoo=Leipzig zoo), and how many observation hours were spent on this focal (Follow Hours).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Focal | DOB | Age Range | Mother | Sex | Site | Follow Hours |
| Albin  Amor  Chindy  Chuck  Cinnamon  Dalia  Diddy  Eden  Ellie  Frankie  Fredy  Lilly  Lois  Luther  Martok  Pepito  Rendang  Rima  Ronaldo  Sari  Simba  Tornado | 01/06/2006  01/09/2014  01/01/2003  01/01/2007  01/04/2012  01/10/2012  01/12/2005  01/11/2014  01/03/1999  01/08/2012  01/01/2005  01/01/2001  01/07/2010  01/02/2016  25/03/2017  01/01/2013  01/04/2013  02/08/2019  01/01/2006  05/08/2017  01/04/2013  01/06/2014 | 1.5  2.5-3  5-6  1  1.5-3, 5-5.5, 6.6-7  2  5, 8  0.5, 2-5  9  1-2, 4.5-5.5, 6.5-7  2.5-4, 6, 8.5-9  6.5-7, 13  0.5, 3-4.5, 6.5-7, 8-8.5  1.5, 3  3  4.5, 5.5, 6.5-7  1  0.5  1.5-2  2.5  0.5-1  3 | Alice  Alice  Cissy  Chick  Cissy  Dodi  Dodi  Ellie  Friska  Friska  Friska  Lisa  Lisa  Lilly  Raja  Piniata  Raffi  Pini  Raffi  Padana  Sarabi  Tiara | male  male  female  male  female  female  male  female  female  male  male  female  male  male  male  male  male  female  male  female  male  male | wild  wild  wild  wild  wild  wild  wild  wild  wild  wild  wild  wild  wild  wild  zoo  wild  wild  zoo  wild  zoo  wild  wild | 22  64  212  7  475  27  27  659  707  692  576  398  867  45  13  31  146  13  155  13  133  21 |

* + 1. Captive Sumatran orangutans

The Sumatran orangutan group at the Leipzig zoo consists of nine individuals. Data was collected on the three immature individuals: Martok, Sari, and Rima (figure 2.3) between January 2020 and March 2020, resulting in 40 observation hours. The basic information of the three zoo focal animals is listed in the table 2.1.

|  |  |
| --- | --- |
| Name: Martok  Taken by Hanna on September 2019 | A close up of an animal  Description automatically generated  Name: Sari  Taken on February 2020 |
| A picture containing outdoor, sitting, small, water  Description automatically generated  Name: Rima (Rima on the rope, the one on top is her mother: Pini)  Taken by Mikeliban on 28 February 2020 |  |

Figure 2.3: **Captive Sumatran Orangutan population of this study**. Pictures in the first row were retried from http://wkprc.eva.mpg.de/english/files/orang.htm.

* 1. Data collection
     1. Wild data and variables

The wild begging data set consisted of begging data collected during 340 focal follows (see appendix 1). Data from 258 of these follows (817 begging events) were already entered in the data set when I started working on the data set. I added the data of the remaining 82 follows that were available, from which I obtained 327 additional begging events. This resulted in a total of 1144 begging events collected from the wild (N=20, age in years: M=3.43, SD=2.14, Min=0.5, Max=13).

For this data set, I included four independent variables and one response variable. Independent variables can be split into two main focuses: the focal and the food item. Regarding the individual attributes of the subjects, I included the age and sex variables; regarding the attributes of the food items, I included the complexity (i.e. Processing Steps) and rarity (i.e. Popfreq, meaning the frequency of this food item in the whole population) variables. Processing steps refer to the procedure of feeding with different steps (i.e. processing steps) which can be quantified up to 5 with pick-and-eat being the baseline (0 step) process and each additional step in between of this process counting as one step. For instance, to eat a banana an orangutan first picks it up from the tree then peels it before ingests it, so this peeling action counts as one step during the baseline step. The general process of eating a banana, hereafter, is standardized as one step (Schuppi et al., 2016; Schuppli, 2020). The rarity of a certain food item is described by the percentage of its occurrence during all the feeding times with all the food items that have been observed either in the zoo or in the wild. The dependent variable is a binary outcome of the acceptance of the orangutan mother during the begging of her offspring and it’s noted as “Success” in my data set with two outcomes, either yes or no. The begging bout where the subject successfully got the food its mother was feeding on was noted down as “yes” and vice versa for “no”. Though there could be a variation amongst different reactive outcomes from the begging target (e.g. active delivery, no sign of any obvious reaction, showing reluctance by turning away, manifesting anger by slapping the beggar’s body part, etc.), I only looked at the outcome of the begging (i.e. did the focal got the food from the target at the end?) for the purpose of analyses in my statistical models.

* + 1. Zoo data and variables

In sum, 133 begging events from the Leipzig zoo were collected on three immature individuals (age in years: M=2.67, SD=0.53, Min=0.5, Max=3). The observation at the zoo mostly took place during the feeding periods (at 10:30, 13:30, and 15:30), as I expected begging to happen around these time points.

The outline as well as the criteria for collecting each of the variables in the zoo data set is almost identical to that of my data set from the wild site except for rarity and desirability variables. The desirability variable is uniquely in this zoo data set, which indicates how popular the food item is among the whole orangutan group. Being a new variable in the zoo data only, it was included due to my special interest in the effect of this variable on the outcome variable which remains as the same as “Success” with two levels. No existing research could be found examining this variable, however, during two months of observation at the zoo, my impression was that the individuals there had distinct food preferences. This led me to include this variable in my statistical model built only on the zoo data, together with other four variables (i.e. age and sex of the focal; complexity and rarity of the food item).

What’s more, although there is rarity variable in both zoo and wild data sets it’s measured differently for the food items at the zoo. In the wild data, the rarity of the food item was calculated by its overall frequency in the population (i.e. the frequency at which it occurred in the diet of the locally resident adult females at Suaq, values are ranged from 0 to 1). In the zoo subset, however, this approach was not applicable since I observed them 2-3 days a week over the course of two months and the observations only took place during the feeding time (at 10:30/13:30/15:30). To assess the rarity and the desirability of the zoo food items I designed a questionnaire with 5-and-7-point scales (see appendix 2) on rarity and desirability variables. I then contacted the head of the zookeepers of orangutans from the Leipzig zoo via email and invited him to fill it out. Because it’s a 5-point and a 7-point scale respectively for each of these variables, they are both considered as categorical rather than numeric predictors.

* + 1. Data exclusion

In my wild focal sample, because only one begging event was noted from the individual named Ian, and not much information is available on this individual, because of his rare appearance at Suaq, I excluded this one data point from the wild data set. Additionally, the local field assistants and Indonesian students working at Suaq filled out 427 of the coding sheets in Indonesian. Due to some translation issues, I had to skip those sheets filled in Indonesian, and it was left with 82 English datasets which I used for this study. Finally, some targets during some begging aren’t the mother, therefore, I had to exclude 14 data points from the wild subset and 52 points from the zoo subset.

* 1. Statistical analyses

I did all statistical analyses and plots of this study in the R programming language (version 3.5.2; R Core Team 2018). With the main models, to analyze which of the predictors (i.e. age of the subject, sex of the subject, complexity of the food item, rarity of the food item, and the and study site) affect the outcome of a begging event (i.e. success, coded as a binary variable with 0 = not successful and 1 = unsuccessful), general linear mixed models (GLMMs) with the binomial error distribution were implemented (Field, Miles, & Field, 2012), using the lme4 package (Bates et al., 2020) and logit link function (McCullagh & Nelder, 1989). I used the psych package (Revelle, 2020) to look at each of the numeric variables in detail (e.g. mean, standard deviation, minimum, maximum, median, skewness and kurtosis, etc.). The mixed effects logistic regression outputs I analyzed with the car package (Fox et al., 2020), and I used ggplot2 package (Wickham et al., 2020) for creating graphics.

I analyzed the data using six different data sets: I the full data frame (begging events N=1277), containing all of the available wild and zoo data, II the wild subset data (begging events N=1144), containing data from the wild only, III the zoo subset data (begging events N=133), containing the data from the zoo only, IV three condensed data sets based on each focal (from both Suaq and Leipzig zoo) and each begged food item during each half-year time window (i.e. age class) within the period of the study. There are three reasons behind this separation. Firstly, my wild data set was established over 13 years while my zoo data set was compiled over the course of two months. Consequently, the age range of each captive subject is too short to be condensed by each half year. The age range of per wild subject from Suaq is large enough to be divided into multiple half-year windows to allow me to discover the effects on begging rate and begging frequency within each subject. Secondly, due to the different approaches applied for scoring the rarity of the food item in the zoo and in the wild (i.e. questionnaire for the zoo items vs regular calculation for the wild items) these variables are not directly comparable. Thirdly, the variable “desirability” exists only in my zoo data because it is not feasible to assess desirability in the wild.

The reason why I have condensed data frames is that, besides the main models, I also looked at the effects of the universal independent variables on begging frequency and begging rate within IV data sets, as the exploratory models.

* 1. Summary of the statistical models

To sum up, there are three main parts (table 2.2) in my eight predictions with different models in my analyses (GLMMs with binomial error distribution for the first and second parts, GLMMs with Gaussian error distribution for the third part). In the first part, I examined the effects of four universal independent variables with an interaction between the age and the sex variables on the begging success in the wild sample (model i), there are three random intercepts included: ① the intercept per mother-infant combination (i.e. Mother/Focal: focal and mother as a nested intercept because not each mother corresponds to only one of the immature subjects) manifests the likelihood of different mother-infant relations, ② the intercept per subject at different age in days (Focal Age) shows the probability that some subjects are older and thus more developed in terms of its feeding competence than the younger ones, ③ the intercept per food item indicates the possibility that there is variation in their traits. To keep type I error rate at the nominal level of 5% (e.g. Barr et al. 2013), I included the slopes of the age effect per mother-infant combination which reveal the chances where it is not the same for all the mother-infant dyads, meaning that the variance of the age effect is assumed. The slopes of the complexity, rarity and desirability (only in the zoo) per food item reveals the likelihood that the complexity, rarity, and desirability effects are not the same for all the food items, meaning that there are presumably variances of these effects (Mundry, 2020a; Mundry, 2020b).

In the second part, I firstly looked at 2a) how two study sites (i.e. wild and zoo) differ in terms of begging success with the random intercept per mother-infant combination (model ii). I then looked into 2b) how the four universal independent variables and the desirability variable impact the begging success in my zoo sample with an interaction between age and sex, and the intercept per food item was included to the mode iii.

In the third part, I firstly looked at 3a) within the wild data merely, how the four universal variables impact the begging frequency including the intercept per mother-infant combination, the intercept per subject at different age in days, and the intercept per food item in model iv; within the zoo data merely, how the four universal variables with the desirability variable influence the begging frequency with the intercept per food item included in model v; within the combined data, how begging frequency changes over different sites, age and sex of the focal in the full data frame with the intercept per mother-infant combination, the intercept per subject at different age in days, and the intercept per food item included in model vi. I lastly looked into 3b) how the universal independent variables affect the begging rate within the wild sample with the intercept per mother-infant combination, the intercept per subject at different age in days, and the intercept per food item included in model vii.

Table 2.2: **summary of all the statistical models in three parts with tested predictions**.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Part | Model | Dataset | Distribution | Prediction | Response variable |
| 1 | i | II | Binomial | One-four | Begging success |
| 2a | ii | I | Binomial | One- three, Five | Begging success |
| 2b | iii | III | Binomial | One-four | Begging success |
| 3a | iv-vi | IV1-3 | Gaussian | Six-eight | Begging frequency |
| 3b | vii | IV1 | Gaussian | Six, seven | Begging rate |

See respective predictions on page number 17-19. Six data sets are I: the full data, II: the wild subset data, III: the zoo subset data, IV1: a condensed wild data on each focal and each begged food item during each half-year time window (i.e. age class) within the period of the study, IV2: zoo data condensed on each begged food item in each age class of a focal, and IV3: a combined data frame of both zoo and wild condensed data.

In each of the seven models, as an overall test of the effect of fixed effects, I compared the full model with a null model lacking the fixed effects but including the same random effects

structure as the full model (Forstmeier and Schielzeth, 2011) using a likelihood ratio

test (Dobson, 2002). Before fitting each of the models, I inspected all numeric predictors (i.e. age, complexity, rarity, and desirability) and the outcome measures (i.e. begging frequency and begging rate) for whether their distributions were normal (i.e. roughly symmetric). In case they were not normally distributed, I tried log and square root transformed the covariates until I reached the skewness of nearly 0 and smallest kurtosis possible (Field, 2005). I considered z-transforming those covariates to achieve an easier interpretable model (Schielzeth, 2010) and ease model convergence but it was not needed in building any of my models. After fitting the model, I checked whether the assumptions of normally distributed and homogeneous residuals were filled using QQ-plot and histograms (Field, 2005) of residuals and residuals plotted against fitted values (Quinn and Keough, 2002). These indicated no deviations from these assumptions. Lastly, I checked for multi-collinearity cases among my predictors to determine potential interactions (Field 2005). There was no interaction other than the age and sex predictors appearing in the wild model only.

Results

* 1. Effects on begging success

*Prediction one: as the immature orangutan grows older, the mother shows less tolerance during begging*

For testing this prediction, I used the full dataset (I) with both wild and zoo data points included to manifest the overall age effect on the begging success (i.e. mother’s tolerance during begging, coded as a binary variable with 0 = not successful and 1 = unsuccessful), the reduced dataset with only the wild sample (II), and the reduced dataset with only the captive sample (III).

In the full data (I), I looked at the mother’s acceptance of the offspring’s begging request to investigate their role in feeding skill acquisition of the offspring and therefore, the target of the begging should be the mother instead of any other individuals. Because there were 66 begging events where the target of the begging wasn’t the mother, hence, I excluded those begging events from my raw data. I also excluded incomplete begging events with no record of the response variable “Success” (N=233), exact age of the focal with reservation of one decimal (N=3), food items (N=2), values for the complexity variable (i.e. processing steps of a food item) (N=71). I fitted my dataset (begging events: N= 912) into my statistical model ii. There are four fixed effects of the age and sex variables as well as the interaction between them, complexity and site variables. By removing the variable of exact age from the model ii and using likelihood ratio tests, I compared the model without age variable to the complete model with the age variable together with other four variables, I got the results (table 3.1) that the probability of the begging success was significantly affected by age (χ2=7.7968, *df*=1, *p*<0.01). More particularly, unlike how I predicted, the relation between the offspring’s age and the mother’s tolerance to the begging was quadratic instead of linear (i.e. the tolerance of the mother decreases continuously with increasing age of the offspring). This indicates that as the orangutan infants grew until the age of 5, the mothers showed increasing tolerance to their begging requests. However, once the immatures reached the age of 5 and grew older, it’s less likely that the orangutan mothers let the offspring take the food from them (figure 3.1). Moreover, in this full model (model ii) the random intercept ② (i.e. per subject at different age in days) showed a standard deviation of 0.5 (table 3.2).

In the reduced dataset with only the wild sample (II), there were 14 begging events where the target of the begging wasn’t the mother, hence, I excluded those begging events from my raw data. I also excluded incomplete begging events with no record of the response variable “Success” (N=223), exact age of the focal with reservation of one decimal (N=3), food items (N=2), values for the complexity variable (i.e. processing steps of a food item) (N=71). I fitted my dataset (begging events: N= 831) into my statistical model i. There are four fixed effects of the age and sex variables as well as the interaction between them, complexity and rarity variables. By removing the variable of exact age from the model i and using likelihood ratio tests, I compared the model without age variable to the complete model with the age variable together with other four variables, I got the results (figure 3.1) that the probability of the begging success was significantly affected by age (χ2=10.3132, *df*=1, *p*<0.01). The relation between the offspring’s age and the mother’s tolerance to the begging was once again non-linear. Moreover, in this full model (model **i**) the random intercept ② (i.e. per subject at different age in days) showed a standard deviation of 0.052 (table 3.2).

In the reduced dataset with only the captive sample (III), there were 52 begging events where the target of the begging wasn’t the mother, hence, I excluded those begging events from my raw data. I also excluded incomplete begging events with no record the rarity variable (i.e. the frequency of the occurrence of a food item in the whole observed food population) processing steps of a food item) (N=1). I fitted my dataset (begging events: N= 80) into my statistical model iii. There are five fixed effects of the age and sex variables, complexity, rarity, and desirability (i.e. a food item is favored by how many orangutans from the same group) variables. By removing the variable of exact age from the model i and using likelihood ratio tests, I compared the model without age variable to the complete model with the age variable together with other four variables, I got the results that the probability of the begging success was not significantly affected by age (table 3.1).

A screenshot of a cell phone

Description automatically generatedA screenshot of a cell phone

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Figure 3.1: **Effect of age in years (square rooted) on the probability of begging success (i.e. the mother being tolerant to the begging call of her offspring) with both wild Sumatran orangutans in Suaq and captive ones in Leipzig zoo (left, model ii), the wild Sumatran orangutans from Suaq only (right, model i).** The vertical lines on the x axis represent frequency of occurrence of begging per binned age and subject. The curves show the fitted probability in 95% of the chance (model ii: N= 912 begging events; model i: N=831 begging events).

Additionally, I found the non-linear relation between the age and the response and decided to keep it my models by comparing the model with age being both linear and quadratic to the model with age being only linear. I kept the same random effect ① (i.e. Mother/Focal: focal and mother as a nested intercept because not each mother corresponds to only one of the immature subjects) and got significant results from the age variable being quadratic by using a likelihood ratio test (χ2= 6.8047, *df*=1, *p*<0.01). Hence, I decided to keep the age variable as quadratic in my full and wild models but not in my zoo model since this transformation of the age variable in my zoo data didn’t differ from the original.

*Prediction two: there is a sex difference in mother’s tolerance towards begging behavior and there is an interaction between the age and the sex variables*

In the full data (I), I fitted my dataset (begging events: N= 912) into my statistical model ii. By removing the interaction between the sex of the immature and immature age from the model and using likelihood ratio tests, I compared the model without the interaction to the complete model with the interaction together with other four variables, I got the results (table 3.1) that the probability of the begging success not significantly differed in the interaction. Because adding this interaction in the reduced model with the captive data wasn’t preferred in an ANOVA test which compares the model with and without this interaction, I didn’t keep the interaction of age and sex in the zoo model.

With the reduced dataset with only the wild sample (II), I fitted my dataset (begging events: N= 831) into my statistical model i. There were 13 male immatures and 6 female immatures. By removing the interaction between the sex of the immature and the immature age from the model and using likelihood ratio tests, I compared the model without the interaction to the complete model with the interaction together with other four variables, I got the results (table 3.1) that the probability of the begging success significantly differed in the interaction of age and sex (χ2=4.558, *df*=1, *p*=0.033). As the age predictor turned out to be quadratic, the relation between this interaction and the mother’s tolerance to the begging was quadratic instead of linear. This indicates that as the orangutan infants grew until the age of 5, the mothers showed increasing tolerance to the begging from both the female and male immatures but with higher tolerance to the males than to the females. However, once the immatures reached the age of 5 and grew older, the frequency of the tolerance of the orangutan mothers decreased continuously to the offspring of both sexes but with higher to the female offspring, comparably (figure 3.2).

A screenshot of a map

Description automatically generatedFigure 3.2: **Effect of age in years (square rooted) interacting with sex of the immature on the probability of begging success (i.e. the mother being tolerant to the begging call of her offspring) with the wild Sumatran orangutans from Suaq (model i).** The vertical lines on the x axis represent frequency of occurrence of begging per binned age and subject. The curves show the fitted probability in 95% of the chance (model i: N=831 begging events).

*Prediction three: the more effort it takes the immature orangutan to acquire a certain food item, the more tolerant the mother is when the offspring solicitates the food item from her*

Complexity of the food item means processing steps of a food item, the higher the value the more complex to process it.

In the reduced dataset with only the wild sample (II), there were 87 distinct food items found in the wild (see appendix 3) with different processing steps (0-5). I fitted my dataset (begging events: N= 831) into my statistical model i. There are four fixed effects of the age and sex variables as well as the interaction between them, complexity and rarity variables. By removing the variable of complexity variable from the model i and using likelihood ratio tests, I compared the model without this variable to the complete model with this variable together with other four variables, I got the results (figure 3.3) that the probability of the begging success was significantly impacted by the complexity of the food item (χ2=4.310, *df*=1, *p*<0.038). The relation between the complexity predictor and the mother’s tolerance to the begging was positively linear (i.e. with the increasing processing steps of the food item, the frequency of mothers’ accepting the begging of their young increased). Moreover, in the wild model (model **i**) the random intercept of ③ (i.e. the intercept per food item) revealed a standard deviation of 0.036; the standard deviation of the effect complexity over all food items showed 0.010 (table 3.2).

In the reduced dataset with only the captive sample (III), there were 22 distinct food items found in the Leipzig zoo (see appendix 3) with different processing steps (0-2). I fitted my dataset (begging events: N= 80) into my statistical model iii. There were five fixed effects of the age and sex variables, complexity, rarity, and desirability (i.e. a food item is favored by how many orangutans from the same group) variables. By removing the variable of complexity variable from the model and using likelihood ratio tests, I compared the model without this variable to the complete model with this variable together with other four variables, I got the results that the probability of the begging success was not significantly impacted by the complexity of the food item (table 3.1). Moreover, the standard deviation of the effect complexity over all food items showed 0.683 (table 3.2).

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Figure 3.3: **Effect of the complexity of the food item on the probability of begging success (i.e. the mother being tolerant to the begging call of her offspring) with the wild Sumatran orangutans from Suaq (model i).** Complexity of the food item means processing steps of a food item, the higher the value the more complex to process it. The boxes on the x axis represent frequency of occurrence of begging per processing step per food item. The line shows the fitted probability in 95% of the chance (model i: N=831 begging events).

*Prediction four: the more uncommon the food item is in the habitat, the higher the tolerance of the orangutan mother*

The rarity of the food item means the frequency of the occurrence of a food item in the whole observed food population, ranging from 0 to 1. In all three models respectively with full data, wild subset data, and the zoo subset data, the rarity variable didn’t influence the begging success of the offspring (table 3.x).

*Prediction five: the general tolerance of the orangutan mothers in the zoo is higher than that of the mothers in the wild*

To compare the overall begging success in the wild and that in the zoo I used the model ii with the merged data. By removing the variable of site from the model and using likelihood ratio tests, I compared the model without site variable to the complete model with the site variable together with other three variables as well as the interaction between age and sex variables, I got the results (figure 3.4) that the probability of the begging success was significantly different in two sites (table 3.1). Particularly, mothers in the zoo were significantly more tolerant to the offspring’s begging than the mothers in the wild (χ2=13.8793, *df*=1, *p*<0.001).

A close up of a map

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Figure 3.4: **Difference in begging success in two study sites (wild vs zoo).** The blue circles show the fitted probability in 95% of the chance, the line in between of them visualizes the gap (model ii: N=912 begging events; wild data: N=831 begging evets; zoo data: N=81 begging events).

Table 3.1

**Results of models investigating the begging success (i.e. mothers’ tolerance during offspring’s begging) from the full model (ii), reduced models with wild (i) and zoo (iii) subsets.** Estimates and standard errors were taken from the summary output of the table, likelihood ration tests (χ2 ), degrees of freedom and the p values were retrieved by dropping the each of the fix effects at a time and comparing the reduced model to the complete model.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Response variable [Model] | Estimate | SE | χ2 | *df* | P |
| **Begging success (yes/no) [Model i]** |  | | | | |
| (Intercept) | -5.602 | 1.355 | a | a | a |
| Immature age (years) b | 4.716 | 1.258 | a | a | a |
| Sex of the immature (male) c | 2.165 | 0.977 | a | a | a |
| Complexity of the food item | 0.179 | 0.083 | 4.310 | 1 | **0.038** |
| Rarity of the food item d | 0.638 | 0.979 | -0.222 | 1 | a |
| Immature age2 b | -1.003 | 0.310 | 10.313 | 1 | **0.001** |
| Sex of the immature (male) c \* Immature age (years) b | -1.013 | 0.482 | 4.558 | 1 | **0.033** |
| **Begging success (yes/no) [Model ii]** |  | | | | |
| (Intercept) | -2.228 | 0.597 | a | a | a |
| Immature age (years) e | 0.740 | 0.205 | a | a | a |
| Site (zoo) f | 2.145 | 0.516 | 13.879 | 1 | **< 0.001** |
| Sex of the immature (male) c | 1.269 | 0.558 | a | a | a |
| Complexity of the food item | 0.133 | 0.086 | 2.148 | 1 | 0.143 |
| Immature age2 | -0.057 | 0.018 | 7.797 | 1 | **0.005** |
| Sex of the immature (male) c \* Immature age (years) e | -0.262 | 0.126 | 3.021 | 1 | 0.082 |
| **Begging success (yes/no) [Model iii]** |  | | | | |
| (Intercept) | 3.895 | 3.136 | a | a | a |
| Immature age (years) | -0.048 | 0.739 | 0.004 | 1 | 0.948 |
| Sex of the immature (male) | 1.668 | 1.019 | 3.209 | 1 | 0.073 |
| Complexity of the food item | -0.617 | 0.547 | 0.915 | 1 | 0.339 |
| Rarity of the food item | 0.039 | 0.427 | 0.009 | 1 | 0.926 |
| Desirability of the food item | -0.454 | 0.392 | 1.623 | 1 | 0.203 |

a: Not shown as having a very limited interpretation.

b: square-root-transformed due to the skewed distribution of the original variable. Skewness (the value of Kurtosis) for the original age variable and the square-root-transformed age variable were 0.47 (-0.25) and -0.1 (-0.98), respectively.

c: Estimate and SE refer to the difference in response between the reported level of the predictor and the reference category (male).

d: square-root-transformed due to the skewed distribution of the original variable. Skewness (the value of Kurtosis) for the original rarity variable and the square-root-transformed rarity variable were 2.19 (4.17) and 0.9 (0.37), respectively.

e. square-root-transformed due to the skewed distribution of the original variable. Skewness (the value of Kurtosis) for the original age variable and the square-root-transformed age variable were 0.57 (-0.01) and -0.06 (-0.83), respectively.

f. Estimate and SE refer to the difference in response between the reported level of the predictor and the reference category (zoo).

Table 3.2

**Estimated standard deviations for the contribution of the random effects and standard deviation (SD)**

**from the full model (ii), reduced models with wild (i) and zoo (iii) subsets.**

|  |  |  |
| --- | --- | --- |
| Term | Effect (1) | SD |
| **Model i** | | |
| Food item | Complexity | 0.010 |
| Food item | Intercept | 0.036 |
| Focal age | Intercept | 0.052 |
| **Model ii** | | |
| Food item | Complexity | 0.099 |
| Food item | Intercept | 0.465 |
| Focal age | Intercept | 0.500 |
| **Model iii** | | |
| Food item | Complexity | 0.683 |

(1): ‘intercept’ refers to a random intercept, others mean random slopes effects.

* 1. Effects on begging rate and begging frequency

*Prediction six: begging frequency and begging rate decrease with age of the immature but increase with complexity and rarity of the food item*

Begging frequency was calculated by dividing the total number of begging events on each observed food item of each focal animal by the total observation hours spent on this focal with the food item in each half year time window. Begging rate is a ratio of the total number of begging events with a certain food item of each focal animal to the number of bouts its mother fed on this food item during the observation period of this study. Begging frequency and begging rate were log-transformed in all four models (iv, v, vi, & vii) due to the skewed distributions of the original response variables (table 3.3). Among my predictors, “Age class” means age of the immature in years but the difference between exact age (like in the begging success model in the previous section) and age class is that I rounded the decimal to the nearest half-year interval for the age class variable.

In models iv and vii built upon the condensed data (IV1) in the wild population, I included the four universal variables (i.e. age and sex of the immature, complexity and rarity of the food item). Before I inspected the distribution of all the predictors, I excluded 60 data points due to the absence of begging frequency and 181 for lack of begging rate. For fitting the data to models iv and vii, I had 160 observations remaining in data IV1. Among my covariates (i.e. age, complexity, and rarity variables) in model iv and vii, I square root transformed age variable and log transformed rarity variable because of the skewness (>1) of the original (table 3.3).

By removing the variable of complexity variable from the model vii and using likelihood ratio tests, I compared the model without this variable to the complete model with this variable together with other three variables, I got the results (figure 3.5) that the probability of the begging rate (log) was significantly impacted by the complexity of the food item (χ2=6.608, *df*=1, *p*=0.010). The relation between the complexity predictor and begging rate was negatively linear (i.e. with the increasing processing steps of the food item, begging rate decreased), suggesting that the immatures begged less for a food item each time its mother was feeding on (i.e. begging opportunity) and has more processing steps (i.e. more complex).

By removing the variable of rarity variable (log) from the model vii and using likelihood ratio tests, I compared the model without this variable to the complete model with this variable together with other three variables, I got the results (figure 3.6) that the probability of the begging rate (log) was significantly impacted by the rarity (log) of the food item (χ2=16.650, *df*=1, *p*<0.0001). The relation between the rarity predictor and begging rate was negatively linear (i.e. begging rate decreased with more uncommon food item), suggesting that the immatures begged less for a rarer food item each time its mother was feeding on.

In model iv with dataset IV, no significant influence found in any of the four predictors on begging frequency of the immature (table 3.3). Moreover, the standard deviation of the random intercept food item showed 0.270 and 0.834 from the intercept focal age in model iv, food item of 0.791 and focal age of 0.321 revealing in model vii (table 3.4).

A close up of a map

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Figure 3.5: **Effect of the complexity of the food item on the probability of log begging rate** (i.e. a ratio of the total number of begging events with a certain food item of each focal animal to the number of bouts its mother fed on the same food item during the observation period of this study) with the wild Sumatran orangutans from Suaq (model vii). Complexity of the food item means processing steps of a food item, the higher the value the more complex to process it. The boxes on the x axis represent frequency of occurrence of begging per processing step per food item. The line shows the fitted probability in 95% of the chance (model vii: N=160 rows).

A close up of a map

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Figure 3.6: **Effect of the log rarity of the food item on the probability of log begging rate with the wild Sumatran orangutans from Suaq (model vii).**  Rarity of a certain food item is described by the percentage of its occurrence during all the feeding times with all the food items that have been observed in this study. The lines on the x axis represent frequency of occurrence of begging per rarity value on per food item. The line shows the fitted probability in 95% of the chance (model vii: N=160 observations).

In model v with the dataset IV2 (i.e. condensed zoo data), due to one data point missing with the rarity variable, I had 38 observations in this model. Similar to the condensed data with the wild sample (IV1), I log transformed the response variable begging frequency in this model due to the skewed distribution of the original (table 3.3) but all the independent variables were roughly normally distributed. Begging frequency is a ratio of the total number of begging events on each observed food item of each focal animal to the total observation hours spent on this focal with the same food item, in each half year time window.

By removing the variable of age (i.e. age class) from model v and using likelihood ratio tests, I compared the model without age variable to the complete model with the age variable together with other four variables, I got the results (figure 3.7) that the probability of the begging frequency significantly differed over age (χ2=6.419, *df*=1, *p*=0.011). More particularly, like the opposite of what I predicted, the relation between the immature’s age and the frequency of its begging was positive. This indicates that orangutan immatures begged more as they aged.

By removing the variable of rarity from model v and using likelihood ratio tests, I compared the model without rarity variable to the complete model with the age variable together with other four variables, I got the results (figure 3.8) that the probability of the begging frequency significantly differed over age (χ2=4.066, *df*=1, *p*=0.044). More particularly, like the opposite of what I predicted, the relation between the immature’s age and the frequency of its begging was positive. This indicates that orangutan immatures begged more as they aged. What’s more, the random intercept of food item showed a standard deviation of 0.509 (table 3.4) in model v.

A close up of a map

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Figure 3.7: **Effect of age on the probability of begging frequency (log) with the captive Sumatran orangutans from Leipzig zoo.** Begging frequency is a ratio of the total number of begging events on each observed food item of each focal animal to the total observation hours spent on this focal with the same food item, in each half year time window.Age class refers to the immature age in years and rounded the decimal to the nearest half-year interval for the. The vertical lines on the x axis represent frequency of occurrence of begging per binned age and subject. The curves show the fitted probability in 95% of the chance (model v: N= 38 observations).

A close up of a map

Description automatically generated

Figure 3.8: **Effect of the rarity of the food item on the probability of log begging frequency with the captive Sumatran orangutans from Leipzig zoo.** Rarity of a certain food item is described by the percentage of its occurrence during all the feeding times with all the food items that have been observed in this study. The lines on the x axis represent frequency of occurrence of begging per rarity value on per food item. The line shows the fitted probability in 95% of the chance (model v: N=38 observations).

*Prediction seven: there are sex differences in begging frequency and begging rate in wild orangutan population*

Throughout these four models, sex difference was not found either in begging frequency or in begging rate (table 3.3).

*Prediction eight: the begging frequency manifests differently from the wild subjects to the zoo subjects (i.e. higher in the wild than it is in the zoo)*

To compare the overall begging frequency in the wild and that in the zoo I used the model vi with the merged data VI3. After excluding 61 missing data there were 379 rows left in the data frame. Due to the skewness of the response variable, I once again log transformed it (table 3.3). By removing the variable of site from the model and using likelihood ratio tests, I compared the model without site variable to the complete model with the site variable together with other three variables as well as the interaction between age and sex variables, I got the results (figure 3.9) that the probability of the begging success was significantly different in two sites (table 3.3). Particularly, immatures in the zoo begged significantly more frequently were significantly than the ones in the wild (χ2=5.843, *df*=1, *p*=0.016), which turned out to be the opposite of how I expected. Moreover, random intercepts of food item and focal age showed a standard deviation of 0.278 and 0.723, respectively (table 3.4) in model vi.

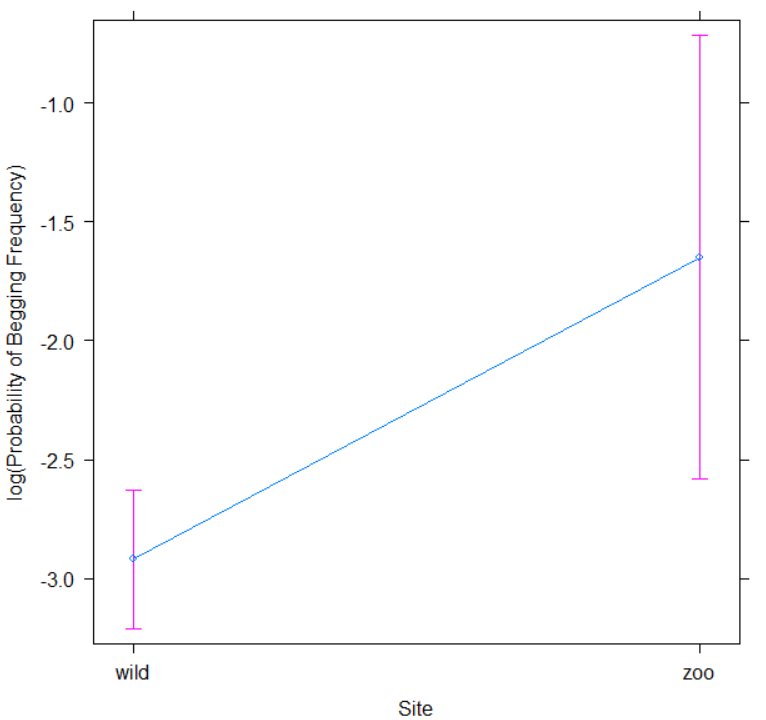


Figure 3.9: **Difference of the probability of begging frequency (log) between two study sites (wild vs zoo).** The blue circles show the fitted probability in 95% of the chance, the line in between of them visualizes the gap (model vi, N=379 observations).

Table 3.3

**Results of models investigating the begging frequency and begging rate from the model iv, v, vi, vii.** Begging frequency was computed by dividing the total number of begging events of each focal animal by the total observation hours spent on this focal during the observation period of this study. Begging rate was calculated as a ratio of the total number of begging events with a certain food item of each focal animal to the number of bouts its mother fed on this food item. Estimates and standard errors were taken from the summary output of the table, likelihood ration tests (χ2 ), degrees of freedom and the p values were retrieved by dropping the each of the fix effects at a time and comparing the reduced model to the complete model.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Response variable [Model] | Estimate | SE | χ2 | *df* | P |
| **Begging frequency b [Model iv]** |  | | | | |
| (Intercept) | -2.640 | 0.701 | a | a | a |
| Age class (in years) c | -0.006 | 0.281 | <0.001 | 1 | 0.984 |
| Complexity of the food item | 0.104 | 0.070 | 1.887 | 1 | 0.169 |
| Immature sex (male) d | 0.106 | 0.378 | 0.079 | 1 | 0.778 |
| Rarity of the food item e | 0.101 | 0.059 | 2.664 | 1 | 0.103 |
| **Begging frequency f [Model v]** |  |  |  |  |  |
| (Intercept) | -2.783 | 0.754 | a | a | a |
| Age class (in years) | 0.404 | 0.149 | 6.419 | 1 | **0.011** |
| Immature sex (male) | -0.175 | 0.206 | 0.715 | 1 | 0.398 |
| Complexity of the food item | -0.149 | 0.176 | 0.687 | 1 | 0.407 |
| Rarity of the food item | 0.237 | 0.111 | 4.066 | 1 | **0.044** |
| Desirability of the food item | -0.140 | 0.097 | 2.029 | 1 | 0.154 |
| **Begging frequency g [Model vi]** |  |  |  |  |  |
| (Intercept) | -3.149 | 0.232 | a | a | a |
| Age class (in years) h | 0.021 | 0.112 | 0.035 | 1 | 0.851 |
| Immature sex (male) i | 0.354 | 0.275 | 1.651 | 1 | 0.199 |
| Complexity of the food item j | 0.106 | 0.063 | 2.790 | 1 | 0.095 |
| Site (zoo) k | 1.271 | 0.504 | 5.843 | 1 | **0.016** |
| **Begging rate [Model vii] l** |  |  |  |  |  |
| (Intercept) | -3.901 | 0.652 | a | a | a |
| Age class (in years) c | -0.050 | 0.176 | 0.081 | 1 | 0.776 |
| Complexity of the food item | -0.289 | 0.107 | 6.608 | 1 | **0.010** |
| Immature sex (male) d | 0.014 | 0.228 | 0.004 | 1 | 0.952 |
| Rarity of the food item e | -0.409 | 0.092 | 16.650 | 1 | **<0.0001** |

a: Not shown as having a very limited interpretation.

b. log transformed due to skew distribution of the original variable. Skewness (the value of Kurtosis) for the original response variable and the log-transformed variable were 7.83 (73.32) and 0.64 (0.06), respectively.

c. square-root-transformed due to the skewed distribution of the original variable. Skewness (the value of Kurtosis) for the original age variable and the square-root-transformed age variable were 0.84 (0.68) and 0.18 (-0.73), respectively.

d. Estimate and SE refer to the difference in response between the reported level of the predictor and the reference category (male).

e. log transformed due to skew distribution of the original variable. Skewness (the value of Kurtosis) for the original response variable and the log-transformed variable were 1.78 (1.79) and -0.44 (-0.67), respectively.

f. log transformed due to skew distribution of the original variable. Skewness (the value of Kurtosis) for the original response variable and the log-transformed variable were 1.49 (1.7) and 0.35 (-1.21), respectively.

g. log transformed due to skew distribution of the original variable. Skewness (the value of Kurtosis) for the original response variable and the log-transformed variable were 8.09 (93.08) and 0.52 (-0.29), respectively.

h. z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 3.61 and 2.06 years, respectively.

i. Estimate and SE refer to the difference in response between the reported level of the predictor and the reference category (male).

j. z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 1.79 and 1.53 processing steps, respectively.

k. Estimate and SE refer to the difference in response between the reported level of the predictor and the reference category (zoo).

l. log transformed due to skew distribution of the original variable. Skewness (the value of Kurtosis) for the original response variable and the log-transformed variable were 5.05 (29.35) and 0.65 (-0.06), respectively.

Table 3.4

**Estimated standard deviations for the contribution of the random effects and standard deviation (SD)**

**from the model iv, v, vi, vii.**

|  |  |  |
| --- | --- | --- |
| Term | Effect (1) | SD |
| **Model iv** | | |
| Food item | Intercept | 0.270 |
| Focal age | Intercept | 0.834 |
| Residuals | - | 0.945 |
| **Model v** | | |
| Food item | Intercept | 0.509 |
| Residuals | - | 0.470 |
| **Model vi** | | |
| Food item | Intercept | 0.278 |
| Focal age | Intercept | 0.723 |
| Residuals | - | 0.916 |
| **Model vii** |  |  |
| Food item | Intercept | 0.791 |
| Focal age | Intercept | 0.326 |
| Residuals | - | 0.948 |

(1): ‘intercept’ refers to a random intercept, others mean random slopes effects.

Discussion

This study investigated how Sumatran orangutan mothers are involved in the acquisition of feeding skills of their offspring. For this purpose, I looked at the reaction of the mother when the young one was begging from her. Because reactions could have multiple ways to be measured, I put my focus on the tolerance of the mother (i.e. letting the offspring have the food or refusing the begging call). In the first and second chapter of my thesis, I investigated which elements could impact the mother’s tolerance when begging occurred to capture some presentation of regulation of the orangutan mother towards the feeding skill acquisition of her immature. There were four aspects in my predictions: age and sex of the immature as well as complexity and rarity of the food item (i.e. four universal independent variables) in this project. I based these four predictors on prior studies. This may bring, on the one hand, an important clue on why orangutans have an exceptionally slow life history with their prolonged immaturity and thereby provides an important message about the evolution of social-cognitive development with social learning of humans. On the other hand, it could also be solid evidence against previous research suggesting that orangutan mothers don’t teach and play only passive role in skill acquisition of their immatures.

The third chapter of this thesis was about a dynamic response to the previous two chapters, which is to shift the focus from the orangutan mothers’ reaction during begging to the offspring’s perspective. I wanted to find out under what circumstances immatures beg from their mothers and if there are variations among the same four predictors as mentioned above.

* 1. Part 1: begging success in relation to four universal independent variables

*Prediction 1 & 2: begging success ~ immature age and sex*

In this thesis, I found that, only in the wild population, the orangutan mother’s acceptance of the begging call significantly changes with the age of the immature and the relation between the offspring’s age and the mother’s tolerance to the begging is quadratic rather than linear. Specifically, as the orangutan infants grow until the age of 5, the mothers show increasing tolerance to their begging requests. However, once the immatures reach the age of 5, it is less likely that the orangutan mothers let the offspring take the food from them. In terms of sex difference, I found that, again only in their nature habitat, there was a relation between age and sex of the immature. In particular, as the age predictor turned out to be quadratic in both sexes, there was a significant difference between them. The difference shows that as the orangutan infants grow until the age of 5, the mothers showed increasing tolerance to the begging from both the female and male immatures but with higher tolerance to the males than to the females. However, once the immatures reach the age of 5 and older, the frequency of the tolerance of the orangutan mothers decreased continuously to the offspring of both sexes but with higher frequency of the tolerance to the female offspring, comparably.

These findings only partly match my predictions about the relation among age and sex of the offspring and begging success. They also only partly confirm the POC theory by Trivers (1974) in which he argues that the older the offspring is, the more competent it will be, and thus needs progressively less parental support and after around the age of 7.5 years, mothers invest less than what is demanded. Here, this was measured as the outcome of the orangutan mothers’ tolerance to their offspring’s begging as they age. Regarding the sex difference revealed in this project, it is in line with the findings from Estienne et al (2019a) studies with young chimpanzees. In a nut-cracking task, chimpanzee mothers were more tolerant to their immature sons’ begging calls than to their immature daughters’ and generally shared more nuts with their sons. However, the tendency of the age and sex interaction suggested in the complex honey extraction task with wild chimpanzees is on the opposite side of what this thesis revealed. In particular, chimpanzee mothers provided more learning opportunities to their daughters, but it decreased as the daughters aged while the opposite pattern was found for sons (Estienne et al., 2019b). These findings also contradict the results on the effect of age and sex Kunz (2019) found in her thesis in which her results yielded no effect of age and sex of Sumatran orangutans from the same study site as this thesis on the mother’s tolerance during begging.

It is very illuminating that instead of continuously decreasing the tolerance to the offspring’s begging, orangutan mothers firstly increase their maternal investment to their young by being increasingly more tolerant to their immatures taking food from them until they are five years old. This coincides with the most frequent begging period found with wild orangutans which is 0-5-year-olds (van Noordwijk & van Schaik, 2005). Mothers are generally more tolerant with begging of their 0-5-year-olds probably because they don’t reach “good enough” skill competences before five years of age and the mothers need to be more supportive to guarantee the survival of their infants. The reason why the highest point where the orangutan mothers are the most tolerant to the begging didn’t show earlier than five years old is that orangutan infants rely merely on mothers’ milk in their first year of life and only start taking solid food between one and one and a half years of age (van Noordwijk et al 2009; van Noordwijk et al., 2013, as cited in Smith et al., 2017). During this period, orangutan mothers might be aware that their young infants can’t digest everything they eat and therefore, restrict their food sharing. Once orangutan offspring grow older than five, termination of maternal invest gradually takes place as the mothers may get ready for the full invest into the next offspring (Trivers, 1974).

Of course, there could be violation of this pattern in regard to the physical condition of the young. Thus, an entire project could be focused on looking into the variation of the physical condition of the offspring and research the outcome of the begging with the focus on the orangutan mother’s acceptance. While there could be other ways of measuring this variable, physical growth of an animal focal could be estimated through non-invasive laser photogrammetry (Schuppli et al., 2016).

*Prediction 3 & 4: begging success ~ complexity and rarity of the food item*

In a previous study it was shown that more complex food items require higher skill level and that competence is reached with enough exposure of mother’s manipulating complex foods (Schuppli et al., 2016). Noteworthily, the measure of complexity of a food item is derived from the number of steps it takes a subject to process the food item (i.e. higher the value, more complex it is to process the food until ingestion), which is also adapted from the measure from Schuppli et al., (2016). In my wild sample from Suaq, I found a positive relation between the complexity of the food item and the begging success, suggesting that the more steps it takes an individual to process the food item, the more liberally the mothers from the natural habitat treat the begging of the immature (i.e. the immature takes the food from its mother more successfully). This finding confirms the results Kunz (2019) got in her thesis which is that the more complex the food item is to ingest, the more successful the immature is in begging for it. This confirms that seemly uninventive orangutan mothers actually do adjust their behavior by giving more opportunities with hard-to process foods to their immatures, which is rather a not-so-easily detectable way of provisioning.

In terms of the measurement of the rarity of a food item, if the occurrence of a food item A is lower than of a food item B in the whole observed food population, then A is considered to have higher rarity and lower availability than B. Therefore, the rarity is always a relative value. As the other very important feeding skill, in the peering data, Schuppli and colleagues (2016) found that the immature orangutans spent more time peering at a less common food item its mother fed on. This can imply that rarer items mean that the immatures have less opportunities to learn them. Hence, I hypothesized that if orangutan mothers want to facilitate the learning process of their offspring, they should be more tolerant for rarer items their immatures beg for. However, my results on the impact of the rarity of the food item didn’t support my prediction. A possible explanation of this would be that the mothers are stingy with rare food items especially if the rare food item is highly helpful for their milk production (van Noordwijk et al., 2013). Another possibility is that the mothers may not be certain about if their young infants can digest the food yet especially when they haven’t tried it much themselves or simply don’t remember if they did in the past since they don’t see rare food items often. Therefore, they would rather testify and explore rare food items on their own.

* 1. Part 2: begging success in relation to site (i.e. wild vs zoo)

*Prediction 5: begging success ~ site (wild vs zoo)*

I predicted that the general tolerance of the orangutan mothers in the zoo is higher than that of the mothers in the wild.I based this prediction on the fact that there are more food resources with smaller variety and more even occurrences in the zoo than there are in the wild. Therefore, the captive orangutan mother can afford to be more tolerant once the offspring begs the food from her. My results supported this hypothesis. However, there might be some limitations from this result due to very uneven distribution of begging events collected from the wild site (N=1144) and the zoo site (N=133). To get more reliable results, one suggestion for future research is to collect more data points from the zoo site.

Although orangutan mothers’ subtle maternal scaffolding was examined in this thesis, it could contribute to young orangutans’ skill acquisition and faster independence from their mothers if the mothers guided their offspring in a more straightforward way. In an interesting study done in captivity (i.e. semi-natural habitat) with orangutans in a re-habituation program, humans assisted orangutan mothers rare their immature, for instance by training the mother to share the food in her possession with her offspring so that there is more opportunities for the young to acquire necessary information and skills regarding the food item through more valuable interaction (Hayashi, 2016). This could be a beneficial practice with mother-infant dyads to help boost the infants’ feeding skills and cognitive abilities. A similar concept called “enculturation” has been stressed by van Schaik & Burkart (2011) which suggests that being their living close cousins, humans shall guide other primate mothers to be more sharing with food and act more actively so they could rear their infants better and faster. At the end it would benefit the mother to be independent earlier and get ready for reproduction sooner which could ultimately promote their overall fitness and survival as a species.

For my begging success models, although I only looked at the outcome of begging (i.e. did the focal got the food from the target at the end?) for the purpose of analyses in my statistical models, there could be a variation amongst different reactive outcomes from the begging target (e.g. active delivery, no sign of any obvious reaction, showing reluctance by turning away, manifesting anger by slapping the beggar’s body part, etc.). If the focus is on the ultimate outcome which is whether the immature took the food successfully, these reactions could be easily omitted while the orangutan mother may have shown obviously low tolerance to the begging behavior. Hence, there could be a guideline to justify valid states of acceptance of begging from the orangutan mother’s standpoint.

* 1. Part 3: begging frequency & begging rate

*Prediction 6: begging frequency and begging rate decrease with age of the immature but increase with complexity and rarity of the food item*

Begging frequency was calculated by dividing the total number of begging events of each observed food item of each focal animal by the total observation hours spent on this focal with the food item in each half year time window. Begging rate is the ratio of the total number of begging events with a certain food item of each focal animal to the number of bouts its mother fed on this food item during the observation period of this study. I found that in the zoo, the begging frequency increases with the age of the immature and the rarity of the food item. Begging rate, in the wild, decreases with the complexity and rarity of the food item. Most of the predictions turned out opposite of how I predicted. The result with the age effect on begging frequency also object a study done with Bornean orangutans where a negative relation between these two variables was concluded (Jaeggi et al. 2008).

In terms of the effect of the rarity variable on the begging frequency I found in my captive sample (i.e. immatures begged more frequently for rarer food item), it disagrees with what the informational hypothesis suggests (Brown et al., 2004). This might have been the case because captive apes are found to be more open to unfamiliar objects by approaching them more fearlessly than wild apes (Forss, Schuppli, Haiden, Zweifel, & Van Schaik, 2015) and maybe the captive and explorative immatures treat unfamiliar food items held by their mothers just as novel objects and are generally more curious about them. However, there might have been a limitation to draw such conclusion because of the number of subjects in the zoo sample. With my wild sample, on the other hand, I found a negative relation (i.e. free-ranging immatures begged less frequently for rarer food items), which stays in line with the study by Jaeggi et al. (2008) with Bornean orangutans. This could be due to the unfamiliarity of the rare food items that the wild immatures feel and therefore are careful and skeptical about such items.

It could also be preliminary with the measurement of the rarity variable in this study that was done at Leipzig zoo as a questionnaire for the head of the zookeeper to fill out and admittedly, single person’s opinion could be subjective. Nonetheless, such experienced person with lots of working experiences with orangutans and full awareness of what and how often they feed at the zoo is still expected to provide valid information. The reason why such questionnaire was designed to assign rarity identifications to the food items in the zoo is that the data from the zoo was all collected during the feeding times whereas in Suaq, volunteers conducted the full follow during the whole day time on each focal. Hence, the method applied in the wild to calculate rarity values for the food items couldn’t be implemented in the zoo. What’s more, due to the same reason, all the begging frequency values were adjusted in the wild site to make them comparable to the captive subjects.

In regards with the complexity finding from my wild sample (i.e. begging rate decreases with the increasing complexity of the food item), this contradicts with Kunz’s thesis (2019) on this prediction and her results. But it agrees with what Jaeggi et al. (2008) concluded that orangutan immatures beg more for hard-to-process food items, together with the results from peering studies (Schuppli et al., 2016; Ehmann, 2019). Immature orangutans beg for complex foods more often and they are more successful in taking them when they beg for more difficult-to-process food items from their mothers. This suggests that the same as their mothers, young orangutans are in fact able to interpret complexity of a food item as a motivation to beg for it in order to get to know what it is and how to process it.

*Prediction 7: there are sex differences in begging frequency and begging rate in wild orangutan population*

I made this prediction regarding what was found in the study with wild chimpanzees in the nut-cracking task whereby the sex difference was revealed significant in begging of immatures (Estienne et al., 2019a). Additionally, in a field study about a very specific feeding skill termite-fishing in wild chimpanzees, immature female chimps acquired this technique earlier and outperformed the young male ones with higher occurrence of replication of the strategies their mothers used. This finding suggests that there are sex differences in terms of observational learning and practicing in young wild chimpanzees (Lonsdorf, 2005). What’s more, Ehmann in her thesis (2019) on the frequency of peering behavior in different contexts among wild Sumatran orangutans in the same study site also found different patterns in male and female immatures. Against these studies, subjects of both sexes in my study, however, didn’t differ in their begging frequency in my thesis.

*Prediction 8: the begging frequency manifests differently from the wild subjects to the zoo subjects (i.e. higher in the wild than it is in the zoo)*

I assumed this difference because regarding the food, there are generally more food resources with overall lower complexity and more even availability among distinct food items in the zoo than in the wild. Regarding the lifestyle, there are more role models available in proximity for the young orangutans in the zoo than in the wild so compared to this in the wild, the reliance on the mother to learn skills is lighter in the zoo. At the end, the difference was confirmed but it was higher in the zoo than in the wild.

Conclusion

Acknowledgments

With the unconditional love and support of my parents, I was able to go abroad and pursue my passion in research in a master’s program at Leipzig university. In the second semester of the program, I was fascinated and inspired by a seminar that opened the world of non-human primates to me. I feel incredibly lucky that I got to know Dr. Caroline Schuppli and her honorable work with orangutans. Her passion motivated me to work with her and get professional training through a very special journey of creating this thesis, which has been my greatest achievement to date. Being my supervisor, she has been extremely patient with my mistakes and was generous with her comments on every detail of my thesis. She is also the most responsive person I’ve ever met. To my other supervisor, Dr. Robert Hepach, I have lots of appreciation especially in regard to the teaching methodology in research. He led the way to teach how to design an empirical study and use R programing language in two separate semesters, which unlocked my potential in doing quantitative research. I admire and respect both of my hard-working supervisors from the bottom of my heart.

Although I haven’t met them in person, I want to thank the colleagues that went to the field and collected high-quality data over the course of 13 years which allowed me to conduct my analysis in the timeframe of a master’s thesis. For the data I collected from the Leipzig zoo, I acknowledge the entry to the Wolfgang Köhler Primate Research Center, that the Max Planck Institute for Evolutionary Anthropology permitted me. During my data collection, I highly appreciated all the support and guidance provided by Hanna Petschauer and the zookeepers.

At the end of this section, I want to give my dearest gratitude to my family for trusting me and giving me the major support, to Johannes Fuhs for loving me, for the company through all the ups and downs, and for always bringing positive energy to my life.

Overall, I am grateful for all the opportunities that have gotten me this far on my path. During this project, I discovered so much fascinating facts about the orangutans by reading lots of field studies done dedicatedly on their behavior. These are all precious learning opportunities which, I have no doubt, will benefit me in my future career.

Appendix

**1: the outline of the digital paper scan (originally in Indonesian, I translated it into English, the time points were only part of the coding scheme)**

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Date: | | | | | | | | | | | | Observer(s): | | | | | Weather: | | | |
| Time | Mother: | | | | Child: | | | | | | | Mother: | | | | | Child: | | | |
| Activity | Item | Type | Height | Activity | | Item | Type | Height | Time | | Activity | Item | Type | Height | | Activity | Item | Type | Height |
| 5:00 |  |  |  |  |  | |  |  |  | 5:18 | |  |  |  |  | |  |  |  |  |
| 5:02 |  |  |  |  |  | |  |  |  | 5:20 | |  |  |  |  | |  |  |  |  |
| 5:04 |  |  |  |  |  | |  |  |  | 5:22 | |  |  |  |  | |  |  |  |  |
| 5:06 |  |  |  |  |  | |  |  |  | 5:24 | |  |  |  |  | |  |  |  |  |
| 5:08 |  |  |  |  |  | |  |  |  | 5:26 | |  |  |  |  | |  |  |  |  |
| 5:10 |  |  |  |  |  | |  |  |  | 5:28 | |  |  |  |  | |  |  |  |  |
| 5:12 |  |  |  |  |  | |  |  |  | 5:30 | |  |  |  |  | |  |  |  |  |
| 5:14 |  |  |  |  |  | |  |  |  | 5:32 | |  |  |  |  | |  |  |  |  |
| 5:16 |  |  |  |  |  | |  |  |  | 5:34 | |  |  |  |  | |  |  |  |  |
| Social activity | time | | | | | who | | | | | what | | | | | with whom | | | | |

**1.1: Coding scheme (wild) after data extraction**

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **FN** | **Date** | **Follow Hours** | **DOB** | **Beggar** | **Age** | **Sex** | **Mother** | **Target** | **Time** | **Food Item** | **RelationtoB** | **Complexity** | **Rarity** | **Success** | **Site** |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
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| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **FN** | **Date** | **FollowHours** | **DOB** | **Beggar** | **Age** | **Sex** | **Mother** | **Target** | **Time** | **Food Item** | **RelationtoB** | **Success** | **Complexity** | **Rarity** | **Desirability** |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

**1.2: Coding scheme (zoo)**

**2: Questionnaire to investigate the rarity and desirability of the zoo food items.**

**Rarity:**

1. How many times a week do orangutans get the following food items? (Please click only **ONE** of the circles for each question)
2. Apple pieces (cubed)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Apple (larger piece than cubed pieces)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Paprika

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Beetroot

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Broccoli

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Zucchini pieces

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Carrot

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Leek

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Fennel pieces (cubed)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Fennel (larger piece than cubed pieces)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Kohlrabi (cubed)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Kohlrabi pieces (larger piece than cubed pieces)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Celery stem

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Celery root (larger piece than cubed pieces)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Celery root piece (cubed)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Cooked carrot wrapped in a paper

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Oatmeal

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Walnuts

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Flour and oatmeal attached to a paper

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Willow tree leaves

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Oak tree leaves

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Lime tree leaves

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Salad

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

1. Chinese cabbage

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Never | Once-twice | Three-four times | Five-six times | Everyday |
|  |  |  |  |  |

**Desirability:**

1. How many of the orangutans like each of the following food items? (Please click only **ONE** of the circles for each question)
2. Apple

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Paprika

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Beetroot

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Broccoli

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Zucchini

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Carrot

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Leek

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Fennel

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Kohlrabi

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Celery stem

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Celery root

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Cooked carrot wrapped in a paper

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Oatmeal

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Walnuts

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Flour and oatmeal attached to a paper

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Willow tree leaves

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Oak tree leaves

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Lime tree leaves

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Salad

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

1. Chinese cabbage

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 0-no one likes it | 1 | 1-2 | 3-4 | 5-6 | 7-8 | 9-everyone loves it |
|  |  |  |  |  |  |  |

**Appendix 3:** **Count of the occurrence of the food items observed in this study.** 108 distinct food items (I= food item; C= count of the occurrence).

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| I | C | I | C | I | C | I | C | I | C | I | C |
| AAB\_FR | 3 | APLS\_FR | 1 | BSG\_BK | 8 | GESBENG | 7 | MDGH\_FR | 11 | RP\_VE | 3 |
| ADDG\_LV | 3 | APPLE\_FR | 1 | BSG\_FR | 41 | GLMB\_LV | 4 | MDGK\_FR | 4 | RP7\_LV | 1 |
| ADDG\_VE | 1 | APSB\_LV | 1 | CARROT\_ROOT | 6 | INSECT\_IN | 1 | MLK\_FL | 1 | RSKB\_BK | 1 |
| AJK\_VE | 3 | APSB\_VE | 1 | CATCH | 2 | JAIR\_FL | 1 | MLK\_FR | 83 | RSKB\_FR | 4 |
| AKAR\_LV | 28 | ASDK\_VE | 11 | CELERY\_ROOT\_PIECE\_ROOT | 7 | KELINCI\_VE | 1 | MNGH\_FR | 18 | RSKB\_LV | 3 |
| AKAR\_NA | 7 | ASK\_FR | 1 | CELERY\_ROOT\_ROOT | 8 | KKCNG\_FR | 2 | OAK\_LEAVES\_LV | 12 | RSKP\_FR | 19 |
| AKAR\_VE | 7 | ASK\_LV | 14 | CELERY\_STEM\_VE | 6 | KOHLRABI\_ROOT | 3 | PAPRIKA\_FR | 12 | RSKP\_LV | 12 |
| AKKT\_LV | 1 | ASK\_VE | 24 | CEREAL\_OAT | 1 | KULBT\_FR | 11 | PKSKW\_VE | 2 | RSKU\_FR | 17 |
| APD\_LV | 3 | AT\_VE | 3 | CHINESE\_CABBAGE\_VE | 2 | KULJM\_FR | 1 | PRD\_FR | 8 | RTKS\_LV | 4 |
| APKS\_LV | 4 | ATB\_VE | 6 | CMG\_FR | 91 | LEEK\_VE | 4 | PWN\_FR | 57 | RTKS\_VE | 32 |
| APKS\_VE | 3 | ATPS\_VE | 1 | COOKED\_CARROT\_PAPERWRAP\_ROOT | 2 | LIME\_LEAVES\_LV | 1 | RAYAP\_IN | 150 | RTN\_VE | 7 |
| APKSB\_LV | 3 | BEETROOT\_ROOT | 6 | DEADWOOD | 8 | MADU\_IN | 4 | RGH\_FR | 4 | RTP\_FR | 1 |
| APKSB\_VE | 2 | BNGPR\_FL | 1 | FENNEL\_ROOT | 3 | MADU\_KERINGAT\_IN | 8 | RNGS\_BK | 7 | RTPB\_LV | 1 |
| APLO\_LV | 2 | BNGPR\_FR | 2 | FISTFISHING | 2 | MDGB\_FR | 10 | RNGS\_FR | 15 | SALAD\_VE | 18 |
| APLO\_VE | 2 | BROCCOLI\_VE | 1 | FLOUR\_OATMEAL\_GRAIN\_OAT | 11 | MDGBR\_FR | 3 | RP\_LV | 11 | SEMUT\_IN | 27 |
| SPG\_FR | 43 | TMPGRW\_FR | 9 | TREEHOLE | 1 | ULAT\_IN | 8 | UNK\_FR | 8 | UNK\_VE | 9 |
| STICK | 2 | TOOLUSE | 3 | TWIG | 4 | UNK | 98 | UNK\_IN | 42 | WILLOW\_LEAVES\_LV | 26 |
| TLS\_BERDURI\_LV | 1 | TPSBT\_FR | 16 | UBR\_FR | 20 | UNK\_BK | 1 | UNK\_LV | 31 | ZUCCHINI\_PIECE\_FR | 2 |

List of figures and tables

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Declaration of Academic Honesty

I have abided by the statutes to ensure good scientific practice at the Leipzig University while writing this thesis (http://www.zv.unileipzig.de/de/forschung/satzung.html). I hereby declare that this master’s thesis was written solely by myself and without any assistance from third parties. Furthermore, I confirm that all sources used in the preparation of this thesis are entirely indicated in the thesis itself. All passages of the thesis which have been taken from other sources, either literally or by analogously, are marked as borrowed with the source(s) cited. The positions of the thesis written in cooperation with other persons are marked accordingly.



Leipzig, DD.07.2020

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