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Master Thesis

The development of social interest in Sumatran orang-utans over age & sex

An observational field study on wild, dependent immature Sumatran Orang-utans (*Pongo abelii*) at Suaq Balimbing, Aceh Selatan, Indonesia

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1. ABSTRACT

Wild orang-utan infants have been shown to acquire their skill sets through socially induced practice. Optimal learning theory predicts that young immatures should learn most of their skills from their mothers, whereas older immatures should widen their pool of role models, but be more selective with skills they show interest in. Because they will have to cope with a change of environment, dispersing individuals are expected to be more attentive to a broader array of role models. In this study, I investigate the development of social interest in immature Sumatran orang-utans (*Pongo abelii*) by looking at peering behaviour, defined as sustained, attentive close range watching, and patterns of associations. My data consists of 3254 peering events by 22 infants (aged 0 – 8 years), 177 peering events by 14 juveniles (weaned immatures) and association data collected from 2007 to 2018 at the Suaq Balimbing research station in South Aceh, Sumatra, Indonesia. Most peering events were directed at either feeding or nesting, both of which are learning-intense contexts. For the infants, I found that they preferentially peered at rare and complex skills, and become increasingly selective with age. They were also more likely to interact with the same food item as the peering target in the hour after the peering event than before. Young infants of both sexes mostly peered at their mother. In males, the interest in other role models increased throughout infancy. In females, however, the interest in individuals other than the mother peaked around mid-infancy and then decreased again. These sex-specific peering patterns were reflected in the proportion of association time infants spent in close proximity of others. In terms of role model identity, I found that when excluding the mothers, males preferentially peered at and associated with juveniles and unflanged males. Females additionally preferred adult females. For the juveniles, I found that they preferentially peered at rare food items but I found no evidence for a complexity preference. Same as infants, juveniles had an increased likelihood to interact with the same food item as the peering target after the peering event. Finally, they seemed to show a preference for their mother and other juveniles. All in all, the development of social interest in orang-utan immatures roughly followed the age-specific patterns predicted by optimal learning theory. The sex-specific peering preferences can be explained by the species' dispersal pattern where, upon reaching adulthood, females settle close to their mother's range and should thus be most interested in acquiring the skills of local residents, while males disperse and thus benefit from learning from a larger number of role models.

2. INTRODUCTION

Animal skill acquisition was long thought to be mediated entirely through innate mechanisms (Lorenz, 1958), or later through individual learning (Shettleworth, 2010; Skinner, 1948), i.e. through trial-and-error learning. Since then, we have come to realise that, especially in primates, this is not the case. Great apes and a hand full of monkeys have long been found capable of observational learning in captivity (*Pongo abelii & Pongo pygmaeus,* Dindo et al., 2010; *Gorilla gorilla gorilla*, Stoinski et al., 2001; *Chlorocebus aethiops,* van de Waal et al., 2010; *Pan troglodytes*, Whiten et al., 2007; reviewed by Whiten & Mesoudi, 2008; Whiten, 2012). Only recently, however, have we begun to understand what this ability is used for in the wild (Aplin et al., 2015; Bastian et al., 2010; Biro et al., 2003; Jaeggi et al., 2008 & 2010; Lonsdorf, 2005; Ottoni et al., 2005; Schuppli et al., 2016). It was shown by means of the method of exclusion that certain complex behaviours are also transmitted socially in the wild (Lameira et al., 2013; van Schaik et al., 2003; Whiten and Mesoudi, 2008; Wich et al., 2012). Nevertheless, it is still unclear to what extent species rely on social learning for the acquisition of every-day skills and knowledge about the social and physical environment. However, more and more studies suggest that for many species social leaning might be the main form of skill acquisition even for basic sustenance skills (Schuppli & van Schaik, 2019; van Schaik et al., 2017; van de Waal, 2013).

Social learning has been defined as "learning (...) that is influenced by observation of or interaction with, another individual or its products" (Heyes, 2012), and comes in many forms and facets (reviewed in Hoppitt & Laland, 2013; van Schaik, 2016c; Figure 1). A first distinction can be made between non-observational social learning and observational social learning. Among the non-observational forms are social- or response facilitation, which describes the mechanism of learning because the presence of others generally increases an individual's activity, and thus also its explorative behaviour. Furthermore, there are local-, and stimulus enhancement which describe that an individual may learn simply because others spend time at a certain place, or with a certain object, respectively, which increases the individuals interest in this specific place or object. Observational forms of social learning, include observational conditioning in which an individual undergoes repeated cycles of observing an action and then selectively practices this action, and contextual imitation in which an individual copies the exact steps of what others do. Additionally, there is production imitation or emulation, also describing the copying of an action but without steps which are plainly unnecessary to achieve the same result. Generally, the observational forms of social learning are deemed to be more cognitively demanding (van Schaik, 2016c).

However complex social learning might seem at first sight, Heyes (2012) proposed that, mechanistically, social learning might be nothing more than modified individual learning. Similarly, it has repeatedly been proposed that most social learning is some form of socially mediated individual learning (Galef, 2015; van Schaik et al. 2017; Whiten, 2015). Additionally to social learning probably being based on simple mechanisms, for learners, it is often advantageous to rely on social learning instead of individual learning for several reasons. For one, it is more efficient because it allows the learner to directly build on something that somebody else had already figured out. Moreover, social learning makes relevant information more salient to the learner because it guides the attention of the learner towards the respective information. Thus, it has a higher signal to noise ratio than individual learning. Furthermore, social learning could potentially lead to cumulative skills, i.e. skills which are built on the basis of other skills to such an extent that a single individual could not learn on its own in its lifetime. Many forms of social learning are quite simple and do not require advanced cognition, though (Hoppitt & Laland, 2013). For example, four different processes have been suggested to all lead to local enhancement. These include aggregation effects or the simple tendency to move around as a group (reviewed in Hoppitt & Laland, 2013). All in all, social learning is more efficient than individual learning and probably mostly based on simple mechanisms. Accordingly, social learning had been proposed to be the real null model of learning for most species (Schuppli & van Schaik, 2019).

If social learning is the main form of skill acquisition of a species in the wild, a whole new series of questions arise in terms of its content, timing, role model choice, and plasticity. In terms of content, species might differ in what they learn socially. They might need to learn specific skills, e.g. how to eat certain foods or how to build nests or knowledge about which foods to eat or where to find them, which individuals to interact with or how. Furthermore, one might investigate who individuals learn from in terms of kinship, social tolerance, sex, age, or competence and whether preferences for certain role models change during development. Moreover, how long individuals learn new skills, i.e. whether learning is restricted to early immaturity or still present during later stages. One might also ask which kind of information is learned at what stages of development. Finally, there are questions of potential differences between the sexes. Males and females might have different learning schedules or role model preferences. The aim of this thesis is to shed light onto these questions by investigating social learning in immature Sumatran orang-utans (*Pongo abelii*).

Social transmission of information is commonly categorised into three distinct directions: vertical transmission from parents to offspring, oblique transmission from adults other than the parents to immatures, and horizontal transmission among peers (van Schaik, 2016a). In general, naïve individuals are expected to learn from older and thus more experienced role models, i.e. through either vertical or oblique transmission (van Schaik, 2016a). With regards to age, three main phases of social learning have been proposed for primates (Schuppli & van Schaik, 2017; Whiten & van de Waal, 2018).

In the first phase, young infants are expected to mainly learn from their primary caregiver, usually mother, through vertical transmission. Young primate infants are still completely naïve. Primates have slow life histories compared to other mammals, often producing only single, slowly-maturing offspring (van Schaik & Isler, 2012). Therefore, maternal investment including nursing and carrying is vital during early development, in the majority of primate species. Such investments are based on close, highly tolerant associations between mother and offspring. Even after weaning, primate mothers are usually tolerant and offer social care for their offspring (van Noordwijk, 2012). Such an association is an ideal basis for social learning. Capuchin monkeys (*Cebus* sp.) were found to adopt foraging techniques from individuals with which they spend the most time in association (Perry, 2011). During early infancy, this is clearly the mother. To be able to learn form a role model, the role model has to be tolerant to be in association or even close proximity. Mothers are thus the first and most important role models. Humans are no exception to this. The parents in Aka and Bofi hunter gatherers were found to mediate the overwhelming majority of skill transmission events under the age of five (Hewlett et al., 2011). In this first phase, because the infants are still completely naïve, they are also expected to be interested in a wide range of skills.

With increasing age of the immatures, their skill competence and knowledge about the environment will increase. In a second phase, after acquiring skills and knowledge of their mothers, the immatures are expected to learn from a widening pool of role models. At the same time, because they know many skills already, they are expected to become more and more selective in their interest. In terms of repertoire stability, this shift of interest during late immaturity makes sense: were the mother the only role model for skill acquisition, any inaccuracies in the skill transmission process would lead to an overall decrease in the size of the skill sets over the generations, even in species with high-fidelity transmission (van Schaik, 2002; van Schaik & Pradhan, 2003). Thus, in species which mainly rely on social learning, individuals are expected to have a phase in which they are interested in individuals other than the mother. Again, this pattern is reflected in humans. After the first five years of dominantly vertical transmission, learning in Aka and Bofi hunter gatherer children, shifted towards oblique and horizontal transmission (Hewlett et al., 2011). Baka children aged five to 16 were even found to gain sustenance-related knowledge predominantly through horizontal transmission (Gallois et al., 2018).

We do not know how long this second phase is. It most likely depends on the amount, frequency and timing of social interaction in older immatures. For example, in gregarious species, this phase probably starts early but is shorter than in more solitary species, because they have more

opportunities to learn and thus might acquire skills more quickly. Species living in large, heterogeneous home ranges or in a changing environment might also have pronounced second phases because they probably rely on learning a wide variety of skills to cope with different circumstances. Therefore, how long individuals learn new skills, i.e. whether learning restricted to early immaturity or also present during later stages, probably depends in part on the social system of the species.

Finally, a potential third phase was proposed, which focuses on the time after dispersal upon reaching maturity. Dispersal is defined as the movement from birth site to breeding site or from breeding site to another breeding site (Ronce, 2007) and occurs in many mammal species (*Chlorocebus pygerythrus,* Cheney & Seyfarth, 1983; *Suricata suricatta,* Doolan & Macdonald, 1996; *Gorilla gorilla gorilla*, Douadi et al., 2007; reviewed in Chepko-Sade & Halpin, 1987). Reasons for such movement might be escaping from overcrowding (Ronce et al., 2000), avoidance of kin-competition (Cote & Clobert, 2010; Ronce et al., 2000), or inbreeding avoidance, with the latter leading to sex-biased dispersal (Gros et al., 2008). Dispersing individuals face challenges in adjusting to their new social and physical environment. Some of these challenges (e.g. learning what, how and where to eat) might be overcome through learning from native individuals. In species with sex-biased dispersal, there might be a discrepancy between the learning behaviour of the sexes. This discrepancy might not only affect the third phase but potentially also the duration, intensity or timing of the first and second learning phase.

Sex-biased dispersal, however, is not the only potential underlying cause for sex differences during the development of social interest. In many species, females and males have different overall needs, show different life-styles, and follow different social strategies. Not only adults exhibit sex-biased behaviours, but many species also have sex differences in the development of physical or social development (reviewed in Lonsdorf, 2017). For example, in order to maximize their reproductive output, chimpanzee males depend on strong social bonds with other males which will ultimately increase their mating success. Female chimpanzees' reproductive outcome, however, depends much more on their physical condition and thus on factors like food intake. This profound sex difference reflected in chimpanzee learning behaviour as well, insofar immature females learn termite-fishing behaviour quicker and have an overall more efficient performance in the task than their male peers (Lonsdorf, 2005). Adult chimpanzee males spend most of their time in association with other males, whereas females spend most of their time alone (Wrangham & Smuts, 1980). These sex-specific social roles were shown to be present early in development. Male infants were more gregarious than females and socialised more with adult males (Lonsdorf et al., 2014). Learning sex-specific behaviours might depend on the opportunities for social learning and thus who individuals spend time with. Tufted capuchin monkeys (*Cebus nigritus*) display sex differences in their foraging techniques, most likely learnt through sex specific attention biases towards adults of the same sex (Agostini & Visalberghi, 2005). In general, many species male and female immatures already adopt the future adult sex differences in their activity budgets (O'Mara & Hickey, 2014 ; van Noordwijk et al., 1993; reviewed in Meredith, 2012). Whenever the adults exhibit strong behavioural sex-differences, we expect immatures to prepare for the respective sex-specific behaviours during development and thus differ in their learning strategies.

Orang-utans are a highly interesting study species to investigate social learning under natural conditions. Orang-utans have a slow life-history (van Noordwijk et al., 2018) with an exceptionally long immaturity lasting about 15-16 years (Wich et al., 2009). While infants get weaned around the age of 7-8 (van Noordwijk et al., 2018), the weaned juveniles are still in tolerant association with their mother until around 11 years of age (van Noordwijk & van Schaik, 2005). Thus, they not only have a lot of time for learning but also the opportunity to frequently interact with at least one skilled individual. Learning from a tolerant and trusted role models seems crucial for orang-utans because they have to learn not only a large variety of basic feeding- and nest building techniques but also knowledge about where to find food sources and what is edible, and depending on the population, they also have to learn many complex skills such as tool use.

It has been shown that orang-utan infants acquire their skill sets through socially induced practice, mainly from their mother (Schuppli et al., 2016b) but also other individuals. Furthermore, orang-utan infants' peering (sustained, attentive close range watching) at the mother in the feeding context was preferentially directed at complex and rare food items. Moreover, Schuppli et al. (2016b) also found that the proportion of peering directed at individuals other than the mother generally increases with increasing age. So far, it remains unclear until what age immatures learn or who the main role models are in terms of sex-age class or relatedness, apart from the mother.

Furthermore, orang-utans have a sex-biased dispersal pattern. The orang-utan's social system is based on male dispersal with strong female philopatry (Arora et al., 2012; Nietlisbach et al., 2012; Singleton and van Schaik, 2002), i.e. upon reaching sexual maturity, males migrate from their natal population to another. Orang-utans have male bimaturism, i.e. adult males come in two morphs (Utami Atmoko & van Hooff, 2004). Young adult males who are lacking secondary sexual characteristics are called unflanged males. These are the ones that disperse. Having dispersed to another area, the unflanged males might later develop into flanged males (Utami Atmoko & van Hooff, 2004).

Females, as the philopatric sex in orang-utans, stay in their natal area and usually settle close to their mother (Ashbury et al., in prep.). Encountering new physical and social environment after dispersal, males need to acquire new knowledge about who is around and what is where. Moreover, female philopatry in orang-utans has led to local traditions and even cultures (van Schaik et al., 2003; Wich et al., 2012; Lameira et al., 2013). Thus, individuals in the area in which unflanged males arrive after dispersal might use different techniques or even eat different food items. For unflanged males, it might be advantageous to learn from the locals, but for locals, it might also be advantageous to learn from unflanged males. Data from Bornean orang-utans (*Pongo pygmaeus*) suggest unflanged males might act as some form of cultural vector insofar that immatures learn new techniques brought to the population by unflanged males (Mörchen, 2016).

For females, learning about a new environment this is not a major concern. While they to slightly expand and shift their home range when they become independent, they still have a big overlap with their mother's home range (Ashbury et al., in prep). However, females do face the huge challenge of having to rear offspring. These sex-specific adult challenges suggest different needs. In fact, orang-utan females and males are known to have different ecological requirements (van Schaik et al., 2009b). On the one hand, adult females depend more on high quality food and spend more time feeding than similarly sized adult males. On the other hand, adult males seem to feed more efficiently (van Schaik et al., 2009b). It is therefore likely that immatures already differ in preparation for these adult challenges and requirements. Such differences might include sex-specific learning strategies.

Orang-utans have the most solitary lifestyle amongst great apes, whereby their sociability level can range from semi-solitary to fission-fusion, depending on populations (Mitra Setia et al., 2009). Orang-utans in most populations spend most of their time on their own, with the exception of females who travel with their dependent offspring. The population at the Suaq Balimbing field site is more gregarious than any other studied orang-utan population. Not only mother offspring pairs spend more time in the company of others compared to other sites, but weaned immatures actually spend more time with others rather than alone (van Schaik et al., 2009a). In fact, in about 70% of follow days, mother offspring pairs are in association with another individual at some point during the day. On average, they spend 52% of their time in association with at least one other individual (Schuppli, unpublished data). With seven individuals per square kilometre, Suaq Balimbing also has the highest density of wild orang-utans (Husson et al., 2009; van Schaik, 2016a). It is likely that the stable high levels of fruit availability found in the area (Husson et al., 2009; Sugardjito et al., 1987), have reduced food competition such that the animals could afford to be more tolerant towards each other. Therefore, at Suaq Balimbing, role models other than the mother are available, even though it is yet unclear to what extent immatures use those role-models for social learning.

Moreover, the orang-utans at Suaq Balimbing are the only wild orang-utans frequently observed to manufacture tools in the foraging context such as for insect feeding or seed extraction

from Neesia fruits (Fox et al., 1999, van Schaik & Fox, 1996). The overall feeding repertoire is more complex than in other populations (Schuppli et al., 2017). Because the orang-utans at Suaq Balimbing have to learn these complex repertoirs, they may rely on social learning more than other populations.

The aim of this study was to investigate the development of social interest in immature orang-utans with a special focus on sex differences and the juvenile period. As a proxy for social interest, I used the peering behaviour, supplemented by data on association patterns. I looked into potential sex differences in the development of role model choice based on the peering behaviour and analysed whether these results are reflected in the proportion of close proximity with association partners. Furthermore, I investigated whether learning is restricted to infancy or extends beyond weaning, as well as who and what juveniles show interest in. Because orang-utans have an exceptionally long juvenile period, juveniles might use this time to learn additional skills. The necessity to learn might actually be a reason why orang-utans' juvenile periods are so long. Previous findings suggest that energetic constraints probably limit the age of first reproductions but highlight the impacts of learning on the life history of orang-utans, especially the age of weaning (Schuppli et al., 2016a). I looked for evidence of social learning by replicating results from Schuppli et al. (2016b) on infant peering directed at their mothers with a new, larger data set. I tested their predictions not only in infants but also in juveniles by utilising all peering events available including those which were not directed at mothers. I did so, by analysing whether peering in the feeding context was predicted by the complexity and/or rarity of the food item. High complexity food such as tool use items might be preferentially peered at because they might take longer to learn. Rare food items are expected to be preferentially peered at as well because there are fewer opportunities to learn and learning them might thus also take long. Furthermore, I replicated their results that exploration rates increase after peering, not only for peering directed at the mother but also at other individuals. Such increased exploration rates indicate socially induced individual practice mediated by peering.

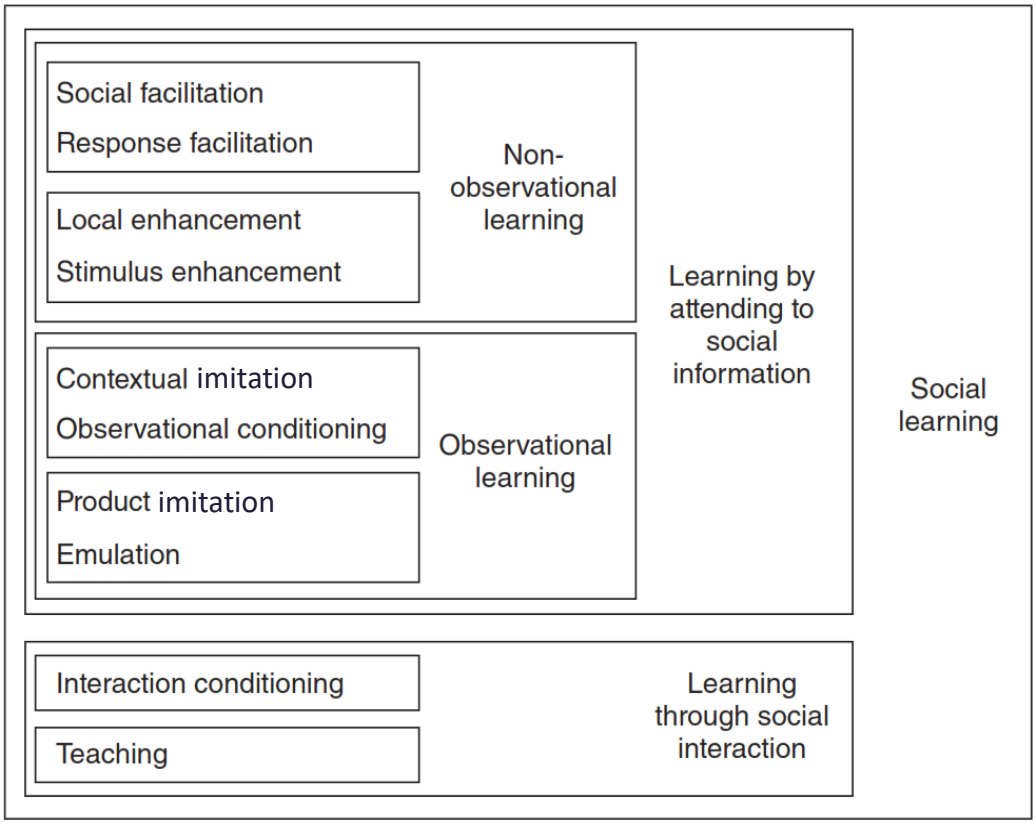


Figure 1: Social learning mechanisms: Schuppli et al., 2017; based on Hoppitt & Laland, 2013; van Schaik, 2016c.

3 QUESTIONS AND HYPOTHESES

The aim of this thesis was to investigate the development of social interest in immature orang-utans in the wild. On the one hand, I replicated previous results on orang-utan infants with a new, larger data set and extended the analyses to include juveniles as well. On the other hand, I looked into the potential use of role models other than the mother, and potential sex differences in the trajectory of age-dependent context-specific social interest. To achieve this, I divided my thesis into four sections.

In the first section, I focused on the activities in which infants are primarily interested in, how this interest changes with increasing age and how it differs between the sexes. In the second section, I focussed on the potential use of role models other than the mother in terms of their sex-age class and degree of relatedness with the peerer, and whether this changes over age and sex. In the third section, I looked into the potential function of peering as a means to social learning. Peering most likely has two different functions, which are not necessarily mutually exclusive. While peering could function as a social tool to elicit tolerance from other individuals, it could also be used as a means to social learning. Here, I was looking for evidence for the second part, by replicating previous results with a larger data set to confirm that the peering behaviour can be a means to social learning in orang-utans. To do so, I investigated whether peering was followed by practice, preferences for complexity and rarity by using all data available. In the final section, I investigated whether juveniles still use peering for social learning or if learning is restricted to infancy. To do so, focused on the three previously mentioned topics and tested the respective predictions in juveniles. As there was much fewer data available on juvenile peering, I could not differentiate between the sexes. For role model choice, I supplemented the information from the peering behaviour with an analysis of association patterns during infancy and juvenility as an additional proxy for social interest.

To pursue the aim of this thesis, I investigated the following questions:

3.1 Infants' interest in specific activities

3.3.1 Which activities are infants mainly interested in?

Predictions:

Under the assumption that peering is means to social learning and thus used in learning intense context, and based on previous findings on orang-utan peering (Schuppli et al. 2016b), I predicted that:

- Most peering is directed at feeding and nest building.

3.3.2 How does the interest in specific activities change over age?

Predictions:

Measuring the development social interest in activities in the proportion of peering events directed at specific activities, I expected that:

- The proportion of peering directed at feeding is high throughout infancy because infants have plenty of opportunities to watch their mother feed on their big repertoire on a daily basis.
- The proportion of peering directed at nesting increases with mobility and then decrease with increasing competence.
- The proportion of peering directed at social interactions increases over age. Sexual interactions, specifically copulations, become more relevant for infants with increasing age, and I expected these to make up most of the social interactions that are targeted by peering.

3.3.2 How do peering rates change over age?

Predictions:

If peering is means to social learning, peering rates should decrease with increasing competence. Schuppli et al. (2016b) found that food peering rates generally decrease over age with increasing food competence. Furthermore, they found nest peering rates to go hand in hand with nest practice, a behaviour in which immatures fail to successfully build a nest or seemingly succeed without using the constructed nest, which increases first with increasing mobility but later decreases with increasing competence. Based on these findings, I predicted that:

- Food peering rates decrease with increasing age and competence.
- Nest peering rates increase at first with increasing mobility but later decrease with increasing competence.
- Overall peering rates follow the general trend of the food peering rates because food peering probably makes up for most of the peering events.

3.2 Infants' interest in specific individuals

3.2.1 Who are the infants' preferred role models?

Predictions:

Young infants are mainly interested in their mother (Schuppli et al., 2016b). When considering everybody else, and assuming peering is at least in part means to social learning, I expected infants to be interested in any individual older and more skilled or knowledgeable than themselves, given the potential role model is tolerant towards the infants. Therefore, I predicted that infants preferentially peer at:

- Juveniles, because they are generally the most gregarious sex-age class (Galdikas, 1985a) and compared to the completely naïve infants, they are more skilled (Schuppli et al., 2016a).
- Adult females who are probably interested in maintaining tolerance towards other infants for the benefit of letting their own infant play even if they suffer energetic costs themselves (van Noordwijk, pers. com.) and even in times of prolonged low fruit availability (de Bellefon, 2017).
- Unflanged males who might be tolerant towards infants because they associate often with their mothers (Galdikas, 1985b; Reukauf, 2019), and because they might possess different skills than the local females.

3.2.2 How does role model choice change over age?

Predictions:

Based on the proposed three phases of social learning (Schuppli & van Schaik, 2017; Whiten & van de Waal, 2018), the transition from the second to the third phase is characterised by a widening of the pool of role models. Under the assumption that the peering behaviour in orang-utans follows these three phases, and based on previous findings that, in general, the interest in others increases with increasing age when compared to the interest in the mother (Schuppli et al., 2016b), I predicted that:

- Male infants direct an increasing proportion of peering at individuals other than the mother as they increase in age.
- Female infants peer at their mother more exclusively than males do, but that they would be interested in individual other than their mothers for at least for some period as well.

3.2.3 How do association patterns change over age?

Predictions:

Due to the limited sample size in female infant peering, I looked at association patterns as an additional proxy for social interest. Specifically, I investigated the proportion of time infants spend in close proximity to others given the opportunity. If both analyses provide a measure for social interest, I expected the same predictions to apply to the association patterns as to the peering patterns. Accordingly, I predicted that:

- The proportion of association time male infants spend in close proximity to association partners other than the mother increases with age.
- Female infants spend a smaller proportion of association time in close proximity to association partners other than the mother compared to males but that they do spend time in close proximity for some period as well.

3.3 Is peering indeed means to social learning?

3.3.1 Do infants practice after peering?

Predictions:

Assuming, peering is means to social learning, rates of individual practice are expected to increase after a peering event. Schuppli et al. (2016b) and Jaeggi (2010) found increased exploration rates in the hour after a peering event. Here, I used the presence of interactions of the peerer with the same object as the focus of the peering event as a proxy for practice. Based on the above assumption and previous findings, I expected that:

- Infants are more likely to interact with the same food item in the hour after the peering event compared to the hour before.

3.3.2 Do infants preferentially peer in complex and rare feeding contexts?

Predictions:

If peering in the feeding context is a means to social learning, infants should be interested in complex feeding contexts until their feeding competence is high. With the same logic, if peering in the feeding context is a means to social learning, infants should be interested in rare feeding contexts in general and should become increasingly selective towards rare items with increasing age. Based on these assumptions and supported by Schuppli et al. (2016b) and Jaeggi (2008) who found that infants preferentially peer in complex and rare feeding contexts, I predicted that:

- Infants preferentially peer at food items which require a high number of processing steps before they can be consumed.
- There is an interaction between age and preference for complexity. Because food competence of infants increases with age (Schuppli et al., 2016b), they are expected to have an increasing preference for complexity with increasing age.
- Infants preferentially peer at food items which are rare in the population diet.
- There is an interaction between age and preference for rarity. Because the repertoire size of infants increases with age (Schuppli et al., 2016a), they are expected to have an increasing preference for rarity with increasing age.

3.4 Juveniles' interests

3.4.1 With whom do juveniles associate?

Predictions:

Juveniles have been suggested to be more gregarious than other sex-age classes of orang-utans (Galdikas, 1985a). Given that I looked at all juveniles, including the ones directly after weaning in this section, and based on previous findings (van Noordwijk et al., 2009), I expected them to spend time with their mother and potentially a younger sibling. Apart from those, I predicted that:

- Juveniles might associate with other juveniles because theys are comparatively gregarious as suggested by Galdikas (1985a).
- Older juvenile females who are already sexually active might associate with unflanged males or flanged males. Unflanged males probably have more incentive to try to father offspring with a juvenile because flanged males are the least social sex-age class once consortships with parous females were excluded (Galdikas, 1985a).

3.4.2 At whom do juveniles peer?

Predictions:

I assumed that social learning in orang-utans goes beyond infancy. They have an exceptionally long juvenile period. Previous findings suggest that this is mainly due to energetic constraints (Schuppli et al., 2016a). However, it seems likely that learning is at least in partly responsible. Even if the long juvenile period is solely a by-product of energetic constraints, juvenile might use this time to learn additional skills. Under the assumption that peering in juveniles is still used for social learning, and follows the proposed three phases of social learning (Schuppli & van Schaik, 2017; Whiten & van de Waal, 2018), juveniles are expected to peer at a wide range of individuals. If peering is means to social learning, they are expected to peer at more knowledgeable individuals then themselves, but potentially also peers, which are at least somewhat tolerant to close proximity with juveniles. Based on these assumptions, I expected that:

- Especially newly weaned juveniles peer at their mothers whenever they have the opportunity.
- Juveniles might peer at unflanged males, because they originally came from a different area and might possess different skills of knowledge that the mother.
- Juveniles might peer at other juveniles because they might be tolerant towards each other and given this prerequisite, they could potentially learn from each other. Infants do not reach adult diet repertoires before weaning (Schuppli et al., 2016a). Even if two mothers have the same repertoire, it is therefore likely, that by the time the offspring is weaned, they have not yet learnt all the same skills.

3.4.3 Do juveniles practice after peering?

Predictions:

In accordance with my predictions on practice in infants, if peering is a means to learning in the feeding context even after infancy, I expected that:

- The likelihood that juveniles interact with the same food item in the hour after the peering event is higher than before.

3.4.4 Do juveniles preferentially peer in complex feeding contexts?

Predictions:

In accordance with my predictions on practice in infants, if peering is a means to learning in the feeding context even after infancy, I expected that:

- Juveniles might potentially have a preference for complex food items. However, if they have such a preference at all, I expected this preference to be weaker than in infants, because juveniles' feeding competence is higher than infants' (Schuppli et al., 2016a).

3.4.5 Do juveniles preferentially peer in rare feeding contexts?

Predictions:

Under the assumption that peering in juveniles is still used for social learning, and follows the proposed three phases of social learning (Schuppli & van Schaik, 2017; Whiten & van de Waal, 2018), juveniles are expected to peer selectively. In accordance with my predictions on practice in infants, if peering is a means to learning in the feeding context even after infancy, I expected that:

- Juveniles preferentially peer at rare food items because they might not yet have encountered them during infancy.

4. MATERIAL AND METHODS

4.1 Study period and study site

I collected behavioural data between November 2017 and July 2018, at the study site Suaq Balimbing (3°42´N, 97°26´E), which is located in a peat-swamp forest in the Gunung Leuser National Park in the province Aceh Selatan, Sumatra, Indonesia. Between 1994 and 1999, and ongoing since 2007. 15 years of extensive behavioural observations on Sumatran orang-utans have already been conducted at the site, resulting in more than 20'000 observation hours on more than 170 different focal animals. With seven individuals per square kilometer, Suaq Balimbing currently has the highest density of wild orang-utans (Husson et al., 2009; van Schaik, 2016a). Furthermore, at Suaq Balimbing the proportion of time orang-utans spend in association with conspecifics and the level of social tolerance is higher than any other studied orang-utan population (van Schaik et al., 2009b). Most likely, this is at least in part due to the comparatively high fruit availability in the forest (Husson et al., 2009; Sugardjito et al., 1987). These stable, high levels of fruit availability might have enabled the orang-utans to be more tolerant towards one another. This means that immatures potentially have the chance to learn from role models other than their mother. Thus, there are likely more overall opportunities for social learning at Suaq Balimbing than in other areas. The combination of these factors makes the site very suitable for my research questions.

4.2 Study subjects

To refer to the specific sex-age classes of the focal animals, I will use the following terms throughout the thesis: Infants (unweaned, dependent immatures), juveniles (weaned immatures with known local mother, including nulliparous females, whereas male offspring tends to disperse before female age of first reprodution at about 15 years or age), mother (the parous female which is the mother the respective infant or juvenile focal animal), adult females (parous females other than the respective mother), unflanged males (adult males lacking secondary sexual characteristics), flanged males (adult males that are fully developed; see Utami Atmoko & van Hooff, 2004). I focused on infants during the first three sections of the thesis (Table 1) and on juveniles during the final section (Table 2). Depending on the analysis, I either used the full data set or a reduction according to certain criteria. For overall descriptive analyses, I used the full data set irrespective of the number of follow hours or total number of peering events per individual. When performing statistical analyses, however, I restricted the inclusion to individuals with either a minimum number of follow hours or peering events.

Table 1: Infant focal animals. Name of infants, their mothers, sex, estimated date of birth (DoB), age range in which they were observed for this study, total follow hours and total number of peering events recorded.

Infant	Mother	Sex	DoB	Age (y)	Follow Hours	Peering events
Frankie	Friska	male	01.08.2012	1 - 6	807	509
Fredy	Friska	male	01.06.2005	2 - 6	645	512
Rendang	Raffi	male	15.07.2013	1	139	43
Ronaldo	Raffi	male	01.01.2006	2 - 3	140	69
Cinnamon	Cissy	female	01.04.2012	1 - 7	697	426
Chindy	Cissy	female	01.01.2003	5 - 6	243	100
Lois	Lisa	male	01.08.2010	1 - 8	1’223	880
Lilly	Lisa	female	01.03.2001	6 - 8	330	87
Eden	Ellie	female	01.11.2014	0 - 4	746	400
Luther	Lilly	male	01.03.2016	1 - 2	67	39
Dalia	Dodi	female	01.10.2012	1 - 5	34	21
Diddy	Dodi	male	01.12.2005	5	46	6
Simba	Sarabi	male	01.03.2015	1 - 2	164	56
Pepito	Piniata	male	01.01.2013	5	26	10
Olala	Okume	female	01.06.2014	3	17	9
Amor	Alice	male	01.01.2015	2 - 4	62	32
Albin	Alice	male	01.07.2006	1 & 7	31	6
Tornado	Tiara	male	01.07.2014	2 - 4	39	17
Chuck	Chick	male	01.07.2007	1	22	7
Ian	Intai	male	01.07.2014	4	41	10
Inky	Intai	male	01.07.2003	8	3	2
Goli	Gani	male	01.07.2007	2	8	12

Table 2: Juvenile focal animals. Name of juveniles, their mothers, sex, estimated date of birth (DoB), age range in which they were observed for this study, total follow hours and total number of peering events recorded.

Juvenile	Mother	Sex	DoB	Age (y)	Follow hours	Peering events
Ellie	Friska	female	01.03.1999	9 - 12	517	24
Fredy	Friska	male	01.06.2005	8 - 9	127	11
Ronaldo	Raffi	male	01.01.2006	8	0	3
Chindy	Cissy	female	01.01.2003	8 - 15	74	10
Cheech	Chick	male	01.07.2000	8	15	1
Lilly	Lisa	female	01.03.2001	10 & 13	302	23
Kronos(2018)	unknown	male	01.07.2009	9	24	2
Oreo	unknown	male	unknown	unknown	0	1
Diddy	Dodi	male	01.12.2005	8	13	1
Sazu	Sarabi	male	01.07.2007	7 & 10	24	7
Shera	Chick	female	01.02.1998	13	208	40
Tina	Raffi	female	01.01.1998	10 - 11	348	4
Trident	Tiara	female	01.07.2006	10 - 11	98	10
Yulia	unknown	female	01.07.2006	9 - 12	398	32

4.3 Data collection

4.3.1 Activity and association data

Through the established behavioural database of Suaq Balimbing, longitudinal behavioural data systematically recorded on the focal animals, their mothers and association partners was available since 2007. Some of the juveniles had already been followed during infancy, and there were data on the infancy and juvenility of two adult females. Thus, on top of the data collected during the time frame of my project, I was also able to assess past social interests in terms of association, and overall activity budgets of their mothers.

Throughout the whole data base, focal animals were followed from their morning to their evening nest whenever possible. Behavioural data were collected using standardized methods of focal animal sampling including instantaneous scan sampling at two minutes' intervals, and ad libitum focal animal sampling (described in detail on www.aim.uzh.ch/de/research/orangutannetwork/sfm.html). The activity, as well as the composition of associations and the distance from focal animal to each association partner, were recorded in two minutes' intervals. A two minutes' interval in which the activity was feeding, is a feeding event. For each feeding event, it was additionally recorded which species of food and which part of the species (i.e. leaf, vegetation, bark, pith, flower or fruit) was fed on, the combination of which is here referred to as "food item". Based on 132'280 feeding events from over 4400 hours of feeding on 20 females, I was able to compute population wide frequencies of these food items.

A focal was considered in an association whenever another individual was recorded to be within 50m of the focal. For every such association partner, I determined sex-age class and maternal relatedness, which had been assessed through a combination of past behavioural and genetic data. I defined the following five categories of maternal relatedness: "mother" for mother infant relationships; "direct" for consecutive siblings, i.e. first and second offspring, as well as second and third, but not first and third offspring; "close" for other siblings, aunts/uncles, grandmothers and cousins of similar age; "distant" for all confirmed relatives such as great-grandmothers, great-aunts or

second-degree cousins; “non” for everybody else. I differentiated between direct, close and distant due to familiarity constraints. Consecutive siblings are generally highly familiar with each other because the weaned immatures usually stay closely associated with the mother for some time even after a younger sibling is born. Other siblings, as well as the other close maternal relations, do not have this intimate familiarity. They are still likely to be somewhat familiar with each other, though, because adult females still associate with their mother from time to time. Therefore, young infants would get to occasionally meet their other siblings, grandmother, aunts or cousins. Other individuals might still be somewhat related but probably not very familiar with each other, so I put them in their own category. For every follow, I computed the number of association hours, i.e. the cumulative time the focal spent in association with another individual, e.g. one hour spent in association with two individuals equals two association hours. On the one hand, one could argue, an individual does not necessarily have double the chances for peering if there are two individuals around instead of just one because it is not possible to peer at two different events at the same time. On the other hand, an additional association partner does mean more opportunities for peering, even if not double. For the analysis, I used association time to compute the proportion of time infants spent in close proximity. Adding the times, the focal animal was together with each association partner, allowed me to compute this proportion for each association partner separately. Again, the distance to one association partner is often not independent from the distance to another association partner but also not completely dependent. Because both options have their merits, the choice for using association time as defined above as opposed to computing the time in association irrespective of the number of association partners was, in the end, a practical one.

4.3.2 Peering data

Amongst others information, the data on the peering behaviour were recorded ad libitum from the focal animal or any of its association partners. Peering is defined as “directly looking at the action of another individual sustained over at least five seconds and at a close enough range that enables the peering individual to observe the details of the action” (Schuppli et al., 2016b). For each peering event, several parameters were recorded: the name of the peerer, i.e. the individual peering at an activity, and the peering target, i.e. the individuals performing the respective activity, the performed activity, as well as presence and distance of additional association partners. In the case of food related peering (“food peering”), we also recorded the food item in accordance with the activity data, as well as presence or absence of any form of attempts to perform the same behaviour with the same food item (henceforth called “exploration”, which includes feeding, try-feeding, exploratory behaviours and object play) within one hour before and after the event. For each food item, a proxy for complexity was determined by the number of processing steps orang-utans perform before ingesting this food item, as described in Schuppli et al., 2016a.

Because the peering behaviour was recorded ad libitum not only for the focal individual but also for association partners, I had to use different samples for different types of analyses. For peering proportions, I used all peering events available because proportions are irrespective of time. However, I computed peering rates as events per hour. To do so, I used the peering events during which the infant itself was a focal animal. In order to get reliable rates, I only used peering events recorded by selected observers. Caroline Schuppli, Ellen Meulman, Julia Kunz, Sofia Forss, Chigusa Keller, Anais van Cauwenberghe, Sonja Falkner, Helvi Musdarlia, Natasha Bartalotta, and Belinda Kunz are all well-trained observers who either had a project focusing on immature learning or had collected data specifically for such projects. Moreover, they had to have recorded a minimum of 50 peering events in total.

4.4 Statistical analysis

Plots and analyses were all done in the R programming language, R 3.4.1 (R development Core Team, 2011) using the base package for all plots and the "lme4" package (Bates et al, 2014) for statistical models. I used general linear mixed effects models (GLMM) with either Poisson or binomial family distribution using the natural link functions of the "glmer" function, and linear mixed effects models (LMM) of the "lmer" function to analyse my data. All model predictions were assessed using the "predict" function. The statistical tests used in this thesis are implemented in the basic "stats" package. In the case of multiple testing, I used the Bonferroni correction.

For analyses with a potential age effect in the data from infants, I pooled data for each individual for each year of their lives. For peering rates, pooling the data meant that I added the number peering events per individual and per year and divided this by the total number of hours the individual was followed by selected observers during the respective year. For peering proportions, the number of peering events that meet the corresponding criteria was divided by the total number of peering events per individual in the specified time frame.

For analysis in which I did not investigate age effects, I either computed overall proportions or pooled the data for each individual irrespective of age. By using the overall proportion, I was able to look into interests with a high resolution because even rare events were included. Pooling the data for the total number of peering events and total follow and association hours of each individual enabled me to compare statistically between e.g. different activities or sex-age classes. To get reliable estimates of an individual's proportions or rates, I reduced the data set to only include individuals with more than a certain amount of peering events, follow hours or association hours. None of the analysis in juveniles included age as a factor. This was not possible, firstly, because the juveniles' ages are based on rough estimates, and secondly, because of the limited sample size in terms of peering and follow hours available for each individual.

I used backward model selection based on the corrected Akaike Information Criterion using the "AICc" function of the "qpcR" package (Spiess, 2018). In a first step, however, I determined by visual assessment of the raw data whether the full model should include age as a linear or quadratic factor. In a second step, I used the AICc values to determine if the age variables should be log-transformed or not. Only in the third step, the actual backward model selection with all variables was performed. Delta AICc values represent the difference in AICc of the best model to the next fuller model from which the last variable was dropped.

5. RESULTS

From 2007 to 2018, 35 observers recorded a total of 3792 peering events, 3431 (90.5%) of which by immatures, which I focused on. These peering events included 3254 by 22 infants and 177 by 14 juveniles. 2906 (84.7%) of these immature peering events were directed at the mother of the peerer.

5.1 Infants' interest in specific activities

As a first step, I looked at what activities infants are interested in and how this interest develops over age. To do so, I analysed peering proportions and rates infants direct at different activities.

5.1.1 Activities of interest

To analyse the context in which peering occurs, I focused only on the peering events directed at the mother because infants are in constant association with their mother but not with other individuals. Furthermore, I did have simultaneous follows only for the mothers, but only rarely for other individuals. Therefore, it was only possible to correct for the number of opportunities for peering which was directed at the mother. I focused on comparing the feeding, nesting, and social contexts of peering because they had been suggested to be the main focus of peering (Schuppli et al., 2016b). From a total of 2842 peering events infants directed at their mother, 2466 (87%) were in the feeding context, 270 (10%) in the nesting context, and 23 (<1%) directed at social interactions. From all the food peering events, 38 (2%) events were directed at insect tool use and 67 (3%) at Neesia tool use. From the social peering, 15 (65%) were directed at copulations.

For every peerer, I computed the proportion of peering events directed at a certain activity, given that we had recorded more than ten peering events by that peerer. Overall, most infant peering events occurred in the feeding context (mean = 0.889, standard deviation (sd) = 0.074), nesting context (mean = 0.080, sd = 0.057), and social context (mean = 0.016, sd = 0.035), while other activities such as moving or resting were barely peered at (mean = 0.015, sd = 0.021, Figure 2). To control for the opportunities an infant has to peer, I looked at the activity budgets of their mothers and found that, where the feeding context is indeed the most prevalent activity (mean = 0.573, sd = 0.081), the nesting (mean = 0.014, sd = 0.002) and social contexts (mean = 0.010, sd = 0.009) were comparatively rare (Figure 3). When comparing the proportion of peering events directed at the mother performing a certain activity to the proportion of time she actually performed this activity (Figure 4), we found that relative peering proportions in the feeding context are lower (mean = 1.52, sd = 0.27) than relative peering proportions in the nesting context (mean = 6.88, sd = 3.15). Peering in the social context relative to the time the mother engaged in social interactions (excluding mother infant interactions because the infant cannot peer at its own interaction), varies substantially (mean = 0.80, sd = 1.02). This came probably from the fact that social interactions were rare in the activity budget of mothers. Despite nesting being similarly rare, it happened regularly, at least once a day for several minutes, while social interactions happened very irregularly. I performed an ANOVA (analysis of variance) assuming unequal variances to compare the means of the relative peering proportions statistically. This resulted in a significant difference between the activities (p-value < 0.0001). In a post-hoc analysis, I then performed pairwise Welch tests while applying the Bonferroni correction for multiple testing. The Welch tests showed significant differences when comparing the feeding context with the nesting context (Bonferroni-corrected p-value = 0.0055), the nesting with the social context (Bonferroni-corrected p-value = 0.0017), as well as the combined other activities (Bonferroni-corrected p-value = 0.0011). The feeding context compared to the combined other activities also had a significant difference (Bonferroni-corrected p-value < 0.0001).

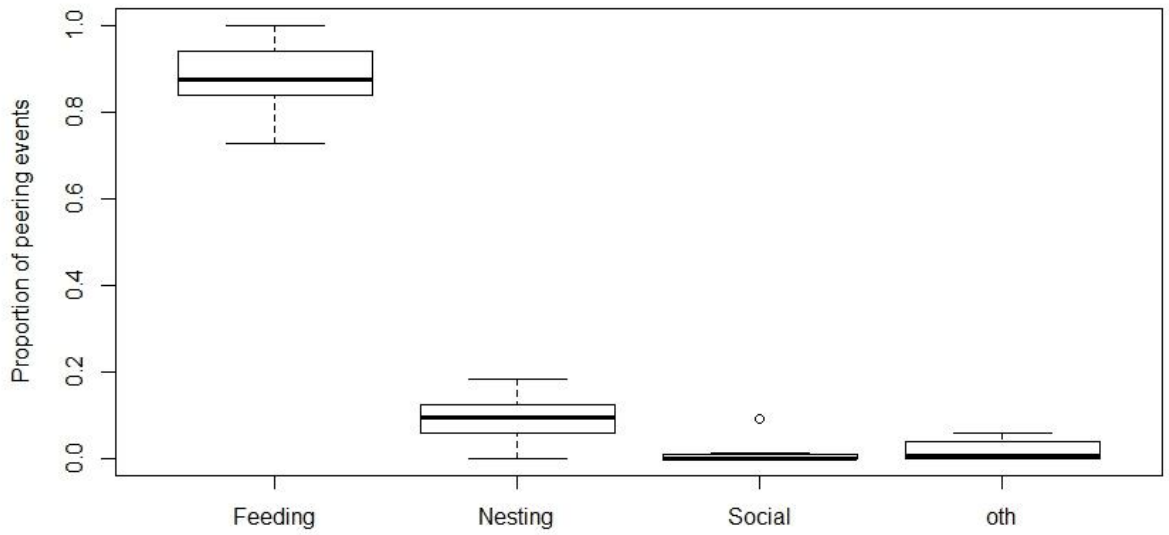


Figure 2: Peering at different activities. Proportions of peering events by infants directed at the different activities of their mothers. Each data point is derived by dividing the number of recorded peering events of one individual at the specific activity by the total number of peering events recorded for this individual, whereby only peerer with more than ten total peering events were included (N = 12).

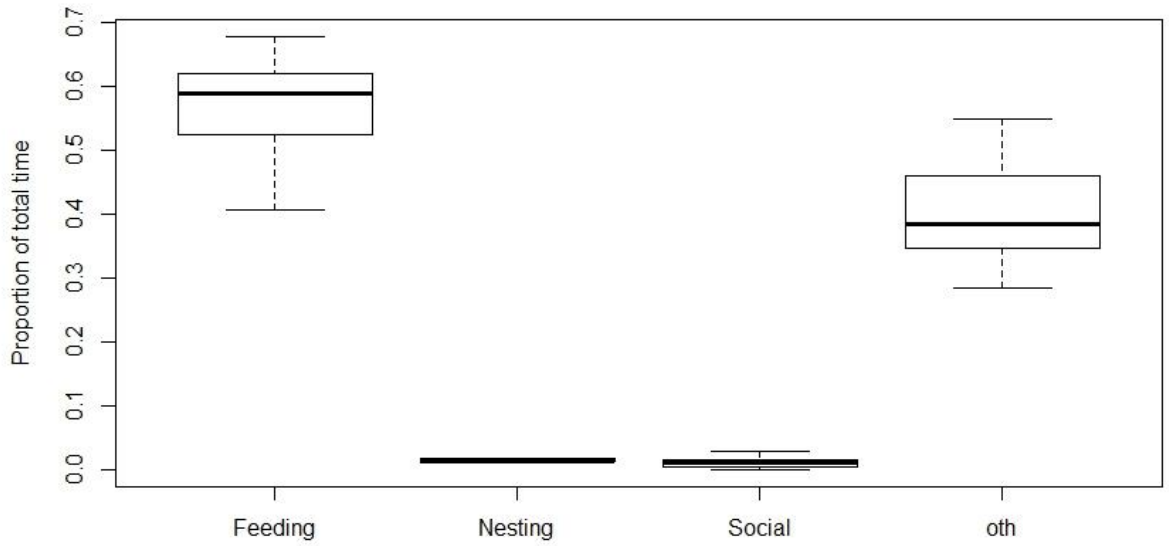


Figure 3: Activity budget of the mothers. The proportion of time the mothers of the immature study subject spent feeding, nesting, in social interactions and performing other activities during focal follows. One data point is derived from the total time a mother was followed (N = 11).

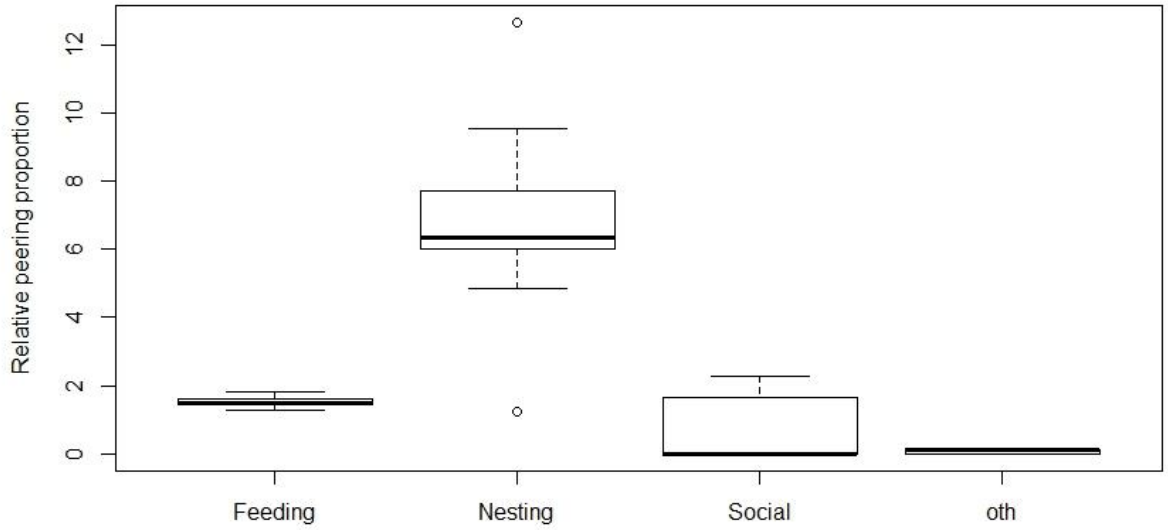
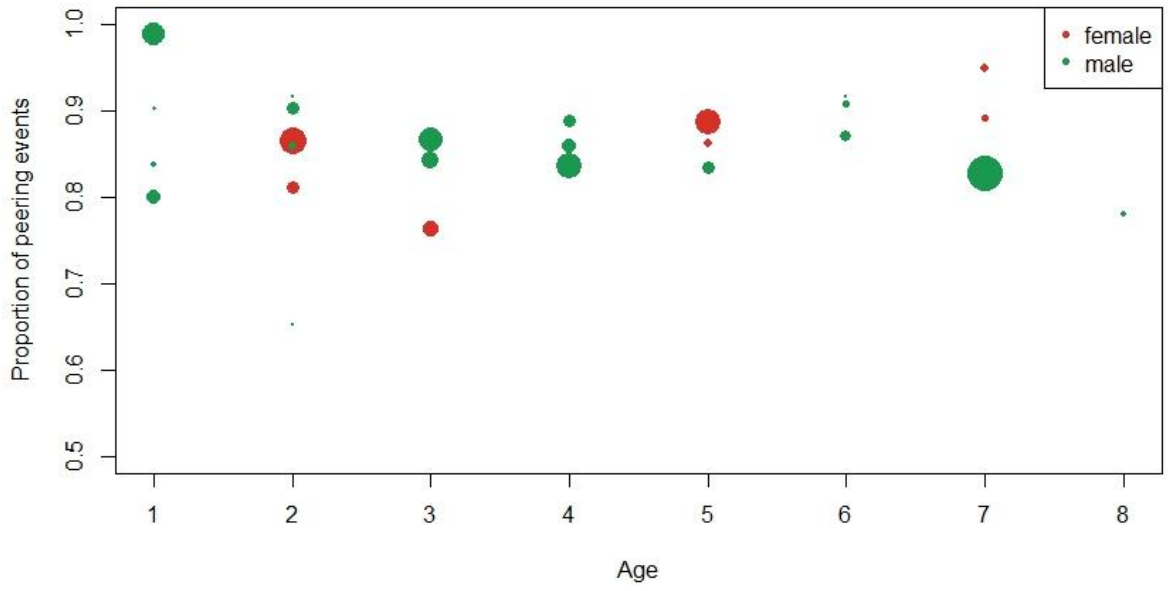


Figure 4: Infant peering corrected for opportunity. Peering proportions infants directed at different activities performed by the mother relative to the proportion of time the mother was performing this activity. One data point is derived from the pooled peering events of one individual peerer with more than ten total peering events and the overall proportion of time the mother performed the respective activities (N = 11). Points above 1 indicate a preference for this activity.

5.1.2 Development of interest in activities

I also looked at the development of the infants' interest in specific activities over age. For this, peering data directed at the mother were pooled for each peerer over 6-month intervals. I used GLMMs with Poisson family distribution and total peering events as offset to analyse the change in interest for the three activities feeding, nesting, and social interactions. To account for the fact that most individuals occurred repeatedly in the data set, I included the focal animal as a random factor. The proportion of peering events directed at feeding was continually high throughout infancy (Table 3, Figure 5a). The proportions of peering events directed at nesting across age, however, followed a quadratic curve, which peaked around 2.5 years of age (Table 3, Figure 5b). The proportion of peering events directed at social interactions increased with age (Table 3, Figure 5c). The model selection according to the corrected AIC did not warrant the inclusion of sex as a factor in either of these models.



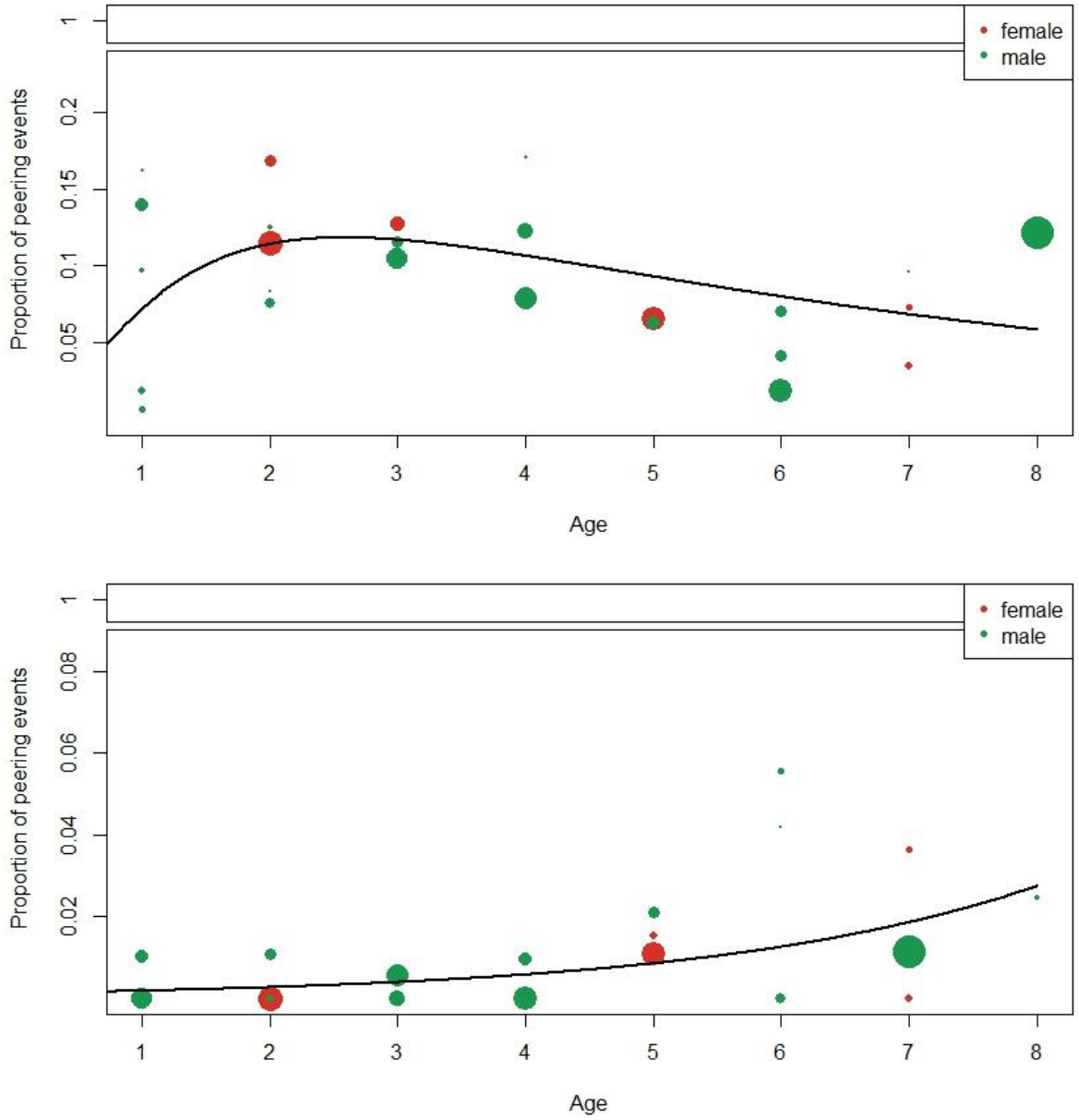


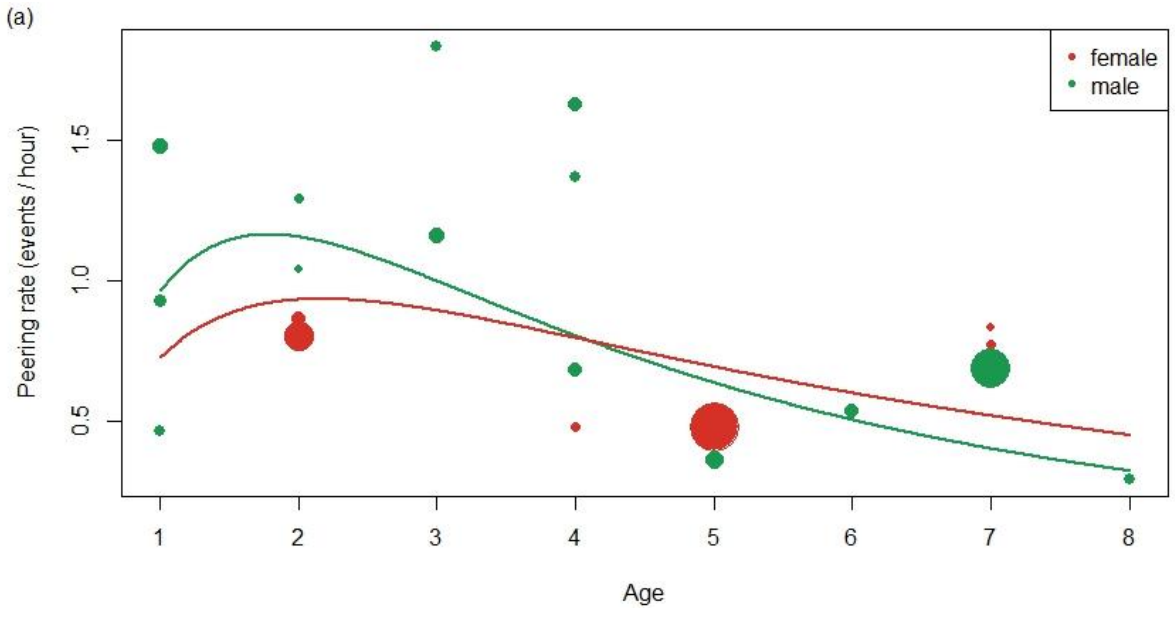
Figure 5: Peering at activity over age. Development of the proportion of peering events directed at a) feeding, b) nesting, c) social interactions, for female and male infants. The raw data is pooled into an averaged proportion over a one-year period for each infant for all with total peering events ≥ 20. The size of the points is proportional to the number of total peering events. The lines are drawn from the respective model predictions (see table 3).

Table 3: Effects on peering at activity. The effects of age on the proportions of peering events directed at different activities of the mother (feeding, nesting, and social interactions), analysed by GLMM with Poisson family distribution, log-link, and total peering events as an offset. Model selection is based on corrected AIC values.

Effect	Effect Type	Estimate	Std. Error	z	P-value	N	95% CI
Food peering: delta AICc = 1.4						28	
Intercept	Fixed	-0.15	0.02	-7.07	**<0.0001**	-	-0.19 to -0.11
Individual	Random	-	-	-	-	12	0.00 to 0.05
Nest peering: delta AICc = 2.0						28	
log(Age)	Fixed	1.05	0.36	2.89	**0.0039**	cont.	0.36 to 1.78
log(Age)^2	Fixed	-0.55	0.17	-3.19	**0.0034**	cont.	-0.90 to -0.22
Individual	Random	-	-	-	-	12	0.00 to 0.24
Social peering: delta AICc = 1.9						28	
Age	Fixed	0.39	0.12	3.25	**0.0011**	cont.	0.16 to 0.64
Individual	Random	-	-	-	-	12	0.00 to 0.78

5.1.3 Development of peering rates

While proportions of peering directed at different activities were highly conclusive about what the infants were interested in, only peering rates (peering events per time) captured social learning frequencies or the interest in certain behaviours during the different stages of infancy. Overall peering rates first increased slightly, then decreased with age (Figure 6a). The best fitting model included significant effects for log-transformed age (P-value < 0.0001), squared log-transformed age (P-value < 0.0001), and the interaction of squared log-transformed age with sex (P-value = 0.00735) (Table 4). As food peering events were by far the most numerous of all peering events, peering rates in the feeding context mainly followed the pattern of the overall peering rates (Figure 6b, Table 4). Nest peering rates increased until a later age, but eventually decreased after peaking around the age of 3.5 years (Figure 6c). The best model for nest peering rates did not include sex but only log-transformed age (P-value = 0.0217) and squared log-transformed age (P-value = 0.0159) (Table 4).



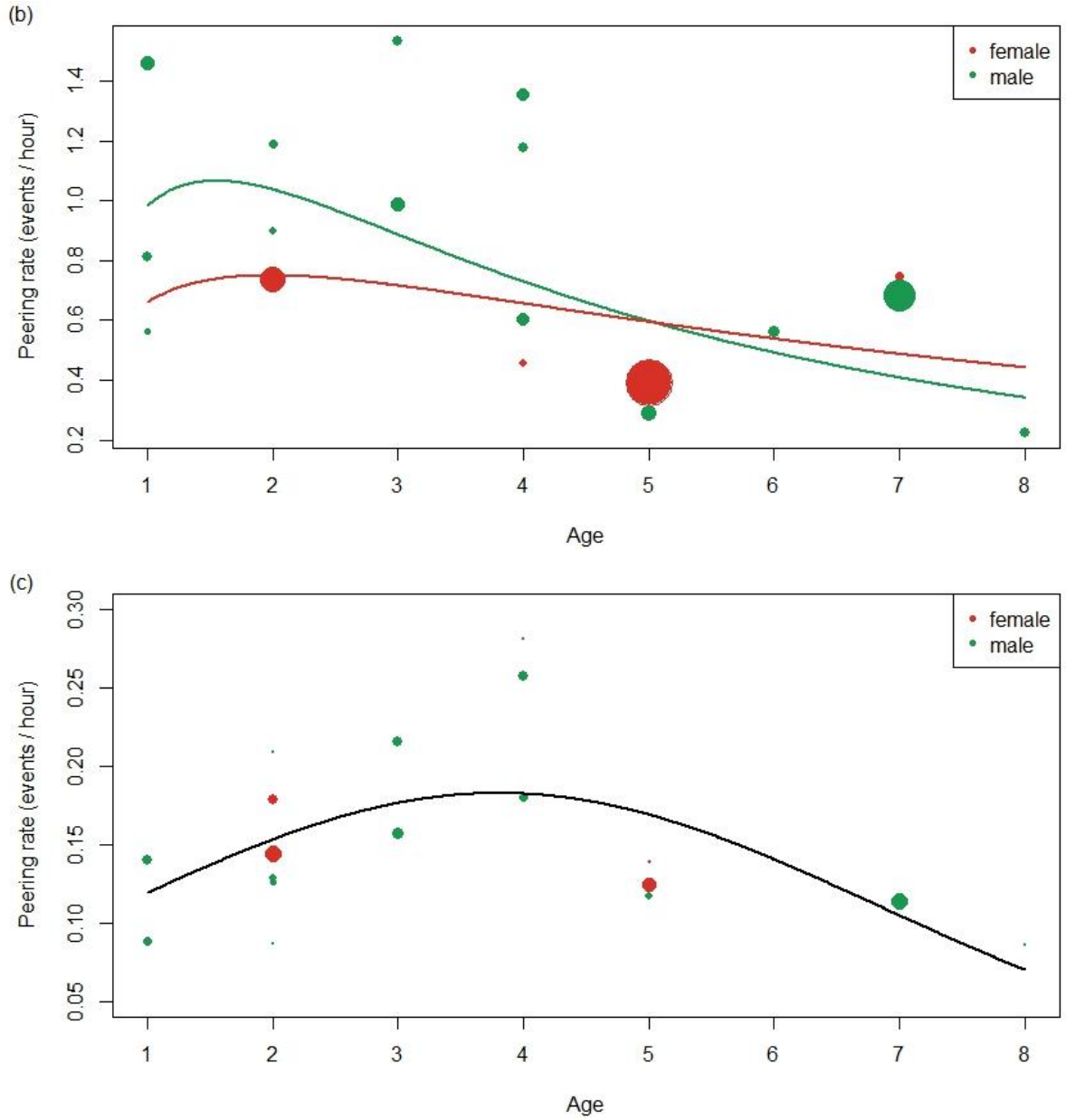


Figure 6: Peering rates over age. a) Overall peering rate, b) food peering rate, c) nest peering rates (events per follow hour), for female and male infants. The number of peering events are pooled over a one-year period for each infant with follow hours ≥ 50 (≥ 20 for nest peering due to fewer overall occurrences). The size of the points is proportional to the number of follow hours. The lines are drawn from the model predictions (see table 4).

Table 4: Effects on peering rates. The effects of age and sex on the peering rates (events per hour) directed at the mother, analysed by GLMM with Poisson family distribution, log-link, and follow hours as an offset, for overall, food and nest peering. The model selection is based on corrected AIC values.

Effect	Effect Type	Estimate	Std. Error	z	P-value	N	95% CI
Overall: delta AICc = 3.2						20	
Sex(male)	Fixed	0.28	0.28	1.01	0.3133	2	-0.36 to 0.86
log(Age)	Fixed	0.66	0.15	4.36	**<0.0001**	cont.	0.36 to 0.95
log(Age)^2	Fixed	-0.43	0.08	-5.44	**<0.0001**	cont.	-0.58 to -0.27
Sex(male) : log(Age)^2	Fixed	-0.14	0.05	-2.68	**0.0074**	-	-0.25 to -0.04
Individual	Random	-	-	-	-	8	0.20 to 0.64
Feeding context: delta AICc = 3.3						20	
Sex(male)	Fixed	0.40	0.24	1.65	0.0993	2	-0.15 to 0.88
log(Age)	Fixed	0.37	0.16	2.3	**0.0212**	cont.	0.05 to 0.68
log(Age) ^{2}	Fixed	-0.27	0.08	-3.27	**0.0011**	cont.	-0.43 to -0.11
Sex(male) : log(Age) ^{2}	Fixed	-0.15	0.06	-2.68	**0.0074**	-	-0.26 to -0.04
Individual	Random	-	-	-	-	8	0.14 to 0.51
Nesting context: delta AICc = 1.4						19	
Age	Fixed	0.41	0.18	2.34	**0.0193**	cont.	0.07 to 0.77
Age ^{2}	Fixed	-0.05	0.02	-2.53	**0.0115**	cont.	-0.10 to -0.01
Individual	Random	-	-	-	-	10	0.00 to 0.21

5.2 Infant's interest in specific individuals

In a second step, I looked at the development of role model choice in infants. I investigated which individuals infants were interested in and how this interest in the mother compared to others develops over age. To do so, I analysed peering proportions infants direct at different peering targets and association time spent in close proximity with individuals other than the mother.

5.2.1 Role model choice

To get to the bottom of role model choice in infants, I investigated the proportions of peering events directed at individuals other than the mother. To correct these proportions for opportunities, I computed the ratio between the peering proportions and the proportion of time spent in association with the respective sex-age class. If infants have a preference for certain role models, we expected this ratio to be above 1. Furthermore, I looked into potential sex differences with respect to such preferences. In the first step, I used every infant peering event available to get the highest possible resolution. In the second step, I redid the analysis only including individuals with more than five peering events to see if the pattern held across individuals by computing means and standard errors. It turned out that the six infants with more than five peering events had a minimum of 18 peering events per individual. However, with only six individuals, I was not able to differentiate between the sexes.

Overall, 252 (9%) of the 2701 infant food peering events were not directed at the mother but at other individuals. Most of these peering events were directed at unflanged males (N = 97, 39%) and juveniles (N = 94, 38%), some at adult females (N = 44, 18%), and hardly any at other infants (N = 9, 3%) or flanged males (N = 8, 3%). The majority of these role models were maternally unrelated

individuals (“non”, N = 165, 65%). However, some were distantly (“distant”, N = 10, 4%), or closely, related (“close”, N = 22, 8%) or even direct siblings (“direct”, N = 55, 22%) (Figure 7). When corrected for, the amount of time infants spent in association with the respective sex-age classes, juveniles, adult females, as well as unflanged males, were peered at preferentially (Figure 8). Looking at the sexes separately, it seemed they have similar preferences (Figure 9). Only their interest in flanged males seemed to differ by much. While males did not seem to be preferentially interested in flanged males, females seemingly did. Considering the small number of peering events directed at flanged males, however, I would treat this result with caution.

The reduced sample consisting of six individuals with a minimum of 18 peering events, confirmed the highest average proportion of infant peering was directed at juveniles (mean = 0.36, sd = 0.3), adult females (mean = 0.23, sd = 0.19), and unflanged males (mean = 0.33, sd = 0.25) (Figure 10). When correcting the proportions for each of the six infants with the amount of time each infant spent in association with the respective sex-age class, adult females and unflanged males were clearly peered at preferentially, while the result was inconclusive on juveniles (Figure 11).

These results are in line with the general prediction. Adult females and unflanged males are sex-age classes which are clearly more skilled than infants. Juveniles are also more skilled than infants but in some tasks potentially less so that adults. Furthermore, adult males are always unrelated individuals due to the male-biased dispersion of orang-utans, and juveniles are known to associate not only with their own mother and younger sibling but also other mother-infant pairs. Therefore, if infants are preferentially interested in skilled individuals, we not only expect these sex-age classes to be of interest, but also a high proportion of role models to be unrelated individuals.

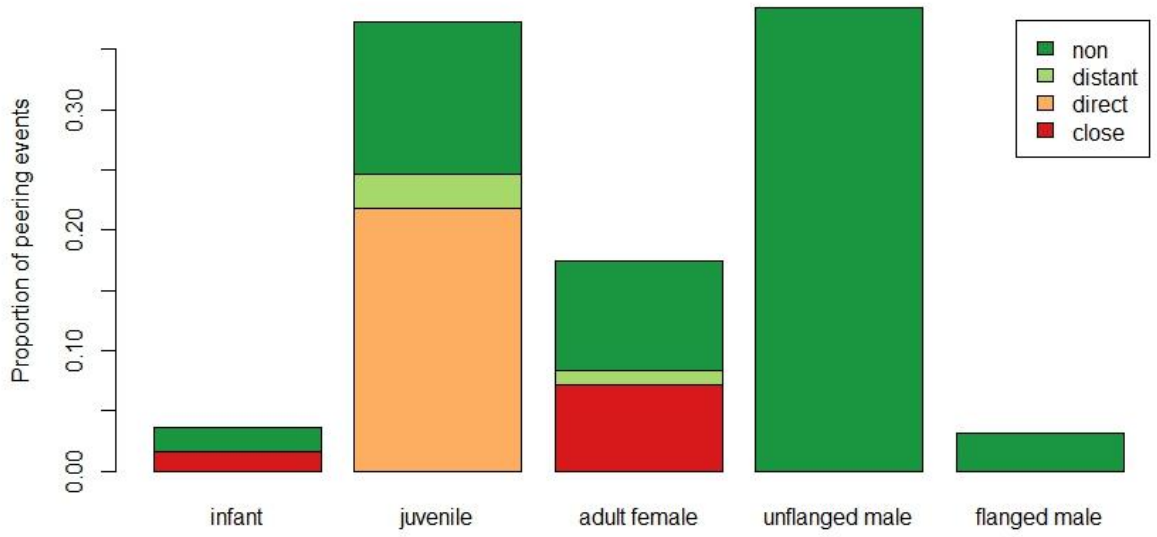


Figure 7: Peering at sex-age classes and different degrees of relatedness. Proportions of the total peering events infant directed at peering targets other than the mother for the different sex-age classes of peering targets and degrees of maternal relatedness.

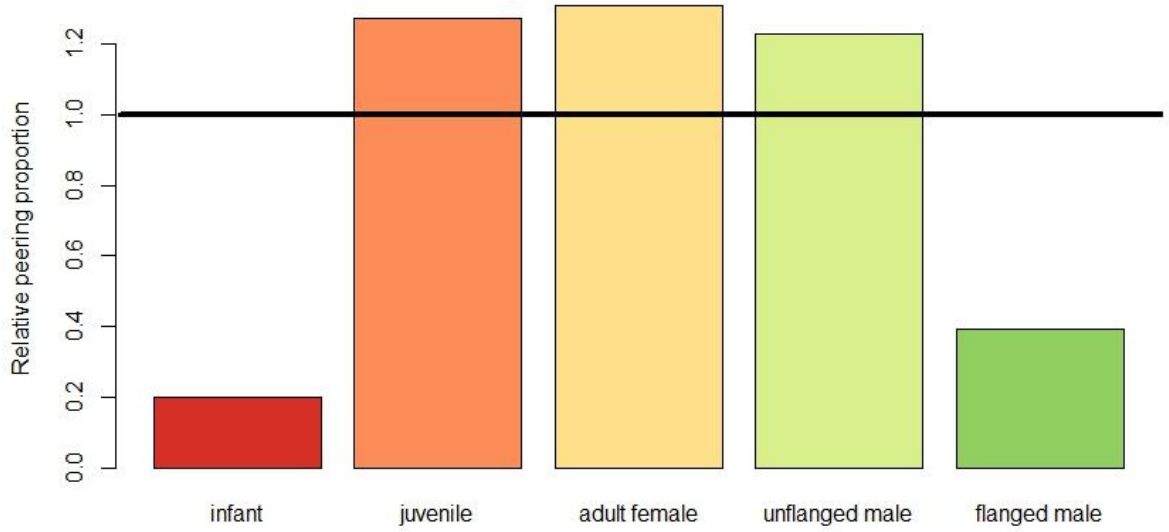


Figure 8: Peering at sex-age classes corrected for opportunity. The proportion of peering corrected for the proportion of time infants spent in association with the respective sex-age class. Values above one indicate a preference for this sex-age class.

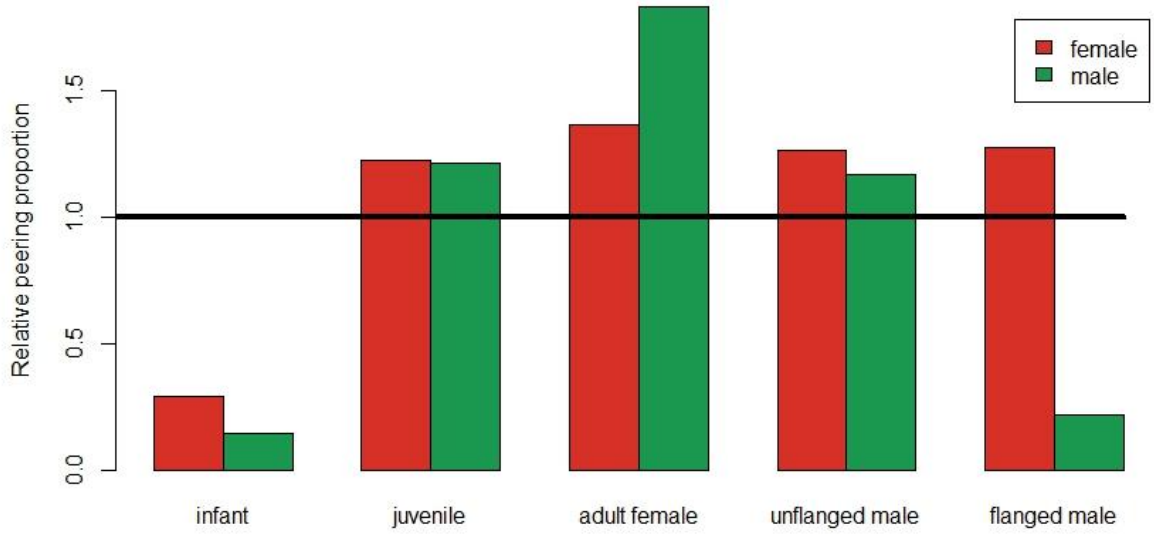


Figure 9: Peering at sex-age classes corrected for opportunity by sex. The proportion of peering corrected for the proportion of time the two sexes of infants spent in association with the respective sex-age class. Values above one indicate a preference for this sex-age class.

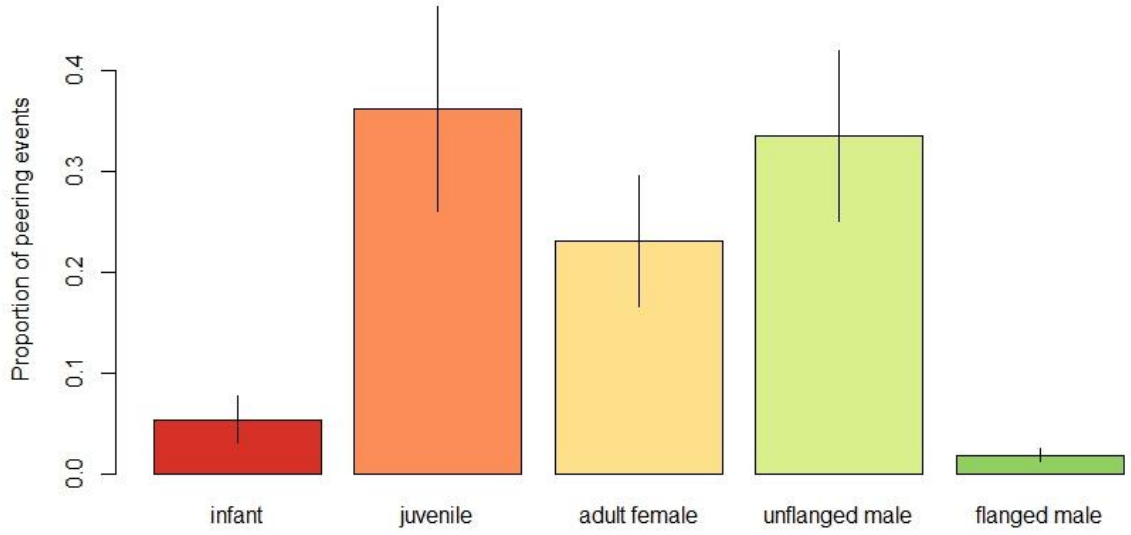


Figure 10: Peering at sex-age classes for each infant. Mean proportion of peering events by infants directed at peering targets other than the mother for the different sex-age classes of the peering targets. The means and error bars in this plot are based on six individuals with more than five peering events.

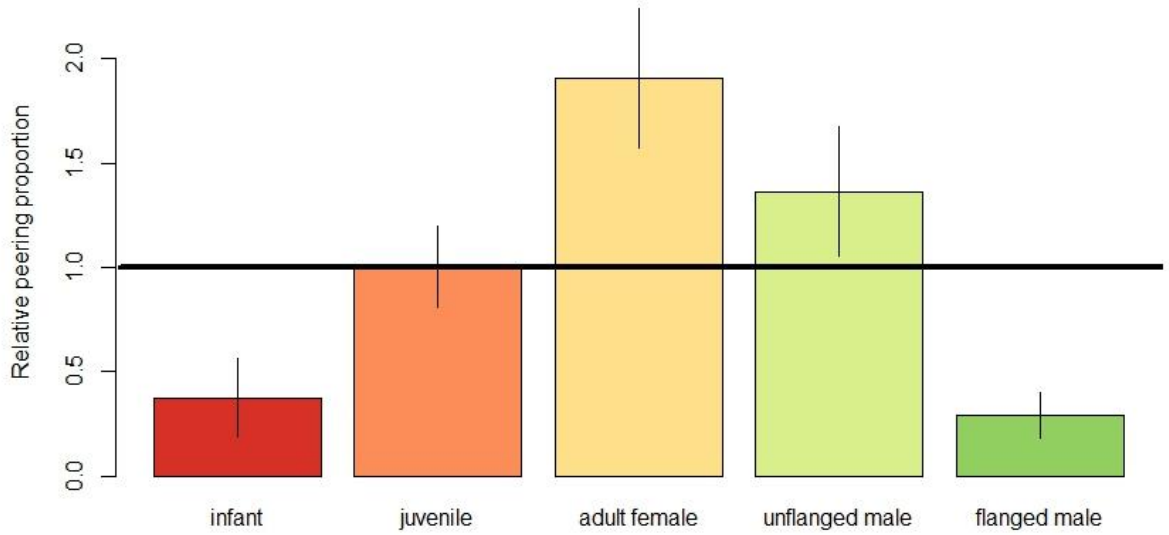


Figure 11: Peering at sex-age classes corrected for opportunity for each infant. The proportion of peering corrected for the proportion of time infants spent in association with the respective sex-age class. Values above one indicate a preference for this sex-age class. The means and error bars are based on six individuals with more than five peering events.

5.2.2 Development of role model choice

The analysis of the development of role morel choice showed evidence for potential differences between the sexes. I performed LMM with the proportion of peering events directed at the mother (pooled over a year for each peerer) as the dependent variable and selected the best model according to the AIC. While the proportion of peering events directed at individuals other than the mothers steadily increased over age in male infants, in female infants the proportion of peering events directed at peering targets other than the mother first increased, but then dropped back to lower levels (Figure 12). In fact, in the best model for females, log-transformed age, the square of log-transformed, as well as their combination were all highly significant (P-value < 0.0001), while only age was significant (P-value = 0.0008) in the best model for males (Table 5).

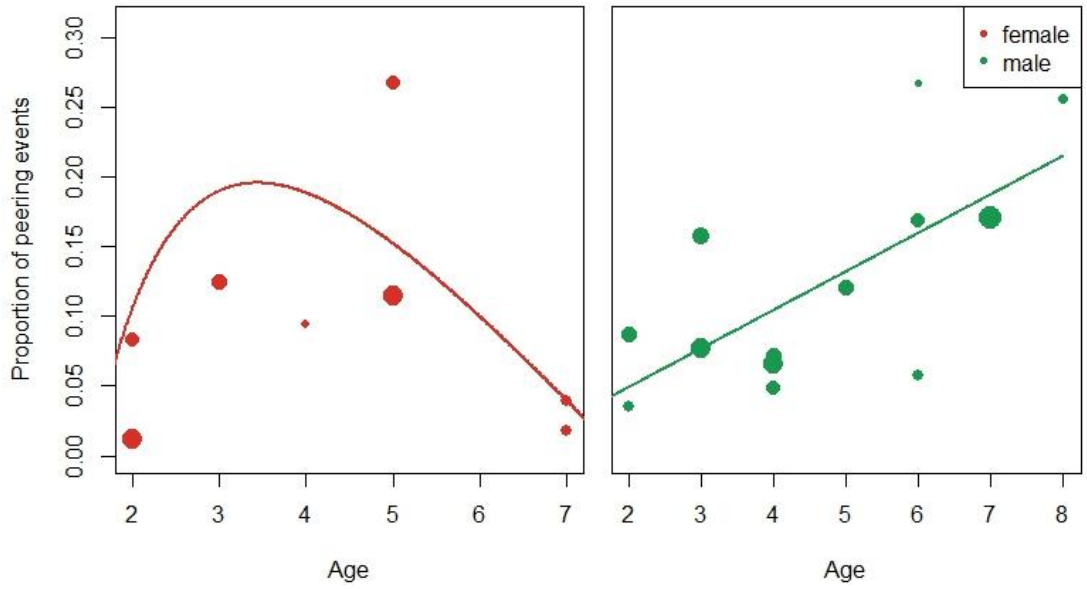


Figure 12: Peering at individuals other than the mother. Development of the proportion of infant food peering events directed at individuals other than the mother for females and males. The raw data is pooled into an averaged proportion over a one-year period for each infant with total peering events ≥ 30 between the age of one to eight years old. The size of the points is proportional to the number of total peering events. The lines are drawn from the model predictions (see table 5).

Table 5: Effects on peering at individuals other than the mother. The effects of age on the proportion of peering events infants direct at their mother, analysed by LMM for female and male infants between age one and eight years old. The model selection is based on corrected AIC values.

Effect	Effect Type	Estimate	Std. Error	z	P	N	95% CI
Females: full model (delta AICc = 9.1 to next slimmer model)						8	
log(Age)	Fixed	-0.76	0.10	-7.80	**<0.0001**	cont.	-1.01 to -0.52
log(Age)^2	Fixed	0.31	0.04	7.85	**<0.0001**	cont.	0.21 to 0.41
Individual	Random	-	-	-	-	4	0.04 to 0.18
Males: full model (delta AICc = 6.2 to next slimmer model)						13	
Age	Fixed	-0.03	0.01	-3.37	**0.0008**	cont.	-0.05 to -0.01
Individual	Random	-	-	-	-	8	0.00 to 0.05

5.2.3 Development of association patterns

In addition to peering, we used association patterns as a second proxy for social interest. For infants which were mobile enough to move in and out of close proximity with association partners, investigating how much time infants spent in such close proximity should reflect their interest in the association partner. We found that the proportion of time an infant spent within close proximity, i.e. 2m distance, to an association partner other than the mother follows a similar pattern as the proportion of peering directed at individuals other than the mother in the previous result. For males, the proportion increased with age, while it first increased then decreased to low levels in females after a certain age (Figure 13). In the best model for females, log-transformed age, square of the log-transformed age, and their combination were highly significant (P-values < 0.0001), but in the best model for males only age was significant (P-value = 0.0003) (Table 6).

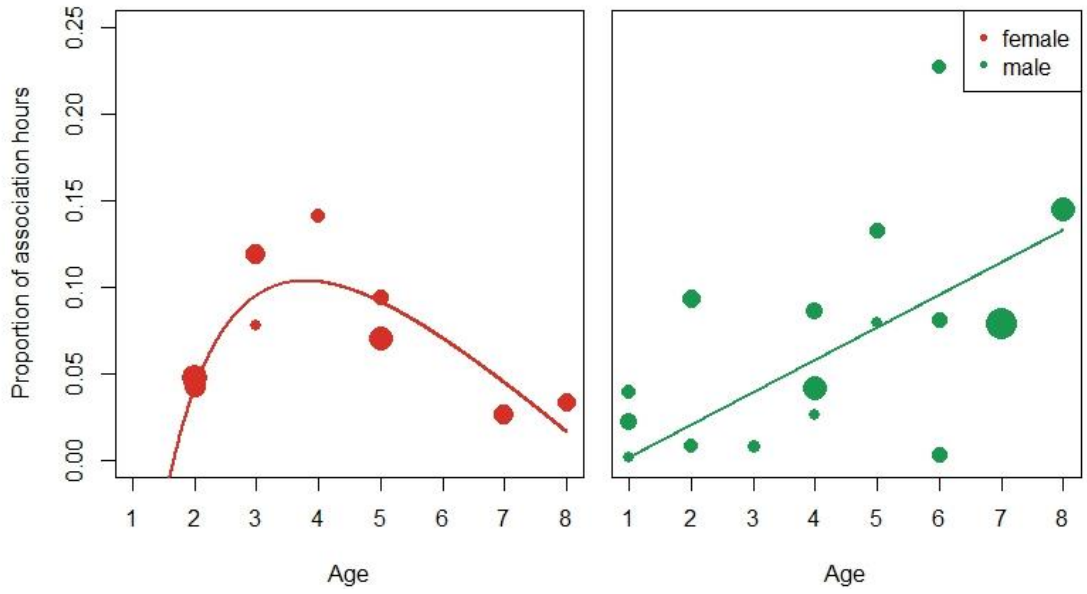


Figure 13: Close proximity to associations other than the mother. Development of the proportion of total association hours infants spent within 2m of an association partner other than the mother, for female and male infants. The raw data is pooled into an averaged proportion over a one-year period for each infant between the age of one to eight years old for all with total association hours ≥ 55. The size of the points is proportional to the number of total association hours. The lines are drawn from the model predictions (see table 6).

Table 6: Effects on close proximity. The effects of age on the proportion of total association hours infants spent within 2m of an association partner, analysed by LMM for female and male infants between age one and eight years old. The model selection is based on corrected AIC values.

Effect	Effect Type	Estimate	Std. Error	z	P-value	N	95% CI
Females: full model (delta AICc = 9.0 to next slimmer model)						10	
log(Age)	Fixed	0.41	0.07	5.99	**<0.0001**	cont.	0.25 to 0.59
log(Age)^2	Fixed	-0.16	0.03	-5.99	**<0.0001**	cont.	-0.22 to -0.10
Individual	Random	-	-	-	-	5	0.00 to 0.04
Males: full model (delta AICc = 8.2 to next slimmer model)						15	
Age	Fixed	0.02	0.004	3.60	**0.0003**	cont.	0.01 to 0.03
Individual	Random	-	-	-	-	6	0.01 to 0.08

5.3 Is peering indeed means to social learning?

In the third part, I replicated results from Schuppli et al. 2016 with my larger data set. In order to test whether peering was a means to social learning in the feeding context, we tested three hypotheses. Firstly, we expected the peerer to interact more with the object of interest after the peering event compared to before. Secondly, we expected peering to target food which is complex to feed on, and therefore that peering rates increased with complexity. And thirdly, we expected peering to target rare food. However, because opportunities to peer at food were higher the more frequent this food was, if peering were performed randomly, we expected a positive correlation between peering frequency and food frequency. If peering targeted rare food, this slope of the regression of food frequency to peering frequency was expected to be lower than one. The new part about what we did in this study, was that we also looked in detail at peering directed at individuals other than the mother, which had never been done before.

5.3.1 Practice after peering

Under the assumption that food peering was a means for social learning, we predicted immatures would interact with the respective food more often in the hour after the peering event compared to the hour before. Any such interaction including feeding, try-feeding, object play and exploratory behaviour with the same food which was handled by the peering target will henceforth be called exploration. They are a proxy for individual practice of the peering skills previously observed. In the first step, I used every infant peering event available to get the highest possible resolution. In the second step, I redid the analysis only including individuals with more than five peering events to see if the pattern held across individuals by computing means and standard errors for each of the sex-age classes.

For 2307 infant peering events, information on the absence and presence of exploration was available for the hour before, as well as the hour after the peering event. 2154 of these peering events were directed at the mother, 78 at juveniles, 75 at unflanged males, 21 at adult females, six at flanged males, and two at another infant. Due to the insufficient amount of peering data on flanged males and infants as peering targets, they were not analysed. For the other four sex-age classes of peering targets, I computed the proportion of peering events with exploration, before as well as after the event. When comparing these two proportions for each sex-age class of peering target, the one after the peering event was always higher than the one before (Figure 14). In fact, the presence of exploration was significantly predicted by the variable before vs. after (P-value = 0.0002) and log-transformed age (P-value = 0.0052) in a binomial GLMM with logit-link (Table 7).

The reduced sample consisting of individuals with a minimum of five peering events, confirmed that the proportion of peering events with exploration in the hour after the event was higher compared to the hour before (Figure 15). This held true not only for peering directed at the mother, but also the other sex-age classes juveniles and unflanged males. Due to the reduction criterion, only a single individual peering directed at adult females would have been included in the analysis, and none for peering directed at flanged males or infants. Therefore, I was not able to include these sex-age classes.

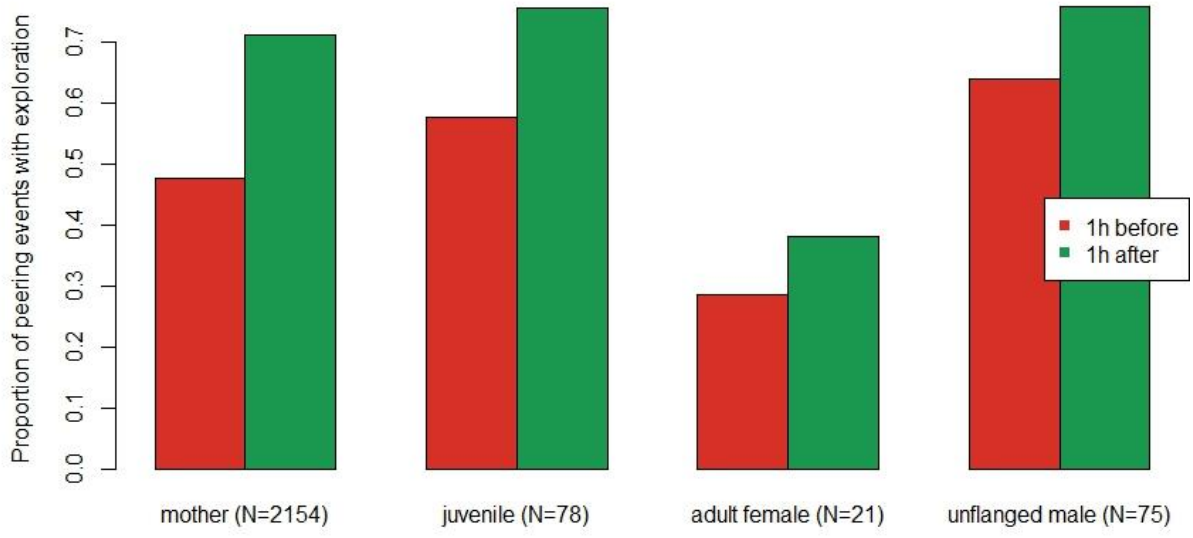


Figure 14: Proportion of peering with exploration. The proportion of infant peering events with exploration within 1h before and 1h after by sex-age class of the peering target. N is the total number of peering events for each sex-age class.

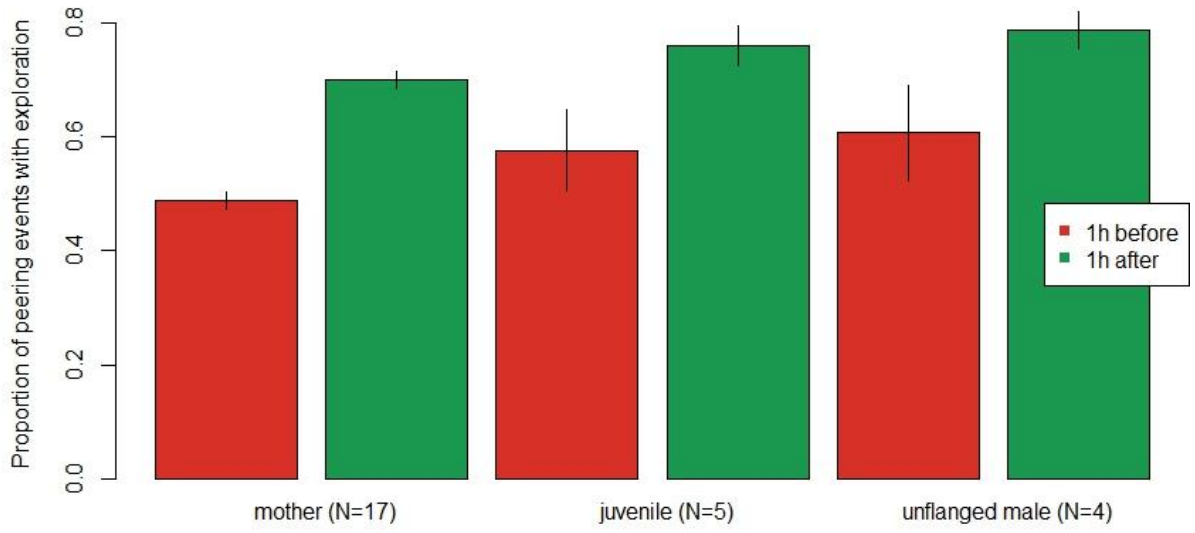


Figure 15: Proportion of peering with exploration for each infant. The proportion of infant peering events with exploration within 1h before and 1h after by sex-age class of the peering target. The means and error bars are based on N individuals with more than five peering events.

Table 7: Effects on exploration. The effects of age and variable 1h before vs. 1h after the peering event on the presence of exploration analysed by GLMM with binomial family distribution and logit-link. The model selection is based on corrected AIC values (full model with delta AICc = 466.1 to next slimmer model).

Effect	Effect Type	Estimate	Std. Error	z	P-value	N	95% CI
variable(after)	Fixed	1.10	0.29	3.77	**0.0002**	2	0.53 to 1.68
log(Age)	Fixed	0.50	0.18	2.80	**0.0052**	cont.	0.15 to 0.85
Sex(male)	Fixed	-0.16	0.42	-0.39	0.6944	2	-1.08 to 0.63
variable(after) : log(Age)	Fixed	0.08	0.23	0.36	0.7165	-	-0.36 to 0.52
variable(after) : Sex(male)	Fixed	-0.34	0.32	-1.06	0.2894	-	-0.97 to 0.29
log(Age) : Sex(male)	Fixed	0.07	0.19	0.36	0.7212	-	-0.31 to 0.44
variable(after) : log(Age) : Sex(male)	Fixed	0.18	0.25	0.72	0.4691	-	-0.31 to 0.66
Individual	Random	-	-	-	-	22	0.32 to 1.02

5.3.2 Rarity & complexity

If peering was used for learning, we expected peering rates to increase with complexity, i.e. the number of processing steps a food requires before ingestion. This effect was expected to get more pronounced with increasing age because young infants still needed to learn everything regardless of complexity but older infants already mastered feeding on low-complexity food. Within the peered-at food items, we found the following patterns. The first model indeed confirmed, that, with increasing age, the number of processing steps had an increasingly positive effect of peering rate (P-value < 0.0001). Furthermore, with increasing age, the frequency of respective food item in the population diet had an increasingly negative effect on the peering rate (P-value < 0.0001) (Table 8).

We expected peering to decrease with increasing food frequency, i.e. the frequency with which the food was present in the population-wide diet of parous females. If infants peered randomly

at what they saw, we expected that a regression line of food frequency to peering frequency to have a slope of 1, because an increased food frequency should lead to increased opportunities to peer (see above). To assess the slope of the correlation between peering frequency and food frequency, we corrected for the number of processing steps instead of including it as a fixed effect. As expected (see above), the 95% confidence interval of the slope was far smaller than 1 (Figure 16, Table 9), which meant the infants preferentially peered at rare food items.

Table 8: Effects on food peering rate. The effects of food complexity (processing steps), food frequency, and age on the peering rate of infants, analysed by GLMM with Poisson family distribution, for female and male infants between age one and eight years old. The model selection is based on corrected AIC values (full model, delta AICc = 29.9 to next slimmer model).

Effect	Effect Type	Estimate	Std. Error	z	P-value	N	95% CI
log(Frequency)	Fixed	0.3	0.05	5.55	**<0.0001**	cont.	0.20 to 0.41
Processing steps	Fixed	-0.25	0.14	-1.76	0.0780	6	-0.52 to 0.03
log(Age)	Fixed	-1.74	0.23	-7.47	**<0.0001**	cont.	-2.34 to -5.07
log(Frequency) : Processing steps	Fixed	-0.06	0.03	-2.33	**0.0201**	-	-0.12 to -0.01
log(Frequency) : log(Age)	Fixed	-0.2	0.04	-4.85	**<0.0001**	-	-0.28 to -0.12
Processing steps : log(Age)	Fixed	0.59	0.11	5.55	**<0.0001**	-	0.38 to 0.91
log(Frequency) : Processing steps : log(Age)	Fixed	0.1	0.02	4.67	**<0.0001**	-	0.06 to 0.14
Individual	Random	-	-	-	-	8	0.17 to 0.56

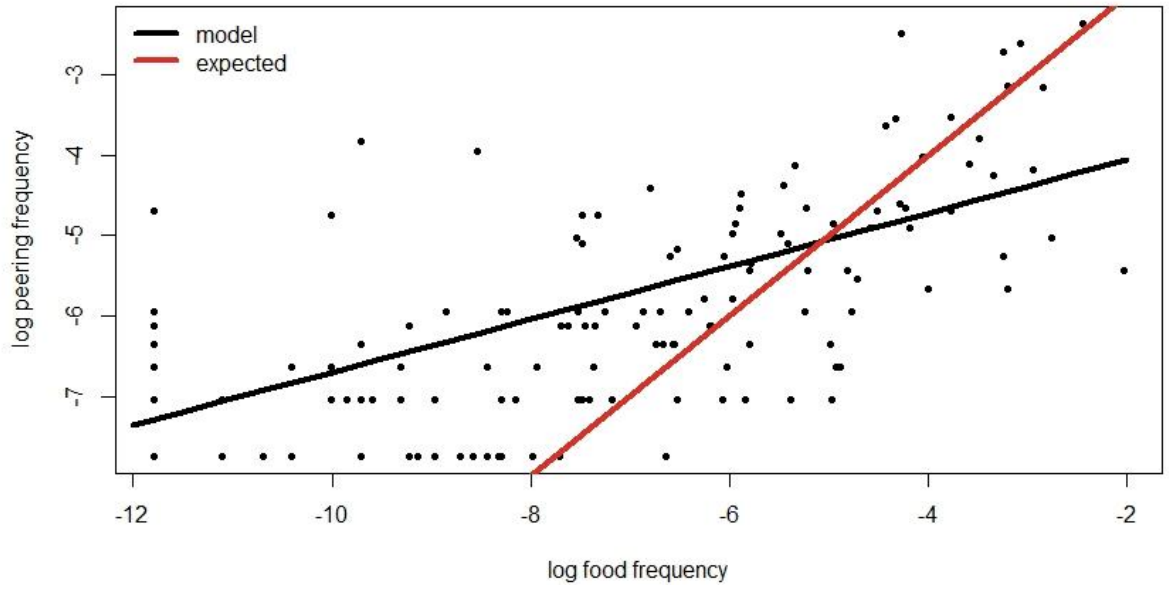


Figure 16: Peering frequency against food frequency. The log-transformed peering frequency plotted against the log-transformed food frequency. The black line follows the model prediction based on the data (see table 9), the red line reflects the expected slope (= 1) under the null-hypothesis.

Table 9: Effects on peering frequency. The effect of food frequency on the peering frequency, analysed by LMM. According to the nature of my prediction, I am comparing the estimate to the expected slope of 1, as opposed to 0. Printed in bold is the confidence interval to be compared to 1.

Effect	Effect Type	Estimate	Std. Error	N	95% CI
log(Frequency)	Fixed	0.11	0.03	cont.	**0.06 to 0.17**
Age	Random	-	-	8	0.25 to 0.82
Individual	Random	-	-	8	0.00 to 0.50
Processing steps	Random	-	-	6	0.11 to 0.59

5.4 Juveniles' interests

I also looked at the social interest in juveniles. I investigated who they spend time with, as well as who and what the peer at. I did this to find out whether learning goes beyond infancy. At this age, peering could have a social function as opposed to learning.

5.4.1 Associations during juvenility

From 2007 to 2018, there have been 307 focal follows of juvenile orang-utans at Suaq Balimbing. During 166 of these, the juvenile was in association with one or more individuals for during the follow. There were a total of 334 associations of juveniles recorded with known sex-age class of the association partner. 26 (8%) of these juvenile associations were with the mother of the juvenile, 62 (19%) with infants including younger siblings, 54 (16%) with other juveniles, 31 (9%) with adult females, 127 (38%) with unflanged males, and 34 (10%) with flanged males (Figure 17).

When focused on the time spent with those association members, the 166 juvenile focal follows with associations comprised a total of 1240.4 association hours. 9% of these were spent with the mother, 19% with infants including younger siblings, 12% with other juveniles, 11% with adult females, 36% with unflanged males, and 12% with flanged males (Figure 18). At the same time, just 1% of the association time was spent in contact with another individual, 8% between 0m and 2m, 12% between 2m and 5m, 27% between 5m and 10m, and 51% between 10m and 50m (Figure 19).

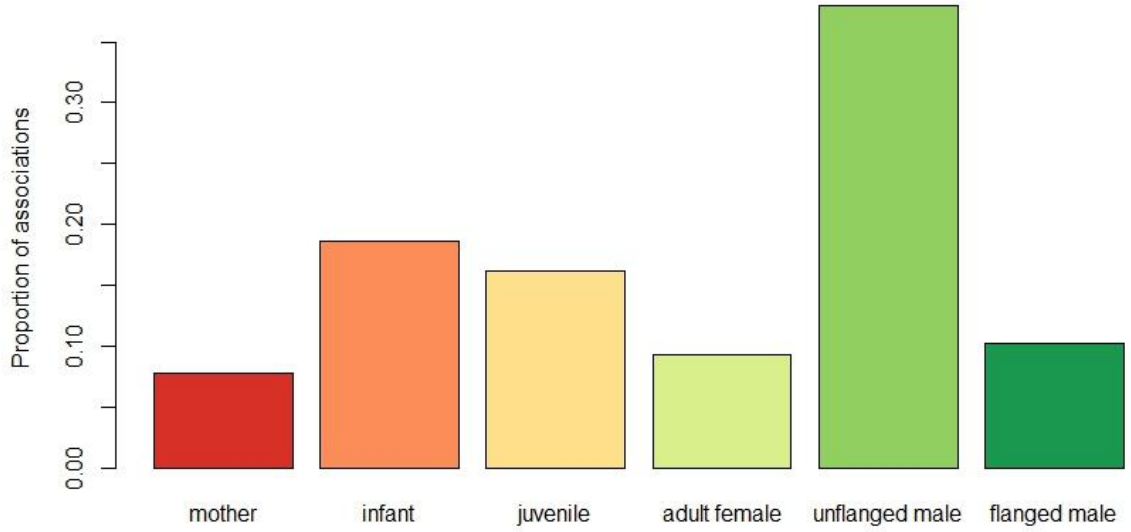


Figure 17: Proportion of associations juveniles spent with different role models. Proportion of juvenile focal follows in association with the respective sex-age class based on occurrence data.

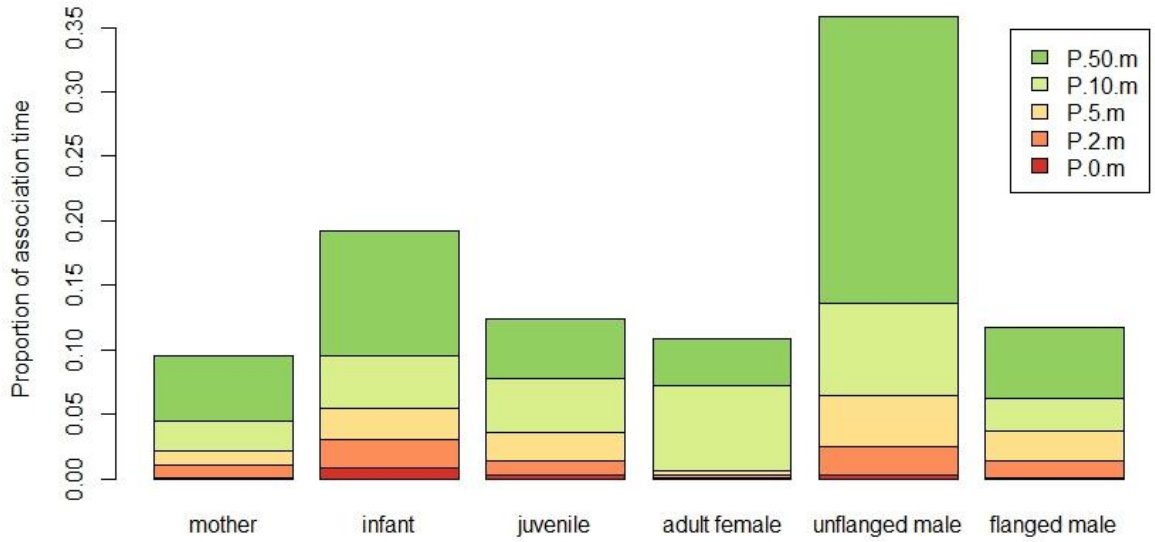


Figure 18: Proportion of association time juveniles spent with different role models. The proportion of association time juveniles spent in association with a sex-age class per amount of time spent in contact (P.0.m), within 0-2m (P.2.m), 2-5m (P.5.m), 5-10m (P.10.m), and 10-50m (P.50.m).

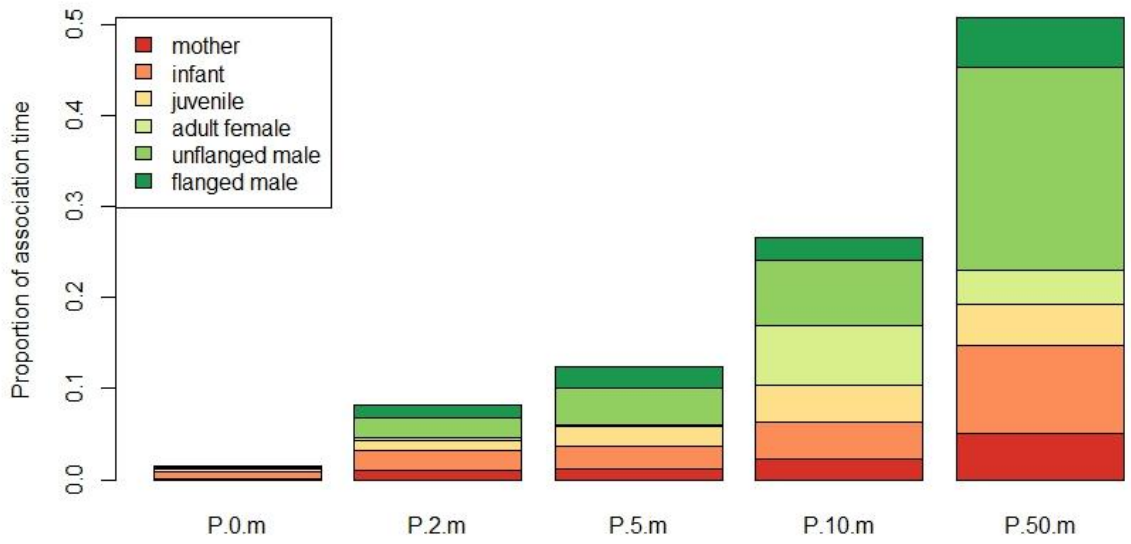


Figure 19: Proportion of association time juveniles spent in different proximity. Proportion of association time juveniles spent in contact (P.0.m), within 0-2m (P.2.m), 2-5m (P.5.m), 5-10m (P.10.m), and 10-50m (P.50.m), per sex-age class of the association.

5.4.2 Juvenile peering

In total, 173 juvenile peering events were recorded. In 147 cases (85%) the peerer was a juvenile female, and only in 26 cases (15%), the peerer was a juvenile male. 152 (88%) were directed at feeding, ten at nesting (6%), one (< 1%) at social interactions, and ten (6%) at other activities (Figure 20). Only four (3%) out of the food peering events were directed at insect tool use, and three (2%) at Neesia tool use. In 36 (21%) events, the peering target was the mother, in eight (5%) each an infant and an adult female, in 57 (33%) each a juvenile and unflanged male, and in seven (4%) a flanged male (Figure 21). Focusing on the patterns of maternal relatedness, it was striking that the majority of peering events directed at role models other than the mother were directed at completely unrelated individuals ("non", N = 135, 78%), none at closely-related individuals, and only two (1%) at distantly-related individuals (Figure 21).

When correcting the proportion of peering by the proportion of association time juveniles spent in association with the respective sex-age class, I found that they only peered preferentially at their mother and juveniles, but not at adult females or unflanged males (Figure 22). After reducing the sample to seven individuals with more than five peering events, I confirmed that the mother, juveniles and unflanged males were frequently peered at (Figure 23). However, I was not able to correct for opportunity, one of the reasons being that two individuals were never seen in association with their mother.

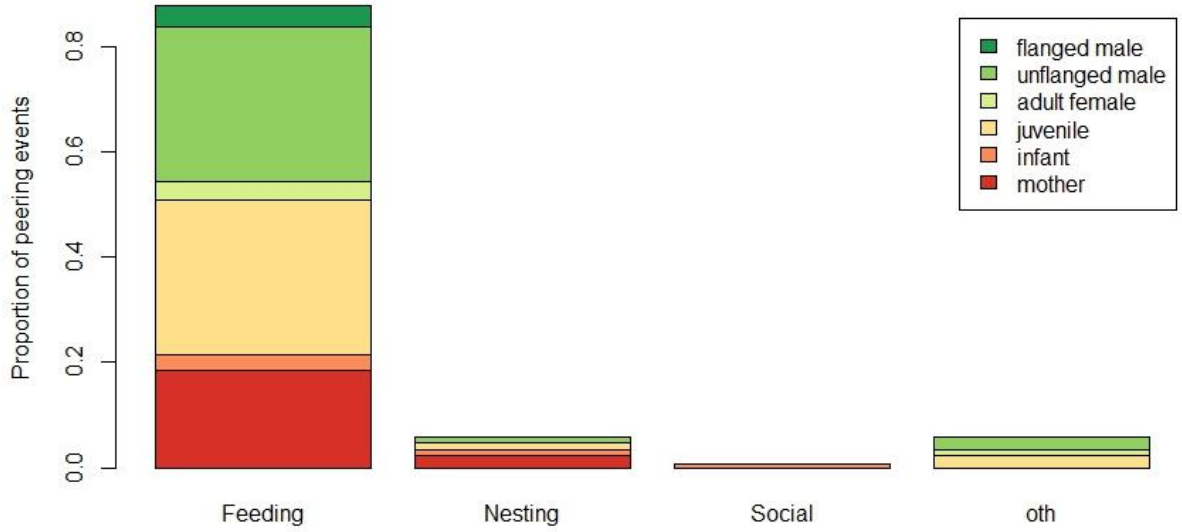


Figure 20: Peering at different activities. The proportion of juvenile peering events directed at feeding, nesting, social interactions, and other activities by sex-age class of the peering target.

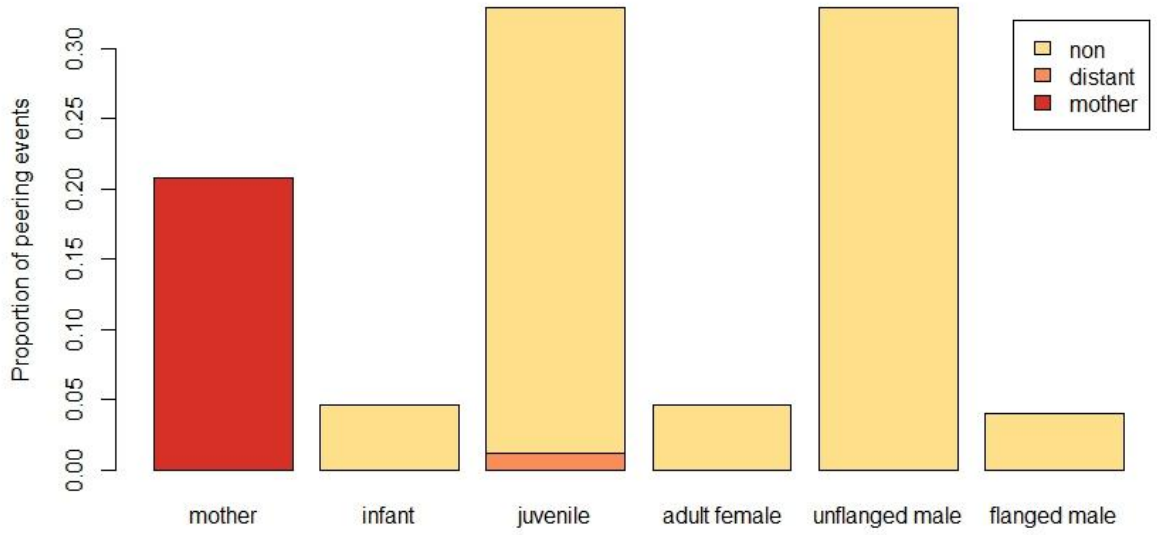


Figure 21: Peering at sex-age classes. The proportion of juvenile peering events directed at a certain sex-age class of peering target by maternal relatedness of peerer and peering target.

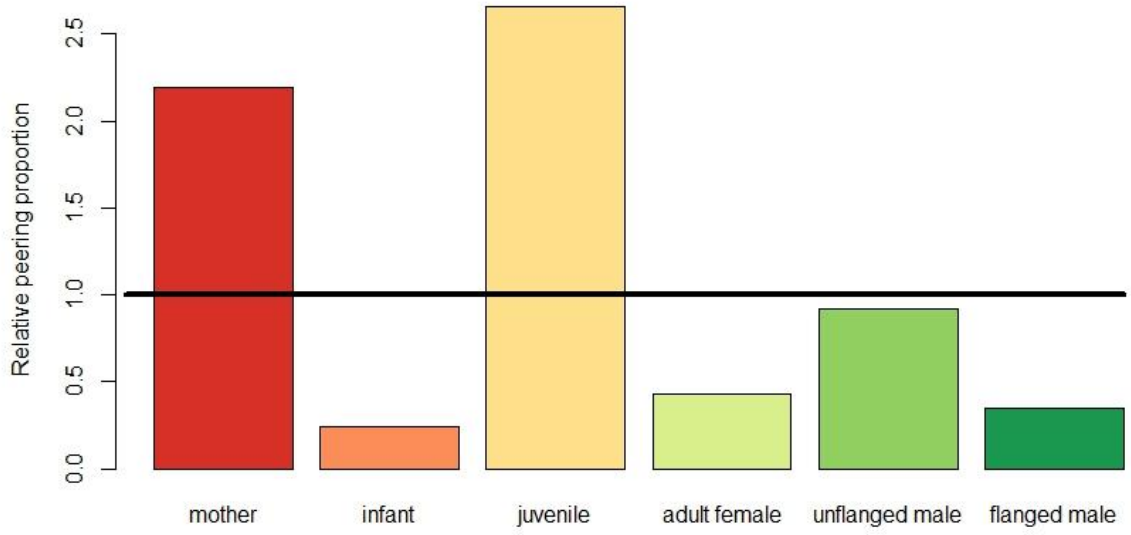


Figure 22: Juvenile peering at sex-age classes corrected for opportunity. The proportion of peering corrected for the proportion of association time juveniles spent in association with the respective sex-age class. Values above one indicate a preference for this sex-age class.

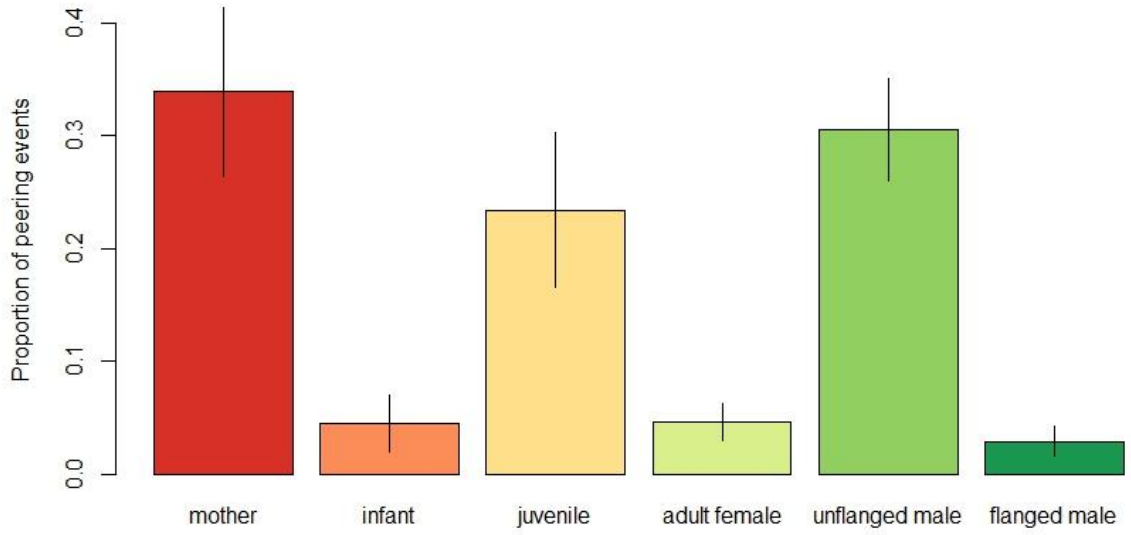


Figure 23: Peering at sex-age classes for each juvenile. Mean proportion of peering events by juveniles directed at the different sex-age classes of the peering targets. The means and error bars in this plot are based on seven individuals with more than five peering events.

5.4.3 Practice after juvenile peering

If peering is also a means for social learning in juveniles, we expect exploration to be a proxy for practice to be present more often in the hour after the peering event than in the hour before. Out of 104 juvenile food peering events with known presence or absence of exploration before and after the event, 76 (73%) had exploration recorded before and 91 (88%) after the event (Figure 24). There was a positive, significant effect of the variable after the event compared to before in the binomial model with outcome variable "presence/absence of exploration" (P-value = 0.0104) (Table 10). I also investigated whether this pattern held when looking at different sex-age classes of peering targets, and when comparing between individuals. When disregarding the peering directed at infants and

flanged males because there were such few events recorded, the pattern of an increased proportion of the presence of exploration in the hour after the peering event compared to the hour before seemed to stand out, not only for peering directed at the mother, but also at other juveniles and unflanged males (Figure 25). When comparing between individuals by reducing the data to seven individuals with more than five peering events, I found the same pattern again (Figure 26).

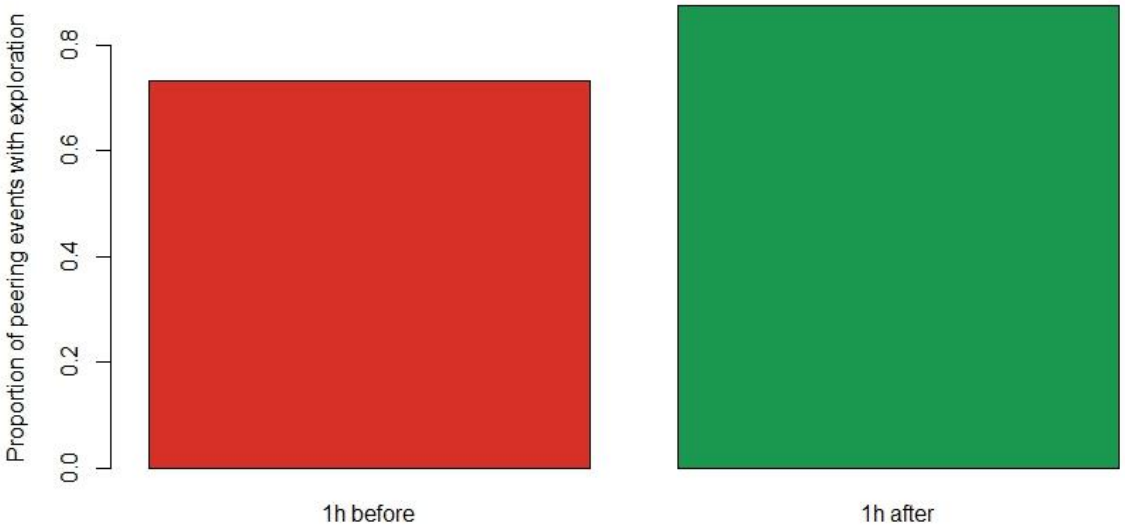


Figure 24: Peering with exploration. The proportion of overall juvenile peering events with exploration within 1h before and 1h after the peering event, based on 104 juvenile peering events.

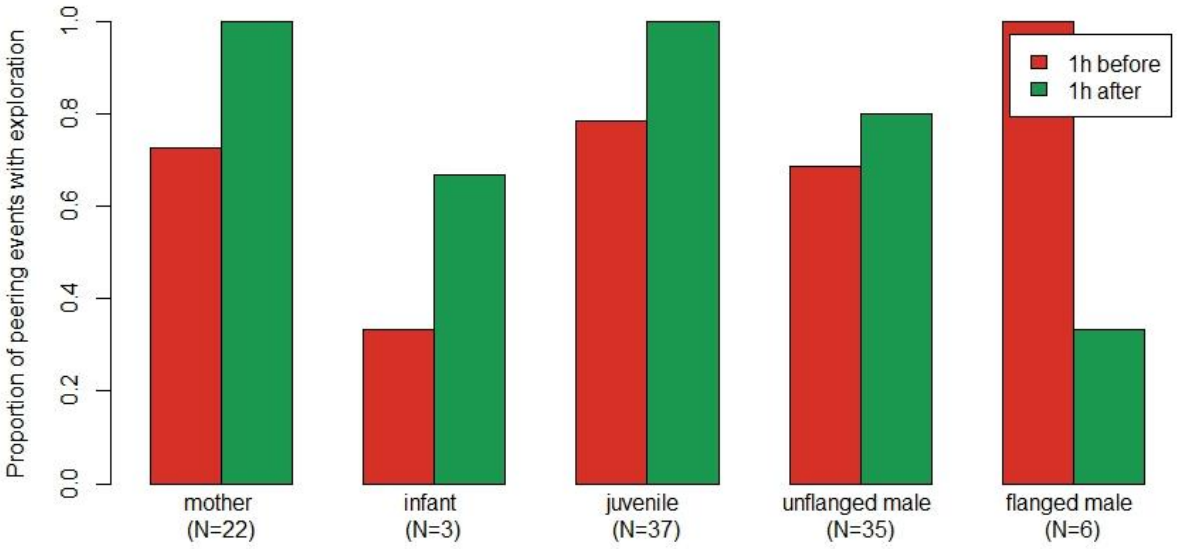


Figure 25: Peering with exploration by sex-age class. The proportion of juvenile peering events with exploration within 1h before and 1h after the peering event by sex-age class of the peering target. N is the total number of peering events for each sex-age class.

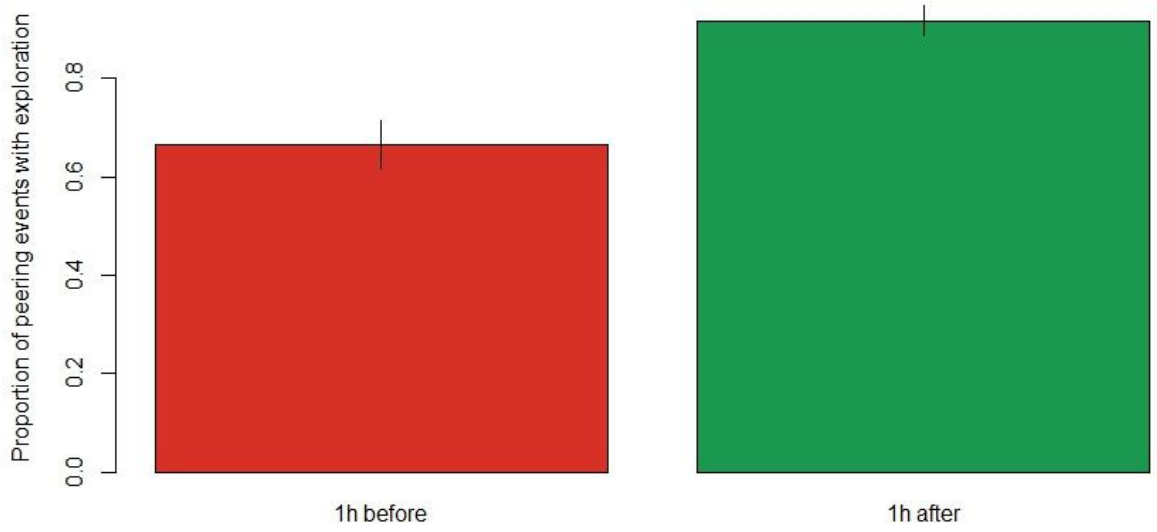


Figure 26: Peering with exploration for each juvenile. The proportion of juvenile peering events with exploration within 1h before and 1h after the peering event. The means and error bars are based on seven individuals with more than five peering events.

Table 9: Effect on exploration. The effect of the variable 1h before vs. 1h after the peering event on the presence of exploration, analysed by GLMM with binomial family distribution with logit-link, for juveniles.

Effect	Effect Type	Estimate	Std. Error	z	P-value	N	95% CI
variable(after)	Fixed	0.95	0.37	2.56	**0.0104**	2	0.60 to 1.04
Individual	Random	-	-	-	-	10	0.29 to 0.98
Maternal Relatedness	Random	-	-	-	-	3	0.25 to 2.07

5.4.4 Juvenile peering by complexity

By the time of weaning, immatures were at about 60% of the feeding rate of their mother for high-level processing techniques, and by the time they become independent from their mother, they were around 80% (Schuppli et al., 2016a). So juveniles already had high food-processing competence. Therefore, we did not necessarily expect juveniles to preferentially peer at food items which required a high number of processing steps even if they do use peering for social learning. Indeed, the best model for the food peering rate of juveniles did not include the number of processing steps (Figure 27, Table10).

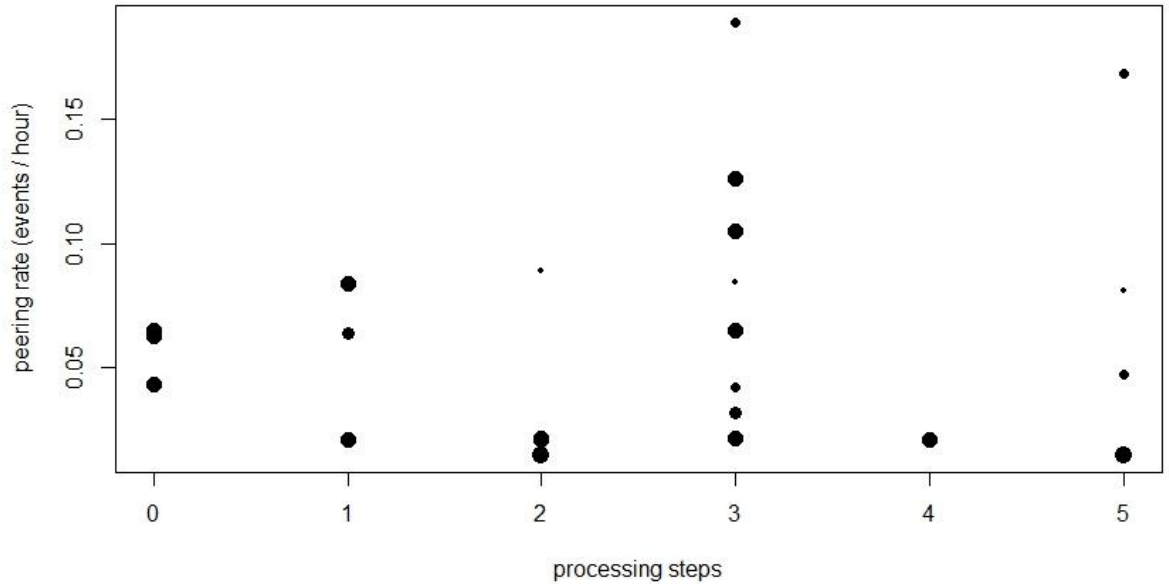


Figure 27: Peering at complexity. Peering rate by the number processing steps for every juvenile with more than ten follow hours.

Table 10: Effect on food peering rate. The effects of food complexity (processing steps), on the peering rate of juveniles, analysed by GLMM with Poisson family distribution. The model selection is based on corrected AIC values (minimal model, delta AICc = 1.7 to the model including the number of processing steps).

Effect	Effect Type	Estimate	Std. Error	N	95% CI
Intercept	Fixed	-2.96	0.14	-	-3.42 to -2.52
Individual	Random	-	-	6	0.00 to 0.92

5.4.5 Juvenile peering by rarity

If peering was still a means to social learning after weaning, we expected juveniles to preferentially peer at rare food items. Under the null hypothesis, juveniles indiscriminately peered at what they saw. Following the same logic as with the infant peering, the null hypothesis would be reflected in a regression slope of 1 when modelling the peering frequency from the food frequency, or the log-transformed frequencies respectively. We found that within the food items that were peered at, the regression slope of the log-transformed peering frequency predicted by the log-transformed food frequency was far from 1 (Figure 28). In fact, the confidence interval was between 0.02 and 0.2 (Table 11).

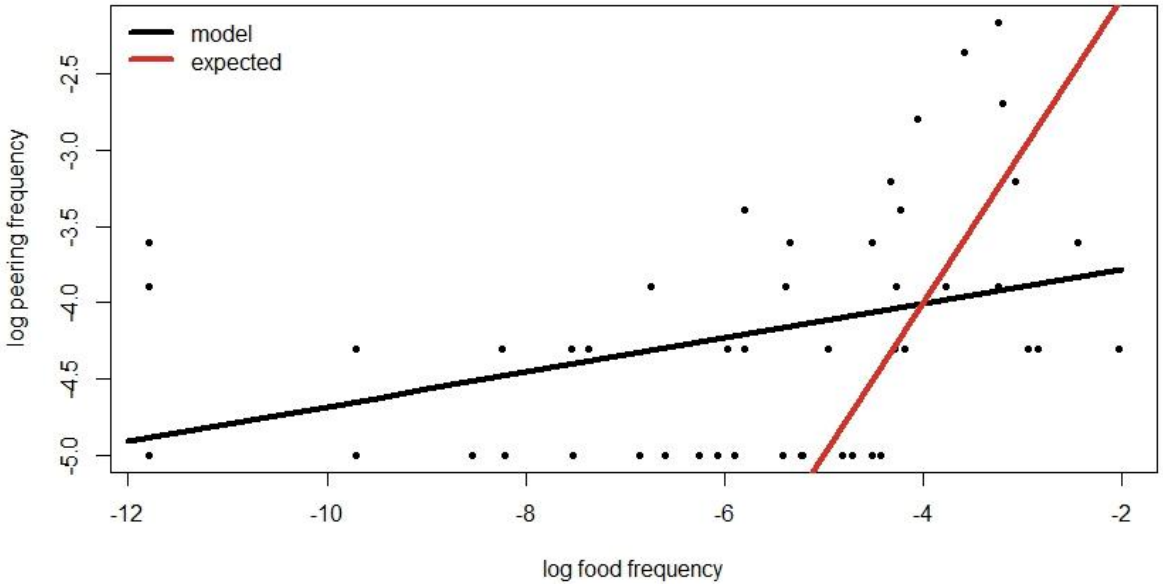


Figure 28: Peering frequency against food frequency. The log-transformed peering frequency of juveniles plotted against the log-transformed food frequency. The black line follows the prediction of the model prediction based on the data (see table 11), the red line reflects the expected slope (= 1) under the null-hypothesis.

Table 11: Effect on peering frequency. The effect of food frequency on the peering frequency, analysed by LMM. According to the nature of my prediction, I am comparing the estimate to an expected slope of 1, as opposed to 0. Printed in bold is the confidence interval to be compared to 1.

Effect	Effect Type	Estimate	Std. Error	N	95% CI
log(Frequency)	Fixed	0.11	0.04	cont.	**0.02 to 0.20**
Processing steps	Random	-	-	6	0.00 to 0.55

6. DISCUSSION

The aim of this study was to analyse how the social interest of Sumatran orang-utan immatures develops with age in the two sexes, and whether learning goes beyond infancy. To do so, I investigated peering contexts, peering targets, proportions, and rates of infants and juveniles, as well as their association patterns. Even though peering could potentially have functions other than social learning, it had already been shown that it can be means to social learning in infants (Schuppli et al. 2016b). With a new, larger data set, I looked for evidence of social learning, not only in infants, but also in juvenile orang-utans to investigate whether peering is still used for learning after infancy. Furthermore, I investigated role model choice and its potential sex differences during development.

I found that immature orang-utans were highly interested in watching others feed and build nests. I also found evidence that social interactions might have been preferentially peered at but overall social interactions were very rare. In infants, overall peering rates and rates of peering directed at feeding decreased with age, likely linked to increasing competence. In terms of peering proportions, however, the interest in feeding was high throughout infancy, suggesting that in relative terms, food peering remained a high priority. The interest in nesting peaked at around the age of 4 years for both peering proportion and peering rate. Nest peering coincides with nest practice behaviour, i.e. unsuccessful attempts to build nests or completion of nests without using them (Schuppli et al., 2016b). This supports the assumption that peering is a means to social learning by inducing individual

practice. The proportion of interest in social interactions, however, increased towards the end of infancy.

Opportunities for infants to peer at feeding and nesting were not expected to differ for young or old infants because they were vital and thus stable components of the mothers' daily activity budget. For social interactions, however, peering opportunities might change with the infant's age because the mother might be more or less engaged in certain social interactions with other individuals at different stages of her offspring's development. For example, one might expect the mother to engage in copulations more frequently shortly before weaning of the infant. This is especially relevant because most of the interactions peered at were copulations. Also, in general, as the infant grows older, it needs less investment from the mother, which leaves her with more time and energy to interact with other individuals. Therefore, it might be the case that the increasing proportion of peering directed at social interactions simply reflected an increased amount of opportunities for an infant to observe its mother interact with other individuals. However, our data showed that the amount of time the mother spent interacting with other individuals did not change with increasing age of the infant (see Appendix Figures A1 & A2).

In terms of role model choice, infants were mainly interested in their mother. Apart from her, they were interested in juveniles, adult females and unflanged males. This followed the prediction that naïve individuals mainly rely on vertical or oblique transmission, i.e. they learn from more senior and thus more skilled individuals. Compared to infants, not only adults are generally more skilled and knowledgeable but also juveniles (Schuppli et al., 2016a). Flanged males would fall into the same category of knowledgeable individuals, but they were the least social sex-age class outside the context of consortships (Galdikas, 1985a). While juveniles were found to be the most gregarious sex-age class in general (Galdikas, 1985a) especially with females with dependent offspring (Mitra-Setia et al., 2009) and thus probably tolerant in most cases, adult females, as well as unflanged males, might actually benefit from being tolerant specifically towards infants.

For adult females, tolerating other infants might give their own infants more opportunities for social play. All immature mammals play, and do so frequently. Its main functions seem to be organizational effects on the neural development for the promotion of lifelong motor skills (Byers & Walker, 1995). Adult Bornean female orang-utan with dependent offspring had higher ketone levels in the urine the day after being in association with another mother offspring pair, suggesting energy stress and therefore direct costs for the females (van Noordwijk, pers. com.). However, even during long periods of very low fruit availability, different mother offspring pairs still spend time together in order for the infants to play (de Bellefon, 2017). If infant play is so important for their own infant's development that mothers put up with increased energetic costs, mothers are expected to be tolerant towards infants of other mothers. This tolerance of other mothers provides infants with opportunities to peer at and thus learn from them. For unflanged males, there might also be benefits for being tolerant towards infants. Unflanged males preferentially associate with adult females (Galdikas, 1985b; Reukauf, 2019). By associating with parous females, unflanged males might get opportunities to learn from local residents, or copulations. It should, therefore, be in their interest to be tolerant towards infants in order to be tolerated by their mothers. This suggests that infants might get opportunities for peering as a by-product from such associations.

When investigating the development of infants' social interest in different types of role models, I found that in males, the interest in role models other than the mother steadily increased with age. This was in line with the framework of the first and second phases of optimal social learning during immaturity (Schuppli & van Schaik, 2017; Whiten & van de Waal, 2018). In females, however, my data suggests the interest in non-mother role models peaked at around the age of five years before decreasing. Due to the relatively small sample size for females, as an additional measure of social interest I further looked at the proportion of association time infants spent in close proximity to other individuals. I found that the infants' sex-specific peering pattern was reflected in their association pattern. However, infants' association patterns did not necessarily solely reflect their interests in

others. The times infants spend at close proximity to others might potentially be influenced by a fear of other individuals or, importantly, the mothers' behaviour. Newly-born infants are in almost constant body contact with their mother (van Noordwijk et al., 2009). For several years later, they get carried when the mother is moving through the canopy. Even after they stop being carried by the mother regularly, the mother often provides help travelling from tree to tree by pulling branches of an adjacent tree close or literally making a bridge between two trees with her body (van Noordwijk et al., 2009). Therefore, the infants are limited geographically by their mothers' travel decisions.

However, when analysing the distances of the mothers to other individuals, I found that the proportions mothers spent in close proximity to association members other than their infants did not reflect the general patterns found in the respective offspring. For mothers with male offspring, I found no evidence of an effect of infant age on the mothers' association patterns. For mothers with female offspring, I did find potential evidence for a relationship between infant age and mothers' association pattern, but it was a logarithmic increase with age which did not peak (see Appendix Figure A8). Because these patterns differ from the pattern of the respective infants, it is likely that the infants' proximity to other individuals is at least in part based on their own decisions and not be fully controlled by the mother.

These differences in the development of role model choice follow the general prediction derived from the sex-biased dispersal in orang-utans. Males leave their natal area once they reach sexual maturity. They were thus expected to show increasing interest in individuals other than their mother. Other individuals might have skills or knowledge which their mothers' do not have. Unflanged males are actually likely to possess skills or knowledge about what is edible from their natal area which the local population does not. To be as well prepared as possible for their own journey to unknown areas through dispersal, they were expected to be interested in individuals with might have such skills or knowledge. Because females stay in their natal area, in fact, females' home range partly overlap with their mothers' home range all their life (Ashbury et al., in prep.), one might at first think that it suffices to learn the mothers' skills. Solely relying on a single individual for the transmission of skills is risky, though. If only the occasional skill per generation is not transmitted, the skill set would steadily shrink in size over time. It is, therefore, necessary to learn skills from more than one individual at some point during development, given a species primarily relies on social rather than individual learning (van Schaik, 2002; van Schaik & Pradhan, 2003). Thus, also for female infants it makes sense to acquire skills and knowledge from individuals other than the mother but it might be less vital for them than for the males.

According to Schuppli et al. (2016b), if peering is a means to social learning, certain predictions are expected to be met. It is expected that infants have a preferential interest in complex and rare skills, as well as an increased likelihood to interact with the object of interest after a peering event compared to before. Orang-utan infants were found to follow these predictions (Schuppli et al., 2016b). I replicated these results in infants successfully with the current data set and slightly adjusted analyses that allowed for including all data. Moreover, I analysed whether the same predictions still hold in juveniles, in other words if juveniles still use peering as means to social learning or not. If learning is not restricted to infancy but expands beyond weaning, this might help explain the exceptionally long juvenile period of orang-utans. However, even if learning is not the main reason for delaying the age of first reproduction, this time might still be used to learn novel skills or additional knowledge.

For the juvenile data, I found that, similarly to infants, they mainly peered in the learning-intensive contexts feeding and nesting. Within the feeding context, I found a preference for rare food items and an increased interaction likelihood after the peering event, as evidence for social learning. In fact, individual practice increased not only after peering directed at the mother, but also most other types of role models. This suggests that juveniles trust a wide range of role models and learn from them. It has been suggested that only attention directed at trusted individuals can induce selective practice (Schuppli & van Schaik, in prep.). Comparing the degree of increase in the likelihood for

practice, peering at the mother results in a slightly larger increase than peering directed at juveniles or unflanged males. Considering the mother is probably still the most trusted individual, these results follow the general prediction that the more trusted the peering target, the more practice is induced.

Investigating potential preferences for complex feeding contexts, I found no evidence for an effect of complexity on peering rates. In fact, only four juvenile peering events were directed at insect tool use, and another three at Neesia tool use. This was not entirely unexpected, though. Juveniles have higher skill competence than infants, even in highly complex contexts such as tool use, eventually reaching adult level competence (Schuppli et al., 2016a). One might have expected peering to stop entirely once adult level feeding competence is reached, but does not seem to be the case. For investigate this in detail, more data on individual feeding competence would be necessary. With the current data, it seems that juveniles stayed attentive. This way, they might have learnt about the occasional novel skill or rare food item. Therefore, even though juveniles might already know how to process complex food items, they might not yet have encountered every rare food item. The rarity preference and increased interaction likelihood are evidence that peering in juveniles is, at least in part, a means to social learning, and not only tool to elicit tolerance as some might have suggested.

In juveniles, role model choice was not as clearly focussed on the mother as in infants. This result was expected, given that juveniles do not spend all their time together with their mother as infants do. However, whenever they are in association with their mother, juveniles do peer frequently at her. When investigating preferences for role models, different strategies have been proposed depending on the species. For example, tufted capuchin monkeys (*Sapajus* spp.) seem to prefer more proficient and dominant, older individuals (Coelho et al., 2015; Ottoni et al., 2005). Juvenile vervet monkeys (*Chlorocebus pygerythrus*) have been shown to focus their social attention mainly on kin (Grampp et al., 2019). Capuchin monkeys learn their feeding techniques from individuals with which they associate the most, suggesting strong links to social tolerance (Perry, 2011). Finally, Mörchen (2016) found that Bornean orang-utans peer at unflanged males more often as their age increases. They suggested that the unflanged males possess knowledge from their natal area which they might bring into new populations by dispersing and thus they might act as a vector for culture. In fact, we found that the juveniles at Suaq Balimbing peered at unflanged males, and also unrelated juveniles, more frequently than at the mother. When corrected for the time juveniles spent in association with other individuals, juveniles did preferentially peer at other juveniles, but not necessarily the unflanged males. Even if unflanged males might not be preferentially peered at, the proportion of peering directed at unflanged males and the increased likelihood of practice indicates that juveniles might learn from them. Juveniles, as well as unflanged males, are frequently found in association with others (Galdlikas, 1985a & 1985b, Mitra Setia et al., 2009), but unflanged males' associations are often driven by the presence of adult females (Galdikas, 1985b, Reukauf, 2019). The findings that juveniles are interested in unrelated peers indicates, that juveniles are not necessarily interested in related or highly proficient individuals, but potentially rather at tolerant individuals. From those, they might be able to learn knowledge about rare activities even if they probably would not be able to learn complex skills. Again, this reflects the finding that juveniles have a preference for rarity but not complexity.

Yet unclear is whether juveniles differentiate between related or familiar and unrelated or unfamiliar juveniles. Once sample sizes have increased, one could investigate whether practice increases equally after peering directed at related or unrelated individuals and whether juveniles preferentially associate with some individuals or if they spend time with whichever juvenile is available. Related individuals are likely to have spent time with each other during infancy because related adult females are more likely to associate than unrelated adult females (Singleton & van Schaik, 2002; Singleton et al., 2009). Through familiarity, related juveniles might be tolerant towards each other. Unrelated juveniles could potentially be more interesting, though. Because juveniles are no longer bound by their mothers' preferences, it is possible they specifically associate with individuals with which they had spent only little time as infants. Social tolerance is probably the most basic factor underlying role model choice in all species. While a certain degree of tolerance to proximity is definitely

required for social learning, the importance of social tolerance on role model choice still needs to be investigated in more detail. Attention biases such as preferences for older, dominant and/or skilled individuals or kin could potentially simply be a bias for tolerant individuals. More likely seems that the observed biases result from a combination of social tolerance as the prerequisite together with biases depending on the social system of the species, the demography of the population and competence of the individual.

All in all, my results confirmed previous findings, indicate that social learning in Sumatran orang-utans is not restricted to young immatures but extends beyond infancy, and gave first insights into potential differences in the development of social interest between the two sexes in orang-utan infants. While females and males did not seem to differ in strength of their overall interest, their learning trajectories, however, seem to differ in terms of role model choice. This probably reflects future differences in the needs of the sexes arising from male-biased dispersal and maternal investment. It remains to be investigated how the different strategies relate to which specific skills or what kind of knowledge is learnt differently with these strategies. For example, older female infants might learn to find high quality food from their mothers in preparation for their future role as mothers. Males might learn to increase their efficiency as would be suggested from the different feeding budgets of the sexes during adulthood (van Schaik et al., 2009b).

Minimal skill competence is required for reaching independence. In females, this needs to be sufficient to sustain raising offspring when they reach adulthood. According to Schuppli et al. (2016a), the age of weaning strongly depends on the skill competence on the immature, but that adult levels are reached before the age of first reproduction. Therefore, while reaching juvenility seems to depend on learning, reaching adulthood is primarily limited by energetic constraints. However, even if skill competence may not be the main limiting factor of reaching adulthood, learning still does play a role during the exceptionally long juvenility of orang-utans. The data of my thesis suggest, learning what to eat is not restricted to infancy but that juveniles still learn about rare food items. Similarly, in humans, we do not necessarily need to know everything before reaching adulthood, but our long juvenility does give us the opportunity to enlarge our skill sets. Yet unclear is how much effort goes into acquiring knowledge about where to find food, where not to go, or who (not) to associate with, and through which mechanisms they do so. While males clearly need to learn about their new physical and social environment after dispersal, females also need to have this information about their natal environment. While females might already learn much by simply being around their mothers, juvenile females do expand and move their home range slightly (Ashbury et al., in prep). One would, therefore, expect females also have to acquire knowledge accordingly.

In conclusion, I replicated previous findings and found evidence for social learning in orang-utan immatures mediated by the peering behaviour. In line with previous findings, I showed that infants heavily rely on social learning. Furthermore, I shed new light onto the role of non-mother role models. Infants preferentially peered at juveniles, adult females, and unflanged males, suggesting a potential bias for individuals which are more skilled than the infants' and tolerant towards them. Moreover, I found that, in infants, the sexes differed in the development of their social interest. While male infants became increasingly interested in individuals other than the mother with increasing age, females' interest seemed to increase at first but then decrease towards the age of weaning. I also found that juveniles still relied on peering to learn new skills implying that learning does go beyond infancy in orang-utans. Juveniles mostly learnt from their mother, other juveniles, and unflanged males. This suggests that the underlying basis for social learning might be first and foremost social tolerance, potentially overlaid with a preference for individuals likely to possess novel knowledge. Overall, the results of this study underline the importance of peering in the acquisition of skill repertoires in wild immature Sumatran orang-utans.

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8. REFERENCES

Agostini, I., Visalberghi, E., 2005. Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group of wild tufted capuchin monkeys (*Cebus nigritus*), Am. J. Primatol. 65. doi.org/10.1002/ajp.20120

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cockburn, A., Thornton, A., Sheldon, B.C., 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature 518, 538–541. doi:10.1038/nature13998

Arora, N., van Noordwijk, M.A., Ackermann, C., Willems, E.P., Nater, A., Greminger, M., Nietlisbach, P., Dunkel, L.P., Utami Atmoko, S.S., Joko Pamungkas, Dyah Perwitasari-Farajallah, van Schaik, C.P., Krützen, M. Parentage-based pedigree reconstruction reveals female matrilineal clusters and male-biased dispersal in non-gregarious Asian great apes, the Bornean orang-utans (*Pongo pygmaeus*). Molecular Ecology 21, pp. 3352–3362.

Ashbury, A.M., Willems, E.P., Utami Atmoko, S.S., van Schaik, C.P., van Noordwijk, M.A., in prep. Home range establishment and the mechanisms of philopatry among female Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan.

Bastian, M.L., Zweifel, N., Vogel, E.R., Wich, S.A., van Schaik, C.P., 2010. Diet traditions in wold orangutans. American Journal of Physical Anthropology 143, pp. 175–187.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., Matsuzawa, T., 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. Anim. Cogn. 6, 213–223. doi:10.1007/s10071-003-0183-x

Boyd, R., Richerson, P.J., 1996. Why culture is common, but cultural evolution is rare, in: Runciman, W.G., Smith, J.M., Dunbar, R.I.M. (Eds.), Evolution of Social Behaviour Patterns in Primates and Man, Proceedings of The British Academy, Vol. 88. Oxford University Press, New York, NY, US, pp. 77–93.

Bray, J., Emery Thompson, M., Muller, M.N., Wrangham, R.W., Machanda, Z.P., 2017. The development of feeding behavior in wild chimpanzees (*Pan troglodytes schweinfurthii*). Am. J. Phys. Anthropol. doi:10.1002/ajpa.23325

Byers, J.A., Walker, C., 1995. Refining the Motor Training Hypothesis for the Evolution of Play. The American Naturalist 146, pp. 25–40.

Cheney, D.L., Seyfarth, R.M., 1983. Nonrandom Dispersal in Free-Ranging Vervet Monkeys: Social and Genetic Consequences. The American Naturalist 122, pp. 392–412.

Chepko-Sade, B.D., Halpin, Z.T., 1987. Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics. The University of Chicago Press, Chicago and London

Cote, J., Clobert, J., 2010. Risky dispersal: avoiding kin competition despite uncertainty, Ecology 91, pp. 1485–1493.

de Bellefon, J.M., 2017. Consequences of forest fires on diet, behavior of ranging and social behavior of wild female Bornean orangutans. Master Thesis, University of Zurich, Department of Anthropology.

Dindo, M., Stoinski, T., Whiten, A., 2010. Observational learning in orangutan cultural transmission chains. Biol. Lett. rsbl20100637. doi:10.1098/rsbl.2010.0637

Doolan, S.P., Macdonald, D.W., 1996. Dispersal and extra-territorial prospecting by slender-tailed meerkats (Suricata suricatta) in the south-western Kalahari. Journal of Zoology 240, pp. 59–73.

Douadi, M.I., Gatti, S., Levrero, F., Duhamel, G., Bermejo, M., Vallet, D., Menard, N., Petit, E.J., 2007. Sex-biased dispersal in western lowland gorillas (*Gorilla gorilla gorilla*). Molecular Ecology 16, pp. 2247–2259

Fox, E.A., Sitompul, A.F., van Schaik, C.P., 1999. Intelligent tool use in wild Sumatran orangutans, in: Parker, S.T., Mitchell, R.W., Miles H.L. (Eds.), The mentalities of gorillas and orangutans, Cambridge University Press, Cambridge, UK, pp. 99–116.

Galdikas, B.M.F., 1985a. Orangutan sociality at Tanjung Puting. American Journal of Primatology 9, 101–119. doi.org/10.1002/ajp.1350090204

Galdikas, B.M.F., 1985b. Subadult male orangutan sociality and reproductive behaviour at Tanjung Puting. American Journal of Primatology 8, 87–99. doi.org/10.1002/ajp.1350090204

Gallois, S., Lubbers, M.J., Hewlett, B.S., Reyes-García, V., 2018. Social Networks and Knowledge Transmission Strategies among Baka Children, Southeastern Cameroon, Hum. Nat. 29, pp 442–463. doi.org/10.1007/s12110-018-9328-0

Grampp, M., Sueur, C., van der Waal, E., Botting, J., 2019. Social attention biases in juvenile wild vervet monkeys: implications for socialisation and social learning processes. Primates 60, pp. 261–275.

Gros, A., Hovestadt, T., Poethke, H.J., 2008. Evolution of sex-biased dispersal: The role of sex-specific dispersal costs, demographic stochasticity, and inbreeding, Ecological Modelling 219, pp. 226–233. doi.org/10.1016/j.ecolmodel.2008.08.014

Hewlett, B.S., Fouts, H.N., Boyette, A.H., Hewlett, B.L., 2011. Social learning among Congo Basin hunter-gatherers, Phil. Trans. R. Soc. B 366. doi.org/10.1098/rstb.2010.0373

Heyes, C., 2012. What's social about social learning? J. Comp. Psychol. Wash. DC 1983 126, 193–202. doi:10.1037/a0025180

Hoppitt, W., Laland, K.N., 2013. Social Learning. An Introduction to Mechanisms, Methods, and Models. Princeton University Press, Princeton.

Husson, S.J., Wich, S.A., Marshall, A.J., Dennis, R.D., Ancrenaz, M., Brassey, R., Gumal, M., Hearn, A.J., Meijaard, E., Simorangkir, T., Singleton, I., 2009. Orangutan distribution, density, abundance and impacts of disturbance, in: Orangutans - Geographic Variation of Behavioral Ecology and Conservation. Oxford University Press Inc., New York, pp. 77–96.

Imanishi K, 1952. The evolution of human nature (in Japanese). In: Imanishi K (ed) Ningen. Mainichi-shinbunsha, Tokyo, pp. 36–94

Isler, K., van Schaik, C.P., 2009. The Expensive Brain: A framework for explaining evolutionary changes in brain size. J. Hum. Evol., Paleoanthropology Meets Primatology 57, 392–400. doi:10.1016/j.jhevol.2009.04.009

Jaeggi, A.V., van Noordwijk, M.A., van Schaik, C.P., 2008. Begging for information: mother-offspring food sharing among wild Bornean Orangutans. Am. J. Primatol. 70, pp. 533–541.

Jaeggi, A.V., Dunkel, L.P., van Noordwijk, M.A., Wich, S.A., Sura, A.A.L., van Schaik, C.P., 2010. Social learning of diet and foraging skills by wild immature Bornean Orangutans: implications for culture. American Journal of Primatology 72, pp. 62–71.

Kummer, H., 1971. "Culture" and the Conceptual Frame of Biology, in: Primate Societies: Group Techniques of Ecological Adaptation. Transaction Publishers.

Laland, K.N., 2004. Social learning strategies. Anim. Learn. Behav. 32, 4–14. doi:10.3758/BF03196002

Lameira, A.R., Hardus, M.E., Nouwen, K.J.J.M., Topelberg, E., Delgado, R.A., Spruijt, B.M., Sterck, E.H.M., Knott, C.D., Wich, S.A., 2013. Population-Specific Use of the Same Tool-Assisted Alarm Call between Two Wild Orangutan Populations (*Pongo pygmaeus wurmbii*) Indicates Functional Arbitrariness. PLOS ONE 8, e69749. doi:10.1371/journal.pone.0069749

Lonsdorf, E.V., 2005. Sex differences in the development of termite-fishing skills in the wild chimpanzees, Pan troglodytes schweinfurthii, of Gombe National Park, Tanzania. Anim. Behav. 70, 673–683. doi:10.1016/j.anbehav.2004.12.014

Lonsdorf, E.V., 2017. Sex differences in nonhuman primate behavioural development. Journal of Neuroscience Research 95, pp. 213–221.

Lonsdorf, E.V., Anderson, K.A., Stanton, M.A., Shender, M., Heintz, M.R., Goodall, J., Murray, C.M., 2014. Boys will be boys: sex differences in wild infant chimpanzee social interactions. Animal Behaviour 88, pp. 79–83.

Lorenz, K.Z., 1958. The evolution of behaviour. Scientific American, Vol. 199, No. 6, pp. 67–82

Meredith, S.L., 2012. Identifying Proximate and Ultimate Causation in the Development of Primate Sex-Typed Social Behavior, in: Building Babies, DIPR 37, pp. 411–433.

Mitra Setia, T., Delgado, R.A., Atmoko, S.S.U., Singleton, I., van Schaik, C.P., 2009. Social organization and male-female relationships, in: Orangutans - Geographic Variation of Behavioral Ecology and Conservation. Oxford University Press Inc., New York, pp. 245–254.

Mörchen, J., 2016. Learning from immigrants: dispersing orangutan males as cultural vectors. Master Thesis, University of Zurich, Department of Anthropology.

Nietlisbach, P., Arora, N., Nater, A., Goossense, B., van Schaik, C.P., Krützen, M., 2012. Heavily male-biased long-distance dispersal of orang-utans (genus: *Pongo*), as revealed by Y-chromosomal and mitochondrial genetic markers. Molecular Ecology 21, pp. 3173–3186.

O'Mara, M.T., Hickey, C.M., 2014. The development of sex differences in ring-tailed lemur feeding ecology. Behavioural Ecology and Sociobiology 68, pp. 1273–1286.

Ottoni, E.B., de Resende, B.D., Izar, P., 2005. Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. Anim. Cogn. 8, 215–219.

Perry, S., 2011. Social traditions and social learning in capuchin monkeys (*Cebus*), Phil. Trans. R. Soc. B 366. http://doi.org/10.1098/rstb.2010.0317

Reukauf, J., 2019. Male affiliative relationships in Sumatran orang-utans: why do unflanged males form temporary associations? Master Thesis, University of Zurich, Department of Anthropology.

Ronce, O., 2007. How Does It Feel to Be Like a Rollong Stone? Ten Questions About Dispersal Evolution, Annu. Rev. Ecol. Evol. S. 38, pp. 231–253. doi.org/10.1146/annurev.ecolsys.38.091206.095611

Ronce, O., Grandon, S., Rousset, F., 2000. Kin Selection and Natal Dispersal in an Age-Structured Population, Theoretical Population Biology 58, pp. 143–159. doi.org/10.1006/tpbi.2000.1476

Ross, C., Jones, K.E., 2001. Socioecology and the evolution of primate reproductive rates, in: Comparative Primate Socioecology. Cambridge University Press, pp. 73–110.

Schuppli, C., van Schaik, C.P., in prep. Social learning among wild orang-utans: is it affective?

Schuppli, C., Forss, S.I.F., Meulman, E.J.M., Zweifel, N., Lee, K.C., Rukmana, E., Vogel, E.R., van Noordwijk, M.A., van Schaik, C.P., 2016a. Development of foraging skills in two orangutan populations: needing to learn or needing to grow? Frontiers in Zoology 13, 43.

Schuppli, C., Koops, K., van Schaik, C., 2017. Cultural Behavior, in: The International Encyclopedia of Primatology. John Wiley & Sons, Inc. doi:10.1002/9781119179313.wbprim0019

Schuppli, C., Meulman, E.J.M., Forss, S.I.F., Aprilinayati, F., van Noordwijk, M.A., van Schaik, C.P., 2016b. Observational social learning and socially induced practice of routine skills in immature wild orang-utans. Anim. Behav. 119, 87–98. doi:10.1016/j.anbehav.2016.06.014

Shettleworth, S.J., 2010. Cognition, Evolution, and Behaviour. Oxford University Press Inc., New York.

Singleton, I., van Schaik, C.P., 2002. The Social Organisation of a Population of Sumatran Orang-Utans. Folia Primatol. (Basel) 73, 1–20. doi:10.1159/000060415

Singleton, I., Knott, C.D., Morrogh-Bernard, H.C., Which, S.A., van Schaik, C.P., 2009. Ranging behavior of orangutan females and social organization, in: Orangutans - Geographic Variation in Behavioral Ecology and Conservation. Oxford University Press Inc., New York, pp. 205–213.

Skinner, B.F., 1948. Superstition' in the pigeon. Journal of Experimental Psychology, 38, 168-172.

Spiess, A.N., 2018. qpcR: Modelling and Analysis of Real-Time PCR Data. R package version 1.4-1.

Stoinski, T.S., Wrate, J.L., Ure, N., Whiten, A., 2001. Imitative learning by captive western lowland gorillas (Gorilla gorilla gorilla) in a simulated food-processing task. J. Comp. Psychol. Wash. DC 1983 115, 272–281.

Sugardjito, J., te Boekhorst, I.J.A., van Hooff, J.A.R.A.M., 1987. Ecological constraints on the grouping of wild orang-utans (Pongo pygmaeus) in the Gunung Leuser National Park, Sumatra, Indonesia. Int. J. Primatol. 8, 17–41. doi:10.1007/BF02737112

Utami Akmoto, S.S., van Hooff, J.A.R.A.M, 2004. Alternative male reproductive strategies: male bimaturism, in: Sexual selection in primates. Cambridge University Press, Cambridge

van de Waal, E., Borgeaud, C., Whiten, A., 2013. Potent Social Learning and Conformity Shape a Wild Primate's Foraging Decisions. Science 340, 483–485. doi:10.1126/science.1232769

van de Waal, E., Renevey, N., Favre, C.M., Bshary, R., 2010. Selective attention to philopatric models causes directed social learning in wild vervet monkeys. Proc. R. Soc. Lond. B Biol. Sci. 277, 2105–2111. doi:10.1098/rspb.2009.2260

van Noordwijk, M.A., 2012. From Maternal Investment to Lifetime Maternal Care, in: The Evolution of Primate Societies. The University of Chicago Press, Chicago and London pp. 221–342.
van Noordwijk, M.A., Hemelrijk, C.K., Herremans, L., Sterck, E.H.M., 1993. Spatial position and behavioral sex differences in juvenile long-tailed macaques, in: Pereira M, Fairbanks L (eds) Juvenile primates. University of Chicago Press, Chicago, pp. 77–85
van Noordwijk, M.A., Sauren, S.E.B., Nuzuar, Abulani, A., Morrogh-Bernard, H.C., Atmoko, S.S.U., van Schaik, C.P., 2009. Development of independence - Sumatran and Bornean orangutans compared, in: Orangutans - Geographic Variation in Behavioral Ecology and Conservation. Oxford University Press Inc., New York, pp. 189–204.
van Noordwijk, M.A., van Schaik, C.P., 2005. Development of ecological competence in Sumatran orangutans. Am. J. Phys. Anthropol. 127, 79–94. doi:10.1002/ajpa.10426
van Schaik, C.P., 2002. Fragility of Traditions: The Disturbance Hypothesis for the Loss of Local Traditions in Orangutans. International Journal of Primatology 23, pp. 527–538.
van Schaik, C.P., 2016a. Social Learning and Culture, in: The Primate Origins of Human Nature. John Wiley & Sons, Inc., Hoboken, New Jersey, pp. 41–58.
van Schaik, C.P., 2016b. The Evolution of Technology, in: The Primate Origins of Human Nature. John Wiley & Sons, Inc., Hoboken, New Jersey, pp. 131–140.
van Schaik, C.P., 2016c. Morality, in: The Primate Origins of Human Nature. John Wiley & Sons, Inc., Hoboken, New Jersey, pp. 351–362.
van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I., Suzuki, A., Utami, S.S., Merrill, M., 2003. Orangutan Cultures and the Evolution of Material Culture. Science 299, pp. 102–105. doi:10.1126/science.1078004
van Schaik, C.P., Fox, E.A., 1996. Manufacture and Use of Tools in Wild Sumatran Orangutans - Implications for Human Evolution. Naturwissenschaften 83, pp. 186–188.
van Schaik, C.P., Pradhan, G.R., 2003. A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. Journal of Human Evolution 44, pp. 645–664.
van Schaik, C.P., Marshall, A.J., Wich, S.A., 2009a. Geographic variation in orangutan behavior and biology, in: Geographic Variation in Behavioral Ecology and Conservation. Oxford University Press, New York, pp. 351–362.
van Schaik, C.P., van Noordwijk, M.A., Vogel, E.R., 2009b. Ecological sex differences in wild orangutans, in: Orangutans: Geographic Variation in Behavioural Ecology and Conservation. Oxford University Press, New York, pp. 255–268.
van Schaik, C.P., Graber, S., Schuppli, C., Burkart, J., 2017. The Ecology of Social Learning in Animals and its Link with Intelligence. The Spanish Journal of Psychology 19, pp. 1–12.
Whiten, A., 2012. Social learning, traditions and culture, in: The evolution of primate societies. The University of Chicago Press, Chicago and London
Whiten, A., Mesoudi, A., 2008. Establishing an experimental science of culture: animal social diffusion experiments. Philos. Trans. R. Soc. B Biol. Sci. 363, 3477–3488. doi:10.1098/rstb.2008.0134
Whiten, A., Spiteri, A., Horner, V., Bonnie, K.E., Lambeth, S.P., Schapiro, S.J., de Waal, F.B.M., 2007. Transmission of Multiple Traditions within and between Chimpanzee Groups. Curr. Biol. 17, 1038–1043. doi:10.1016/j.cub.2007.05.031
Wich, S.A., de Vries, H., Ancrenaz, M., Perkins, L., Shumaker, R.W., Suzuki, A., van Schaik, C.P., 2009. Orangutan life history variation, in: Orangutans - Geographic Variation in Behavioral Ecology and Conservation. Oxford University Press Inc., New York, pp. 65–76.
Wich, S.A., Krützen, M., Lameira, A.R., Nater, A., Arora, N., Bastian, M.L., Meulman, E., Morrogh-Bernard, H.C., Atmoko, S.S.U., Pamungkas, J., Perwitasari-Farajallah, D., Hardus, M.E., van Noordwijk, M.A., van Schaik, C.P., 2012. Call Cultures in Orang-Utans? PLOS ONE 7, e36180. doi:10.1371/journal.pone.0036180
Wrangham, R.W., Smuts, B.B., 1980. Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. Journal of Reproduction and Fertility, Supplement 28, pp. 13–31.

9. APPENDIX

9.1 Infants' interest in activities

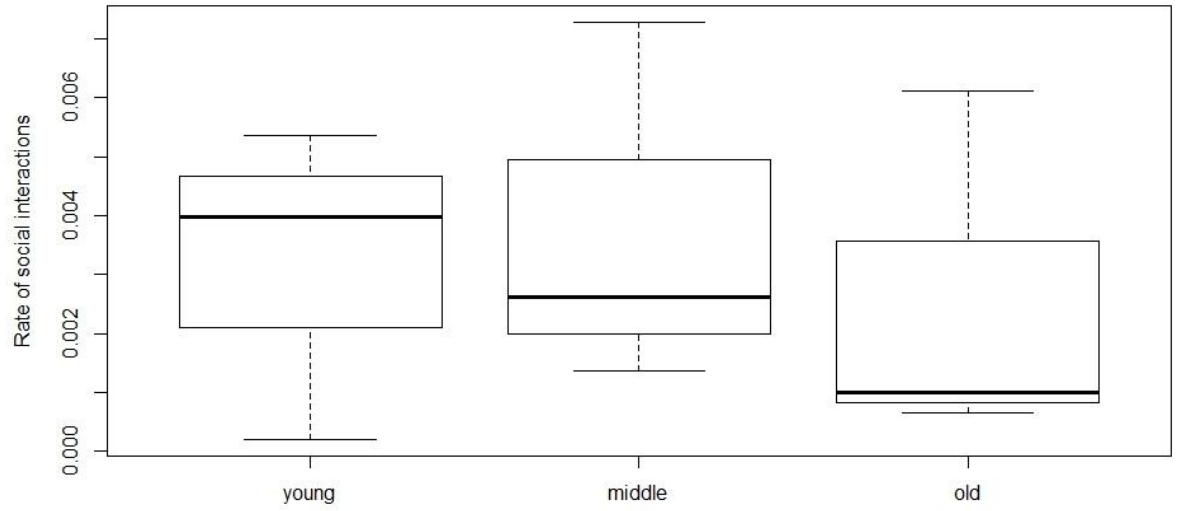

Figure A1: Mothers' rates of social interactions. The rates of social interactions in number of 2-min interval with social interactions in relation to the total number of 2-min interval of activity data of focal animal follows from the three most frequently followed mothers, Friska, Cissy, and Lisa. The rates were computed for follows when the respective dependent infant was young, i.e. younger than three years old, middle, i.e. between three and five and a half years, and old, i.e. between five and a half and eight years of age.

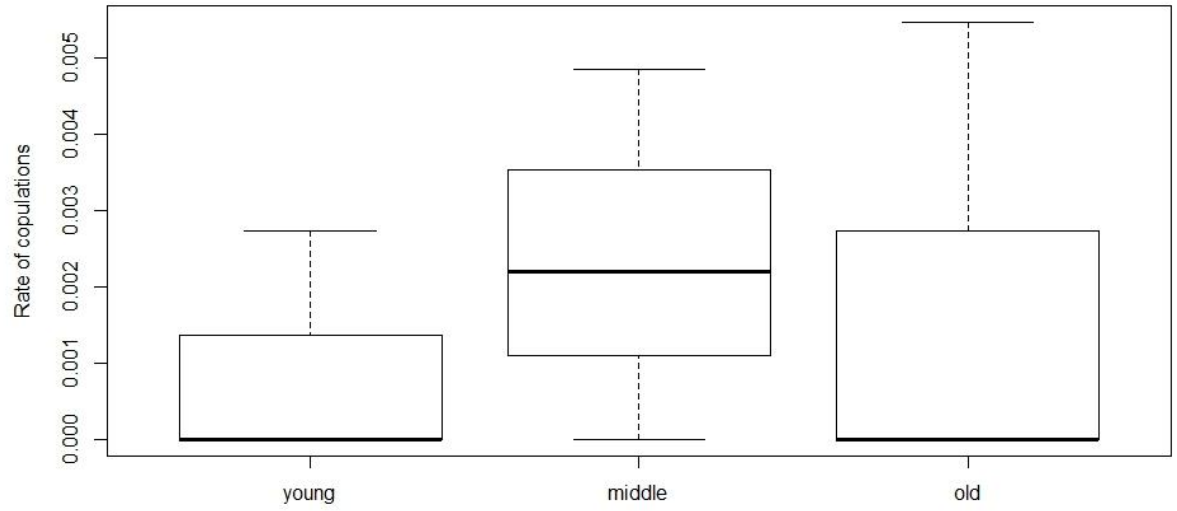

Figure A2: Mothers' rates of copuations. The rates of copulations in number of 2-min interval with copulations in relation to the total number of 2-min interval of activity data of focal animal follows from the three most frequently followed mothers, Friska, Cissy, and Lisa. The rates were computed for follows when the respective dependent infant was young, i.e. younger than three years old, middle, i.e. between three and five and a half years, and old, i.e. between five and a half and eight years of age.

9.2 Infants' interest in others

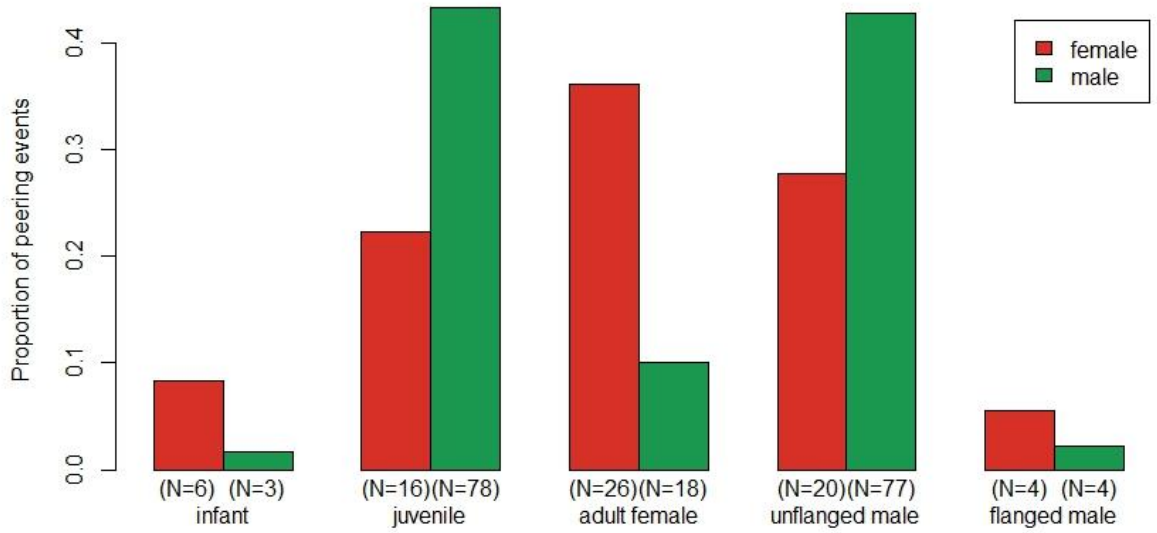

Figure A3: Peering at sex-age classes by sex. The proportion of infant peering events directed at a certain sex-age class of peering target separately for the two sexes of infants.

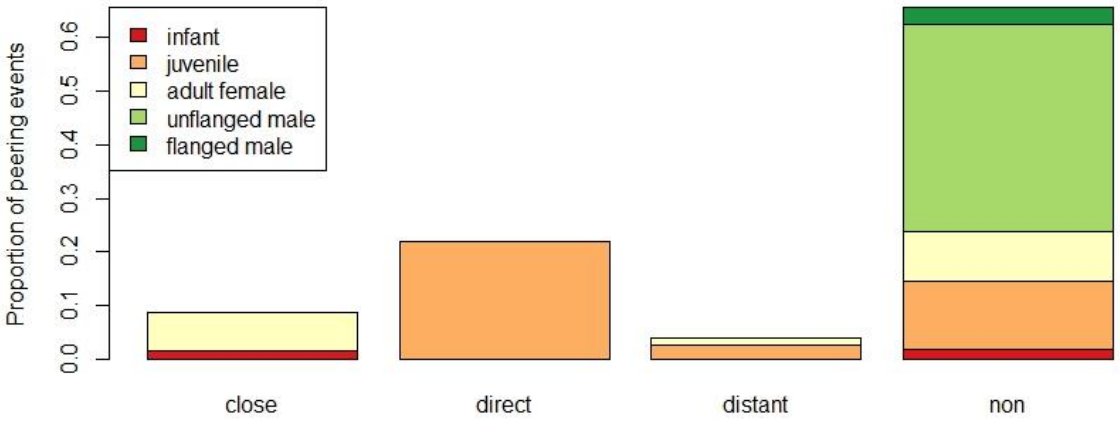

Figure A4: Peering at individuals of different maternal relatedness categories. The proportion of infant peering events directed individuals with certain maternal relatedness of peerer and peering target by sex-age class of peering target.

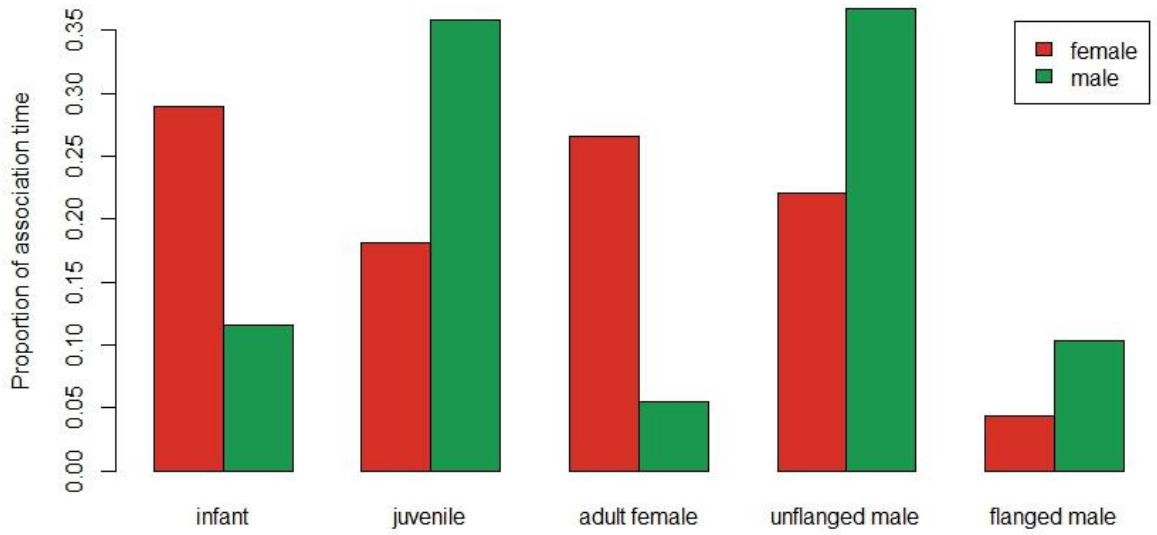

Figure A5: Proportion of association time infants spend with different role models by sex. The proportion of association time juveniles spent in association with a sex-age class per amount of time spent in contact (P.0.m), within 0-2m (P.2.m), 2-5m (P.5.m), 5-10m (P.10.m), and 10-50m (P.50.m).

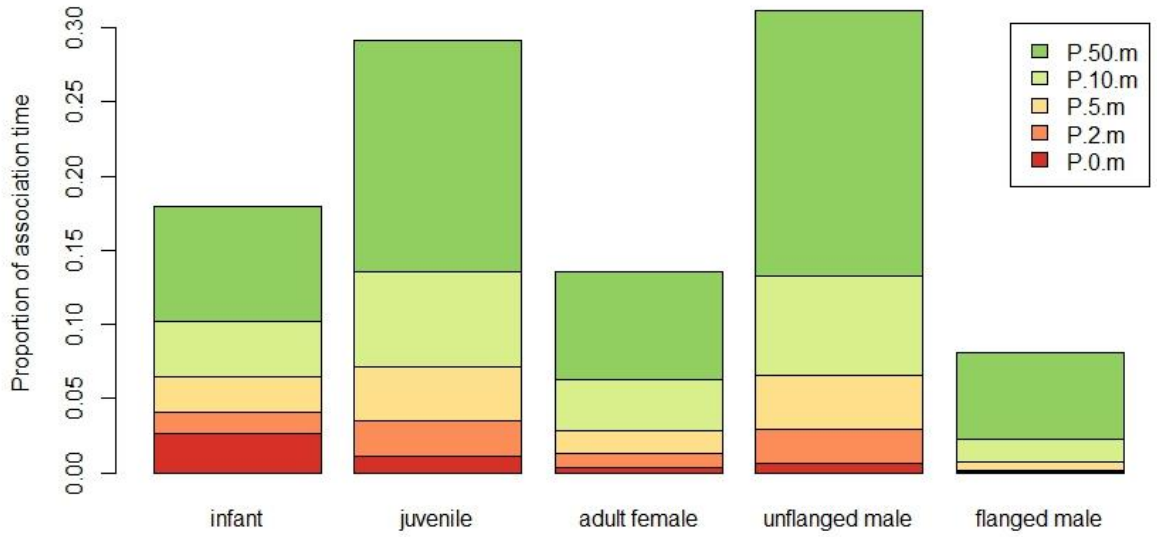

Figure A6: Proportion of association time infants spend with role models other than the mother. Proportion of association time infants spent in association with a sex-age class per amount of time spent in contact (P.0.m), within 0-2m (P.2.m), 2-5m (P.5.m), 5-10m (P.10.m), and 10-50m (P.50.m).

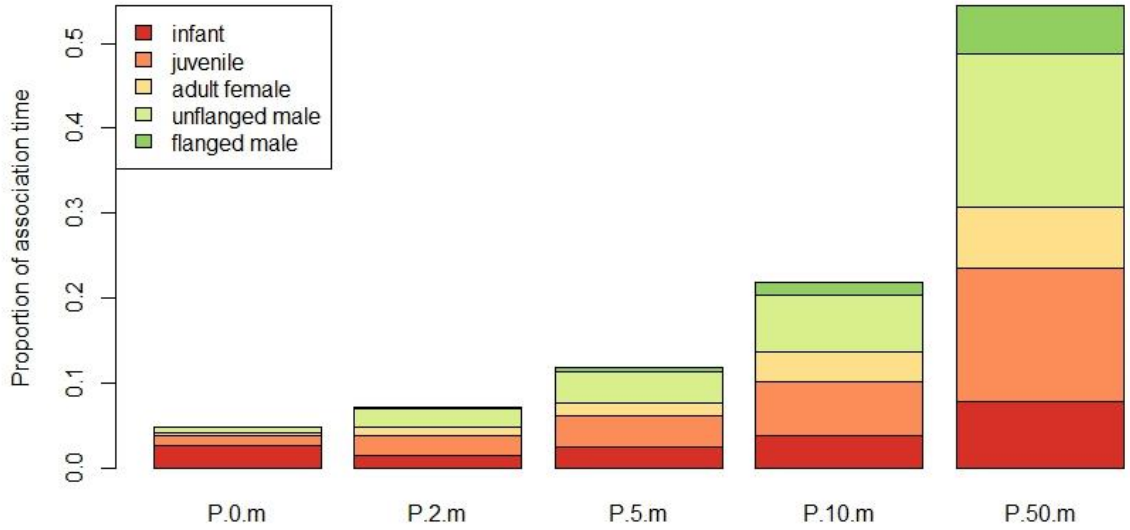

Figure A7: Proportion of association time spent in different proximity. Proportion of association time infants spent in contact (P.0.m), within 0-2m (P.2.m), 2-5m (P.5.m), 5-10m (P.10.m), and 10-50m (P.50.m), per sex-age class of the association, excluding mothers.

9.3 Mothers' distance to others

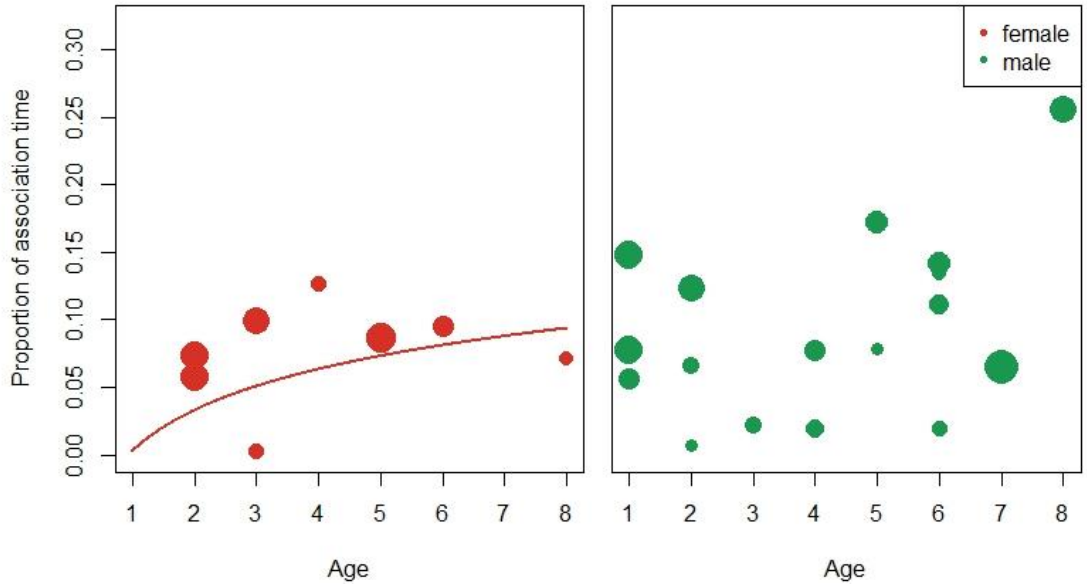

Figure A8: Associations of mothers by the age of the infant. Development of the proportion of total association time mothers spent within 2m of an association partner over the age of the respective infant, for mothers of female and male infants. The raw data is pooled into an averaged proportion over a one-year period for each mother with an infant between the age of one to eight years old for all with total association hours ≥ 55. The size of the points is proportional to the number of total association hours. The lines are drawn from the model predictions (see table A1).

Table A1: Effects on close proximity. The effects of infants' age on the proportion of total association hours their mothers spent within 2m of an association partner, analysed by LMM for mothers of female and male infants between age one and eight years old. The model selection is based on corrected AIC values.

Effect	Effect Type	Estimate	Std. Error	z	P-value	N	95% CI
Females: (delta AICc = 0.6)						8	
log(Age)	Fixed	0.04	0.01	4.72	**<0.0001**	cont.	0.02 to 0.07
Individual	Random	-	-	-	-	4	0.02 to 0.09
Males: minimal model (delta AICc = 0.9 to model including infant age)						18	
Intercept	Fixed	0.09	0.01	6.35	**<0.0001**	cont.	0.06 to 0.12
Individual	Random	-	-	-	-	7	0 to 0.05

9.4 Development of infant associations

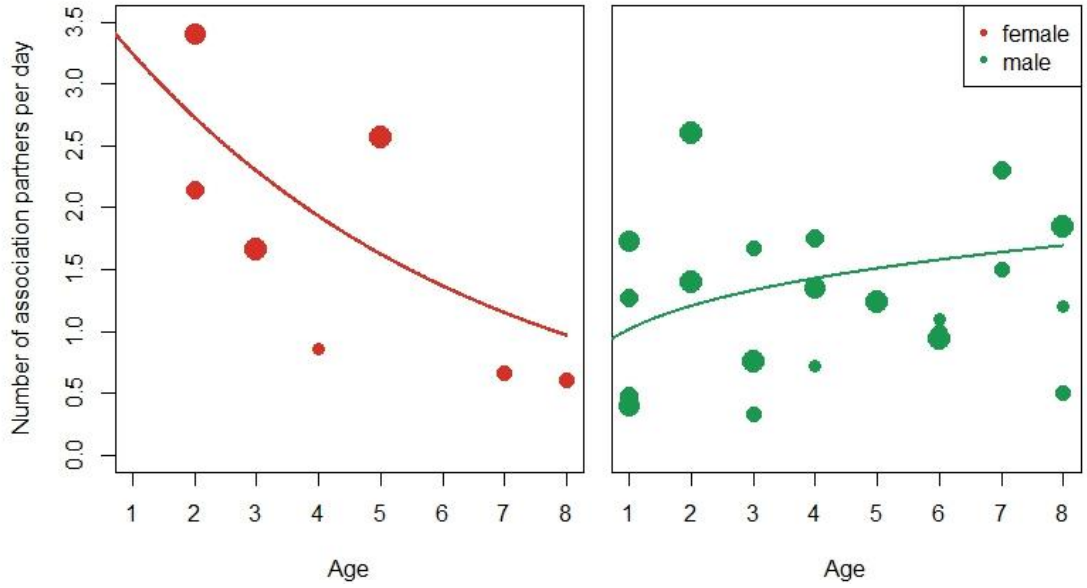

Figure A9: Number of association partners. Number of non-mother association partners per infant follow day. The raw data is pooled into an averaged proportion over a one-year period for each infant between the age of one to eight years old for all with follow days ≥ 5. The size of the points is proportional to the number of total peering events. The lines are drawn from the model predictions (see table A2).

Table A2: Effects on the number of association partners. The effects of age on the number of association partners, analysed by GLMM with Poisson distribution and the log-transformed number of follow days as offset, for female and male infants between age one and eight years old. The model selection is based on corrected AIC values.

Effect	Effect Type	Estimate	Std. Error	z	P-value	N	95% CI
Females: full model (delta AICc = 14.5 to next slimmer model)						7	
Age	Fixed	-0.17	0.04	-4.02	**<0.0001**	cont.	-0.26 to -0.09
Individual	Random	-	-	-	-	3	0 to 0.50
Males: full model (delta AICc = 7.1 to next slimmer model)						22	
log(Age)	Fixed	0.25	0.10	2.74	**0.0061**	cont.	0.08 to 0.44
Individual	Random	-	-	-	-	8	0.02 to 0.49

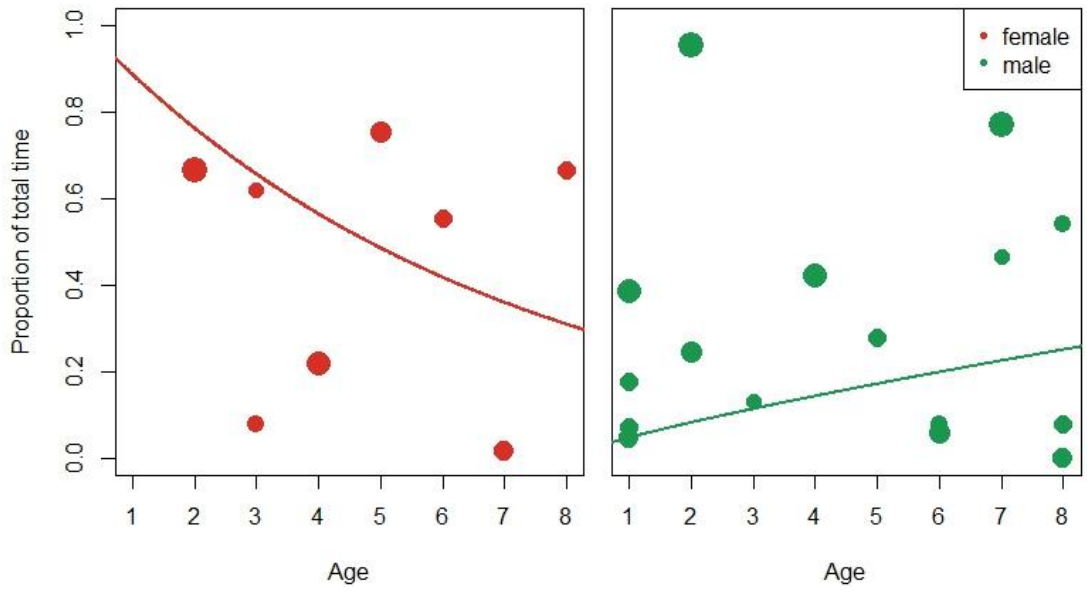

Figure A10: Association time per follow hour. Development of the proportion of non-mother association time per total infant follow time. The raw data is pooled into an averaged proportion over a one-year period for each infant between the age of one to eight years old for all with follow hours ≥ 30. The size of the points is proportional to the number of total peering events. The lines are drawn from the model predictions (see table A3).

Table A3: Effects on association time. The effects of age on the association time of infants, analysed by GLMM with Poisson distribution and the log-transformed total follow hours as offset, for female and male infants between age one and eight years old. The model selection is based on corrected AIC values.

Effect	Effect Type	Estimate	Std. Error	z	P-value	N	95% CI
Females: full model (delta AICc = 458.6 to next slimmer model)						7	
Age	Fixed	-0.15	0.01	-20.8	**<0.0001**	cont.	-0.17to -0.14
Individual	Random	-	-	-	-	3	0.30 to 1.70
Males: full model (delta AICc = 1019.5 to next slimmer model)						16	
log(Age)	Fixed	0.81	0.02	53.4	**<0.0001**	cont.	0.78 to 0.84
Individual	Random	-	-	-	-	8	1.59 to 5.31

9.5 Juvenile peering

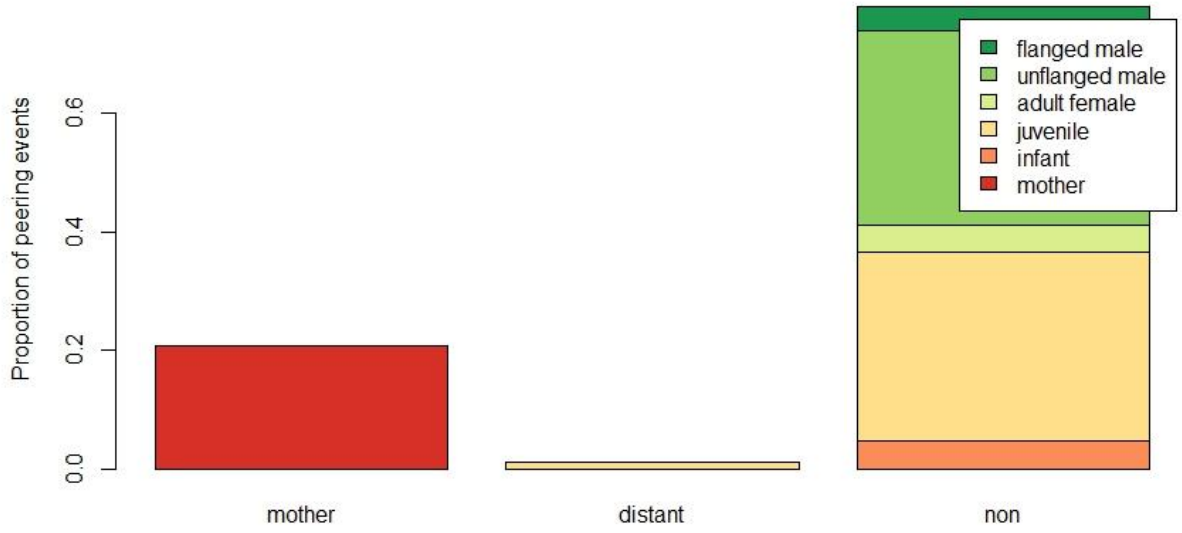

Figure A11: Peering at individuals of different maternal relatedness categories. The proportion of juvenile peering events directed individuals with certain maternal relatedness of peerer and peering target by sex-age class of peering target.

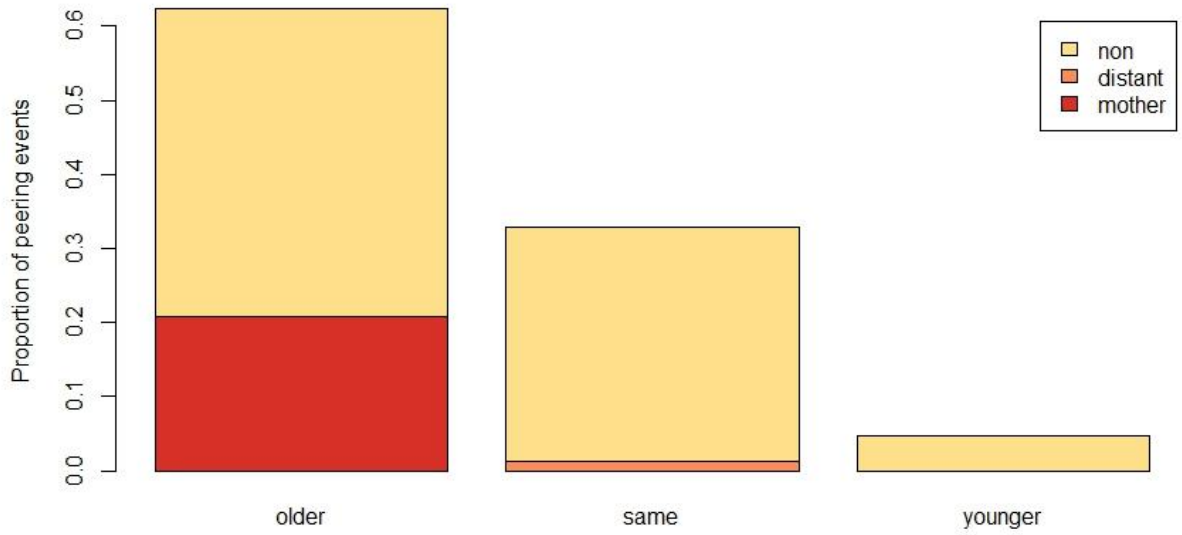

Figure A12: Peering at age categories. The proportion of juvenile peering events directed older (mother, adult females, unflanged males, or flanged males), similarly aged (juveniles), and younger (infants) individuals by maternal relatedness of peerer and peering target.

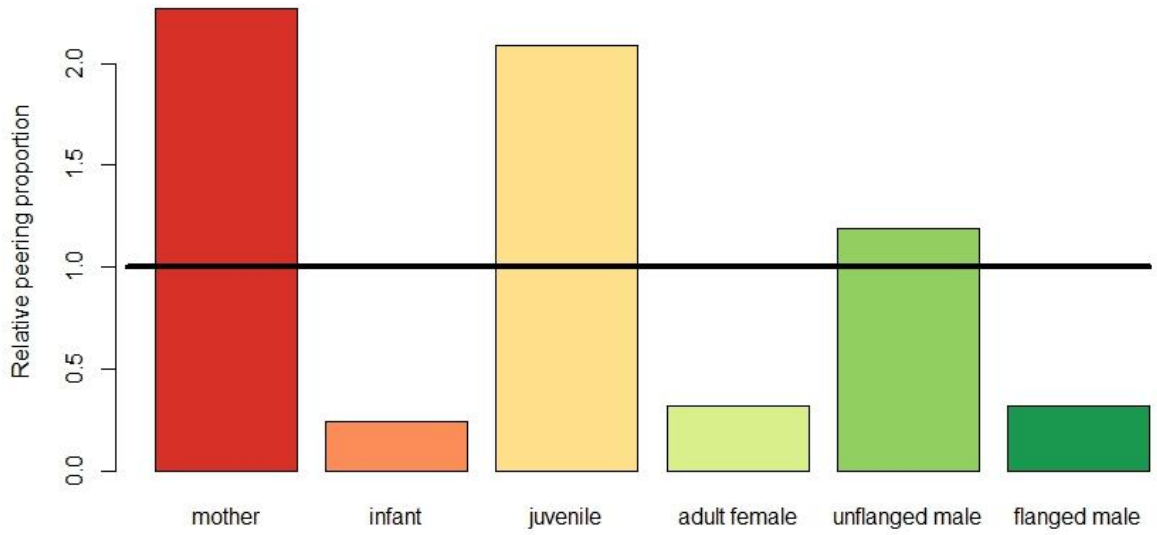

Figure A13: Juvenile peering at sex-age classes corrected for time in proximity. The proportion of peering corrected for the proportion of association time juveniles spent within 10m with the respective sex-age class. Values above one indicate a preference for this sex-age class.

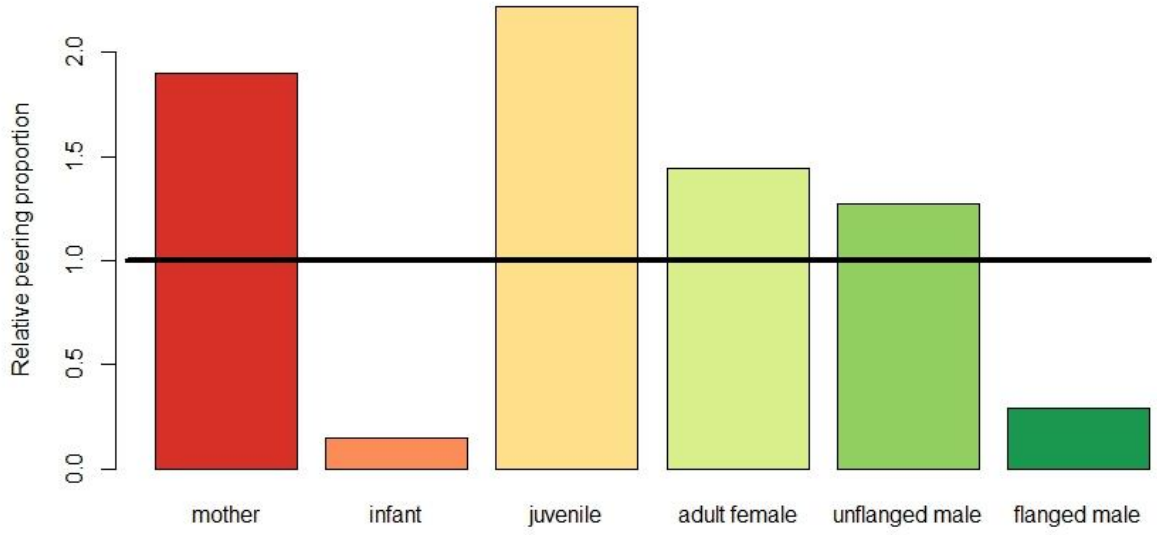

Figure A14: Juvenile peering at sex-age classes corrected for time in close proxmitiy. The proportion of peering corrected for the proportion of association time juveniles spent within 2m with the respective sex-age class. Values above one indicate a preference for this sex-age class.

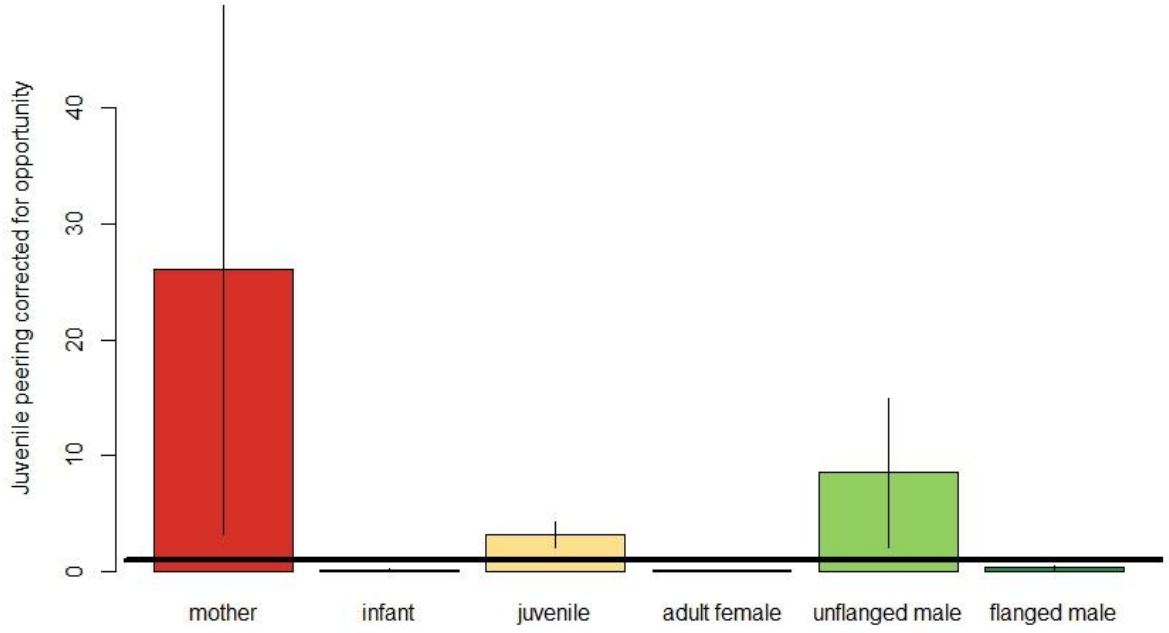

Figure A15: Peering at sex-age classes corrected for opportunity for each juvenile. The proportion of peering corrected for the proportion of time juveniles spent in association with the respective sex-age class. Values above one indicate a preference for this sex-age class. The means and errorbars are based on seven individuals with more than five peering events.

9.6 Juvenile associations

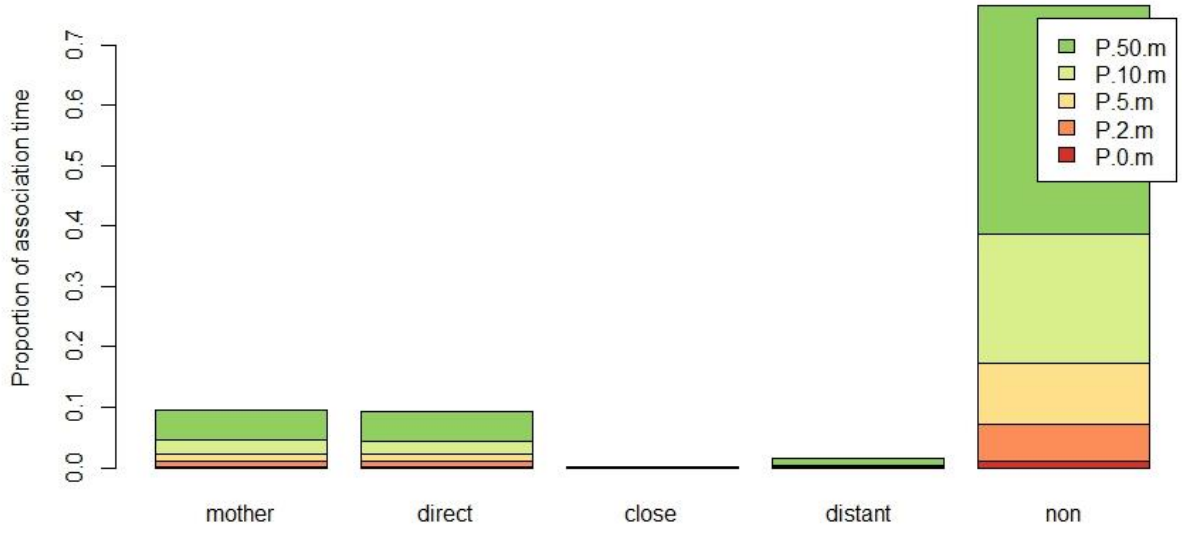

Figure A16: Proportion of association time with different sex-age classes. The proportion of association time juveniles spent in association with a sex-age class per amount of time spent in contact (P.0.m), within 0-2m (P.2.m), 2-5m (P.5.m), 5-10m (P.10.m), and 10-50m (P.50.m).

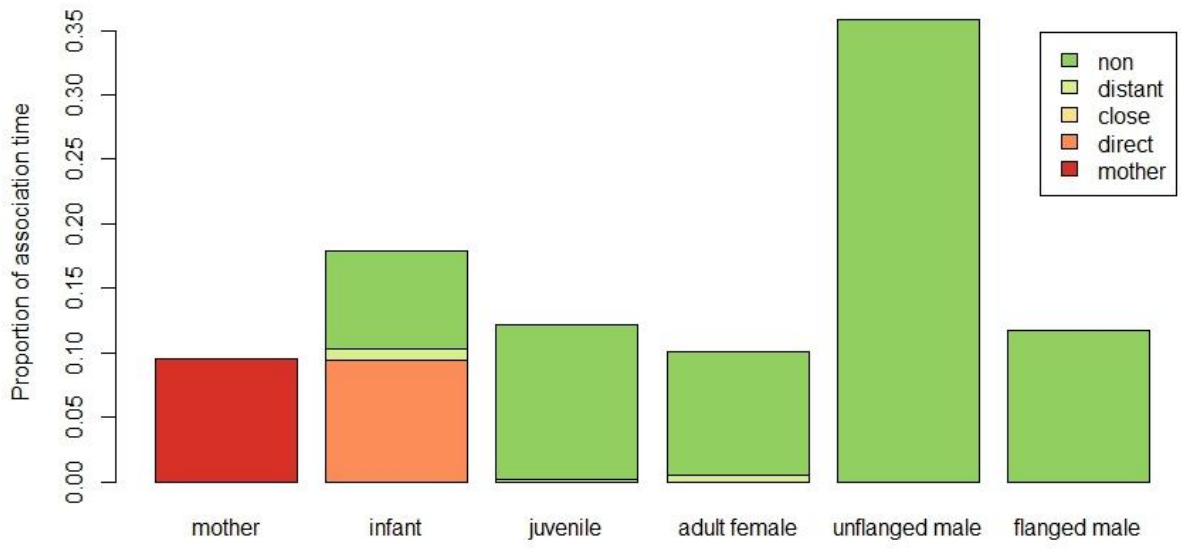

Figure A17: Proportion of association time with different sex-age classes. The proportion of association time juveniles spent in with different sex-age classes, by maternal relatedness of peerer and peering target.

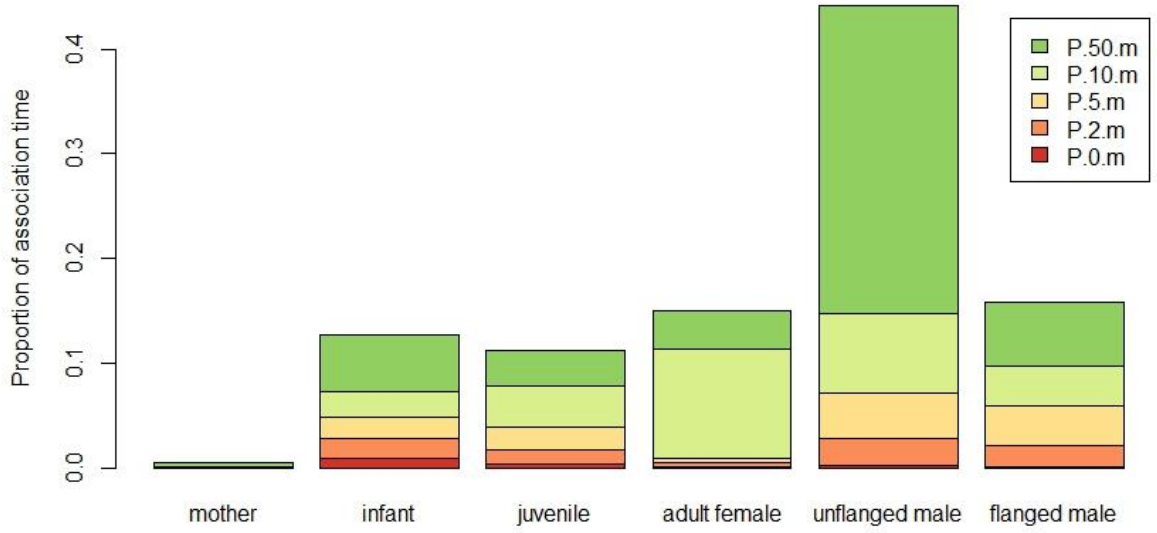

Figure A18: Proportion of association time independent juveniles spent with different role models. The proportion of association time juveniles aged eleven or older spent in association with a sex-age class per amount of time spent in contact (P.0.m), within 0-2m (P.2.m), 2-5m (P.5.m), 5-10m (P.10.m), and 10-50m (P.50.m).

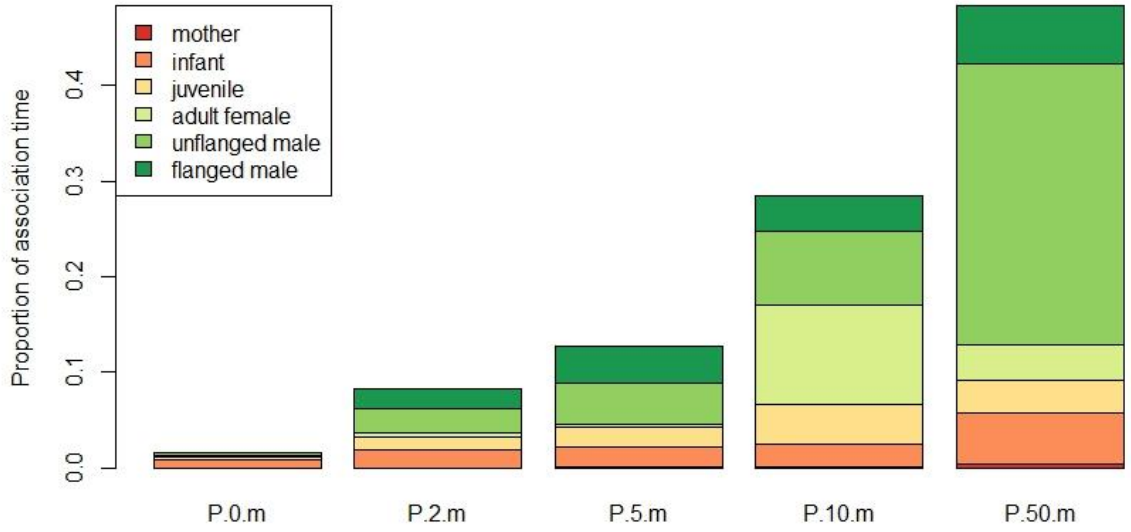

Figure A19: Proportion of association time independent juveniles spent in different proximity. Proportion of association time juveniles aged 11 or older spent in contact (P.0.m), within 0-2m (P.2.m), 2-5m (P.5.m), 5-10m (P.10.m), and 10-50m (P.50.m), per sex-age class of the association.

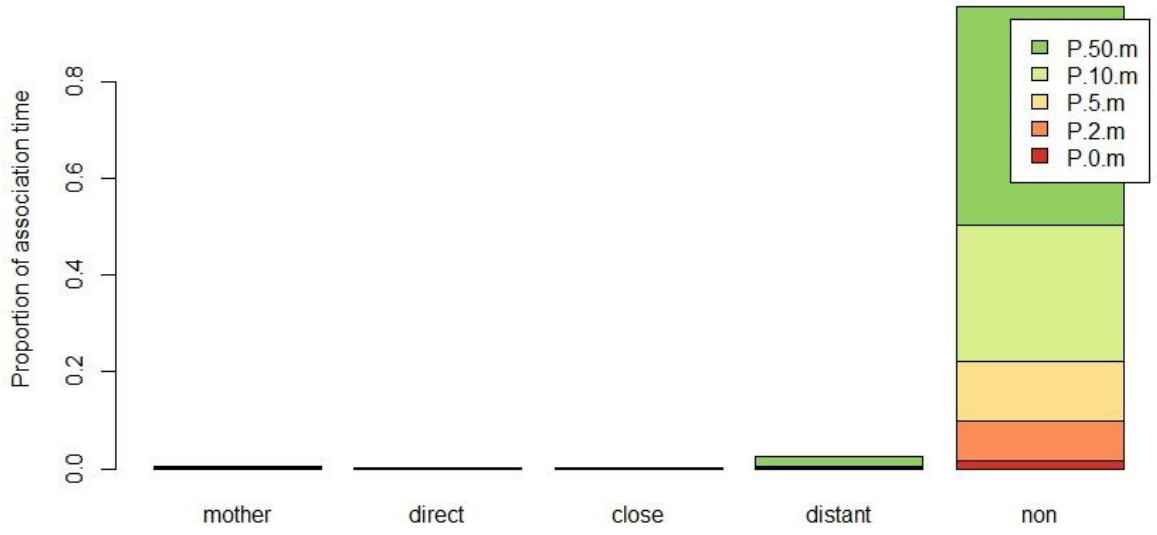

Figure A20: Proportion of association time with at individuals of different maternal relatedness categories. The proportion of juveniles aged 11 or older spent with individuals with certain maternal relatedness per amount of time spent in contact (P.0.m), within 0-2m (P.2.m), 2-5m (P.5.m), 5-10m (P.10.m), and 10-50m (P.50.m).

10. STATEMENT OF AUTHORSHIP

I declare that I have used no other sources and aids other than those indicated. All passages quoted from publications or paraphrased from these sources are indicated as such, i.e. cited and/or attributed. This thesis was not submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Place, Date Signature