How to be the new guy? Strategies of unflanged Sumatran orangutans to cope with their new environment after dispersal

Master thesis

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I. Abstract

It is becoming increasingly evident that throughout the animal kingdom, species rely on social learning in their skill acquisition. The most frequently studied context of social learning in nature is immatures' skill acquisition. However, also adult animals may need to socially learn in certain contexts. One of these contexts is dispersal. Dispersal is the movement from one's natal area to one's breeding site and occurs in all great ape species. Dispersing individuals are expected to show behavioural strategies to cope with their new physical and social environments, one of which could be social learning. Social learning after dispersal is expected in species that are capable of social learning and that disperse over long distances, such as the Sumatran orangutan. Orangutans show extensive geographic variation in behaviour – including variation in diet repertoires, feeding and nest building techniques – which is the product of ecological differences and cultural processes. As the dispersing sex, unflanged males must adjust to the physical and social environment of their new neighbourhoods, which likely differs substantially from their natal area. In my master thesis, I investigated (i) the sex-specific genetic patterns caused by dispersal, (ii) the social strategies that males use to establish themselves in their new neighbourhoods and (iii) the extent to which males learn from locally resident individuals by peering (attentive close range watching). I used faecal samples of 14 female and 31 male orangutan collected between 2007 and 2010 at Suaq Balimbing, South Aceh, Indonesia, and ten years of association data collected including 1,240 hrs of behavioural data and 270 peering events (close range watching of a conspecific's activity) by 20 unflanged males. To assess the sex-specific genetic structure I investigated a set of 18 paternally transmitted Y-chromosomal marker and examined the maternally transmitted HVR I Region of the mitochondrial DNA. I found 11 Y-chromosomal haplotypes and two mitochondrial haplotypes. Y-chromosomal diversity was detected to be higher than mitochondrial diversity. Unflanged males' associations were mostly tolerant and included many positive social interactions. They seemed to occupy positions of high connectivity in the population's social network. Furthermore, unflanged males' peering occurred mostly in learning intense contexts (such as feeding and social interactions) and was mostly directed towards locally resident females. There were also higher interaction rates with the same object as the peering target after a peering event and a positive correlation between peering rates and rarity of the observed activity. Unflanged males that had arrived only recently in the area peered more frequently than established males. In summary, I found a sex-specific genetical pattern indicative for male-biased dispersal. The relatively low mitochondrial diversity suggested a recent genetic bottleneck. Also, I found evidence that dispersing unflanged males adjust to the environment of their new neighbourhood by establishing themselves socially via frequent and highly tolerant associations. Further, they seem to use observational strategies to learn socially from resident females.

II. Statement of Authorship

I declare that I have used no other sources and aids than those listed in the references. All passages from publications or other 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 other university or institute of tertiary education.

Zurich, 16.10.2019 Olivia Wassmer

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1. Introduction

1.1 Social learning

For a long time, skill acquisition was believed to be mediated through innate mechanism (Lorenz, 1958) or through individual learning, including trial-and-error learning (Skinner, 1947). Since the start of studying learning-behaviour in animals, we came to realize that the ability for social learning is widely spread in the animal kingdom (Galef and Giraldeau, 2001; reviewd by Galef and Laland, 2005). Social learning is defined as "learning (...) that is influenced by observation of or interaction with, another individual or its products" (Heyes, 2012). In lab experiments many different taxa have been shown to be capable of social learning (Insects: Alem et al., 2016; Fishes: Brown and Laland, 2003; Reptiles & Amphibia: Ferrari et al., 2007; Mammals: Griffin, 2004).

However, it becomes more and more evident that many species are not just capable of social learning under laboratory conditions but also rely on social learning for habitual skill acquisition in their natural habitats. The transmission of complex learning behaviour was found to especially rely on social learning in nature (Fragaszy and Perry, 2008; Marshall-Pescini and Whiten, 2008; Vale et al., 2017). Recently, we came closer to realize that this might only be "the tip of the iceberg" (Schuppli and Schaik, 2019) and that for many species, even for basic subsistent skills, social learning might be the most prevalent form of skill acquisition (Shorland et al., 2019).

Heyes (2012) separated social learning in non-observational and observational learning. Non-observational learning involves local-, and stimulus enhancement described as the learning due to an increased interest of an individual in a specific place or object only by others spending time at this certain place or interacting with this certain object (Tomasello, 2009). Observational learning includes conditioning where an individual repeatedly observes and selectively practices an action, as well as imitation in which an individual copies the exact behaviours of others. In general, observational forms of social learning are considered to be cognitively more demanding (Schaik et al., 2016).

Especially primates seem to rely on observational learning. For example, observationally learnt tool use has been observed in several non-human primate species (*Pan troglodytes*: Marshall-Pescini and Whiten, 2008; *Cebus*: Perry, 2011; *Pongo abelii*: Schaik and Knott, 2001). Furthermore, there evidence for observational learning of subsistent skills such as diet and foraging behaviour (reviewed by Rapaport and Brown, 2008; *Pongo abelii* and *Pongo pygmaeus*: Schuppli et al., 2016a; M*acaca fuscata yakui* Tarnaud and Yamagiwa, 2008; *Gorilla gorilla:* Watts, 1985).

If social learning is the main form of subsistent skill acquisition of species in the wild, a whole new series of questions arise in terms of its content, role model choice and intensity. Because the underlying factors that lead to social learning change throughout life, timing is a central aspect of natural of social learning (reviewed by Whiten and van de Waal, 2018). Regarding content, there might be differences in what individuals learn socially. Individuals of different ages might have different requirements concerning their skill set, e.g. about which foods to eat or where do find them, how to build nests or which individuals to interact with. In addition, individuals' preferences for certain types of role models might change during life. Sex, age, or competence of the respective role model are likely to influence role choice. Also, the intensity of learning will change during life. We know that a period of particular intensity in social learning happens during the infant and the juvenile phase of non-human primates (Whiten and van de Waal, 2018). Individuals are then still naïve and need to learn the basics. However, also adult individuals might have to learn under certain conditions during which they are confronted with novelty (for example unknown physical and social environments), such as the time after dispersal.

1.2 Dispersal

Dispersal is defined as both the movement from a birth site to a breeding site and from one breeding site to another. By increasing the amount of total genetic diversity contained within rather than between populations (Wright, 1969), dispersal may have consequences for the level of genetic connectedness and diversity between populations in space and time (Ronce 2007; Saastamoinen et al. 2018). Furthermore, dispersal may also affect speciation (Barton, 2001), inbreeding depression (Roze and Rousset, 2005), cooperation and sociality (Galliard et al., 2005) as well as many life-history traits (Pen, 2000). However, in order to evolve, dispersal must provide the dispersing individuals with benefits.

One benefit of gene flow could be to avoid competition (Lambin et al., 2001) from either conspecifics or relatives. To escape from competition with conspecifics, an individual can improve indirect and direct fitness by exploiting new food sources and finding new mates. This favours dispersal and leads to a net flow from individuals from a highly populated area to a less populated one (Hastings, 1983). Although dispersal might not always reduce the density of conspecifics, it does reduce relatedness. This does not provide the dispersing individual with any direct environmental benefits, but reduces competition with kin. By reducing competition with kin via dispersal, individuals increase the fitness of breeding parents or siblings in the natal area and, indirectly, their own inclusive fitness (Lambin et al., 2001; Taylor, 1988; Waser et al., 2013).

An alternative explanation for the evolution of dispersal is inbreeding avoidance. Inbreeding may have negative fitness consequences for the resulting offspring due to an increase in homozygosity (Charlesworth and Charlesworth, 1987). Especially in small populations, the effects of heterosis result in increased fitness of offspring born to parents originating from different populations when compared to offspring of parents from the same population. This phenomenon is also known as the outbreeding effect (reviewed by Wakchaure & Ganguly, 2015). Whereas kin competition tends to have a stabilizing effect in the sense that both sexes disperse at the same ratio – heterosis favours divergence in sex-specific dispersal rates. In a high-density population of white-footed mice, it has been shown that when the parents of one sex are removed, the dispersal of the opposite sex will be delayed (Gandon, 1999; Perrin and Mazalov, 2000). Greenwood (1980) has argued that the direction of the sex bias is a consequence of the type of mating system. In monogamous species, females tend to disperse more because the benefits of philopatry are higher for males. Conversely, male-biased dispersal is expected in polygynous mating systems, as seen in most mammals, because male reproductive success is limited by mating opportunities (Perrin and Mazalov, 2000). Therefore, males disperse in most mammalian species. However, Trochet et al. (2016) have proposed that sexual asymmetry in morphology and parental care might be the main determinant of the evolution of sex-biased dispersal across species and not mating systems, as proposed in Greenwood's hypothesis.

Although dispersal does provide the dispersing individual with benefits, it also comes at a major cost (Bonte et al., 2012; Kingma et al., 2017; Maag Nino et al., 2019; Nevoux et al., 2013, Overview in Table 1). Whereas energetic and time costs refer to investments that cannot be spent on other activities (e.g. eating or mating), risk costs entail the probability of dying or suffering injuries during dispersal all three costs are direct consequences of dispersal. Forfeiting benefits related to prior residence and familiarity result in indirect fitness costs and are commonly referred to as opportunity costs (Bonte et al., 2012).

Table 1: Costs of dispersal. *Definitions from Bonte et al. 2012.*

Type of cost	Definition
Energetic costs	Direct costs that arise due to metabolic energy invested in movements. This may also entail costs as a consequence of the development of certain features associated with dispersal, i.e. energetic investments in specific dispersal organs (wings) and tissue (muscles).
Time costs	Direct costs incurring by the time that is invested in dispersal and thus cannot be invested in foraging, mating or recuperating.
Risk costs	Direct costs due to mortality risk (e.g. because of increased rates of predation or colonization of unsuitable habitat) and risk of injuries in the form of deferred attrition costs by accumulated damage (e.g. wing wear or other physical harm) or physiological change.
Opportunity costs	Indirect costs, beard by individuals that gave up prior residence advantages and familiarity-related advantages when they dispersed. This might also come into effect by not having the benefit of local adaptation anymore.

The consequences of dispersal are a result of either locational dispersal, meaning leaving a accustomed home range, or social dispersal, meaning leaving familiar conspecifics (Isbell and Van Vuren, 1995). Genetical adaptations, but also cultural adaptations (i.e. skills and behaviour transmitted socially within and between generations, Boyd and Richerson 1985), provided the individual with advantages to the local environment of its natal area. In terms of location dispersal, differences in food abundance and availability between an individual's natal area and its new home range are likely to result in challenges to the dispersing individual. Especially individuals that disperse over long distances might lack certain skills and knowledge about what kind of foods there are in the area, where to find and how to eat them, as well as familiarity with hideout spots (Yoder, Marschall, and Swanson 2004; Galef and Giraldeau 2001; Russon 2003). In terms of social dispersal, the new environment may result in a loss of social status and dispersing individuals may be confronted with xenophobic behaviours by the resident individuals of their new population (O'Rian and Jarvis, 1997). Furthermore, by dispersing, individuals sacrifice the opportunity for cooperation with related individuals (reviewed by Lambin et al. 2001).

1.3. Social learning after dispersal

To counterbalance the aforementioned consequences of dispersal, social learning could be a powerful tool. Dispersing individuals can acquire knowledge about important foraging sites and shelter opportunities, as well as the local food spectrum possibly including food types that migrant individuals have not experienced yet, from locally resident individual. Resident individuals have spent all their lives in the area and resident adults are, therefore, presumably ecologically competent and bearer of local cultural knowledge.

Specific challenges of local environments may require local innovations, which, if they are transmitted from individual to individual, may likely show a geographical variation between populations or groups (Krützen et al., 2011). Hence, the need for social learning might be especially pronounced for species that live in challenging environments (Brockmann and Van Schaik, 2012), show complex feeding techniques (Van Noordwijk and Van Schaik, 2005) and have an extensive-, socially-learned diet repertoire (Russon et al. 2004).

Social learning after dispersal remains poorly studied (see Whiten and van de Waal for an overview of existing studies). In primates, a hand full of studies showed that individuals switch to behaviour to match the one of residents after dispersal: In vervet monkeys van de Waal et al. (2013) showed experimentally that adult males, which were trained to eat corn dyed a certain colour during their infancy, later on adopted the preference of their new group. This also happened even when this meant switching to another colour when they were free to decide from which colour to eat. Similar patterns have been observed in chimpanzees where females that transfer between communities with different nut-cracking techniques, have been found to switch to the local technique (Luncz et al., 2012).

Adjusting one's behaviour after dispersal to the behaviour of residents is particularly adaptive when it is uncertain what the optimal local foraging strategies are and if the behaviour of the local residents offers a good model. Another explanation for changing one's own behaviour to the behaviour of residents is when dispersing individuals seek social acceptance in their new social environment. Paukner et al. (2009) have found that capuchin monkeys show more affiliation towards humans who imitate them. However, it remains challenging to clearly distinguish between these two strategies. Nevertheless, both explanations show the presence of social learning in adulthood after dispersal.

1.4 Orangutan as a study species

Orangutans are arboreal great apes found on the island of Sumatra (Sumatran orangutan: *Pongo abelii;* Tapanuli orangutan: *Pongo tapanulisensis*) and Borneo *(*Bornean orangutan: *Pongo pygmaeus sp.*, Wich et al. 2009). If not otherwise stated, details on specific life history variables and association patterns, refer to *P.abelii*. Sumatran orangutans live in high densities (Husson et al., 2008) and are more gregarious than Bornean orangutans (van Schaik, 1999). The social tolerance in Sumatran orangutans provides individuals with many opportunities for social learning. In summary orangutans are a highly interesting species to study the effects of dispersal on social learning because they have extensive skill repertoires with a great variation in geographic variation (Krützen et al., 2011). Moreover, we know that most of these skills are learnt socially (Schuppli and Schaik, 2019). Lastly, the male-biased dispersal allows us to clearly distinguish between resident and migrant individuals.

Orangutans have a rich behavioural repertoire consisting of many complex behaviours (i.e. tool use in feeding context; van Schaik et al., 1996) and specialized nest building techniques (Prasetyo et al. 2009). They also show an extensive catalogue of subsistence skills. In some regions, they feed on over 250 different species of plants (pers. communication with Caroline Schuppli). There is extensive geographic variation in diet repertoires, behavioural ecology, social organization throughout orangutan populations (Russon et al., 2004; Van Schaik et al., 2009). Krützen et al. (2011) have shown that this geographic variation in behaviour is explained little by genetic differences, but more by environmental and cultural differences.

1.4.1 Social learning in orangutan

To acquire their extensive adult skill sets, immature orangutan rely heavily on social learning, where by most social learning happens during infancy and early juvenility (Jaeggi et al., 2010). Schuppli et al. (2016b) have found that immature orangutans learn their subsistence skills by peering at their mothers and, to a limited extent, other role models. Peering, defined as attentive close-range watching, happens in a variety of contexts and is followed by selective practice of the observed

behaviour. It has been shown that peering in the feeding context correlates positively with complexity and negatively with the frequency of the involved food item in the mother's diet (Figure 1), providing us with strong evidence for peering as a tool for social learning.

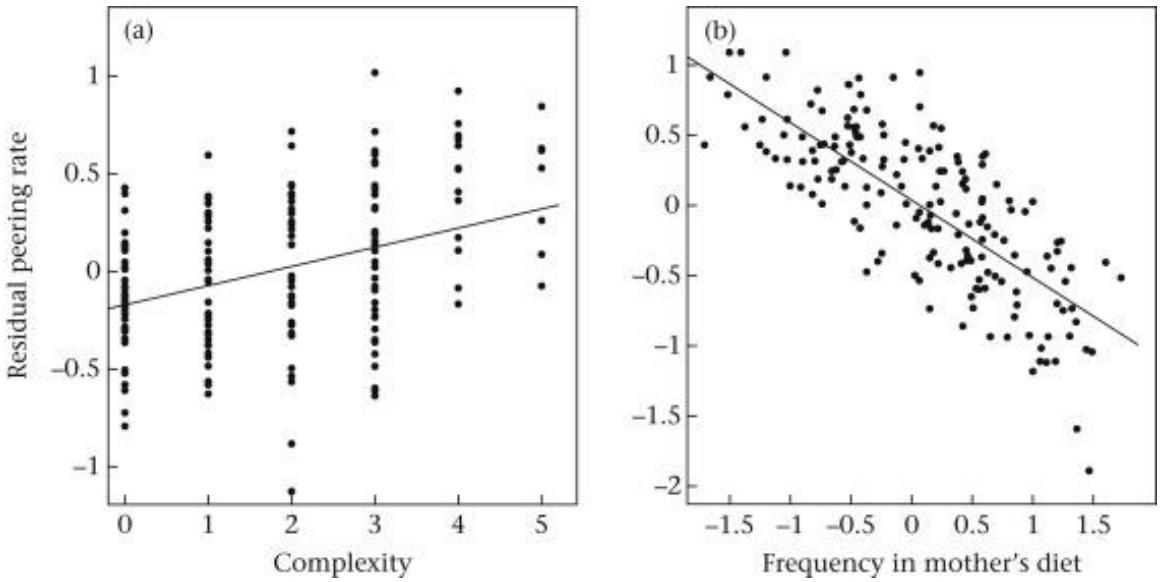


Figure 1*: Peering in relation to food complexity and frequency in the mother's diet:* *"(a) residual peering rates (corrected for frequency) versus complexity and (b) residual peering rates (corrected for complexity) versus frequency in the mother's diet (log transformed) for dependent Suaq immatures peering at their mothers in the feeding context. Residuals and the regression lines calculated based on them were used for illustrative purposes only" (Schuppli et al. 2016b)*

1.4.2 Dispersal in orangutan

A striking life-history characteristic of male orangutans is the presence of a bimaturism (Maggioncalda et al., 2002; Utami et al., 2009). Upon reaching sexual maturity, males first go through a so-called unflanged phase during which they are only marginally bigger than females (Banes et. al, 2015). Unflanged males can stay in this state for anywhere between a couple to more than 30 years (Utami et al., 2002; Utami-Atmoko, 2000). Only through a secondary growth spurt do males transition into the flanged phase by growing cheek pads, a throat sack and gain a substantial amount of weight and strength (Utami et al., 2002). The two male morphs cannot just be differentiated by physical appearance, but they also show differences in their social strategies. While flanged males live rather solitarily in their somewhat established home ranges (Mitani, 1985; Mitra Setia and Van Schaik, 2007), unflanged males are far more gregarious and cover larger distances (Utami et al., 2009; van Schaik et al., 2009). Upon reaching the unflanged male stadium, orangutan males leave their natal area to disperse into a new area.

At several long-term study sites behavioural observations have shown maturing females to settle near their mothers while males tend to be more in a transient state (van Schaik & van Hooff, 1996; Delgado & van Schaik, 2000; van Noordwijk et al., 2012). These findings indicated a male-biased dispersal, whereas genetic studies on autosomal markers found high mean relatedness in both adult sex classes in Borneo (Goossens et al. 2006) and a lower mean relatedness among males in Sumatra (Utami et al., 2002), suggesting no clear sex-biased dispersal pattern in Borneo and a male-biased dispersal pattern in Sumatra.

Results stayed ambiguous until Nietlisbach and colleagues (2012) study on the differentiation of sex-specific genetic markers across geographic distance provided evidence for strong male-biased dispersal in orangutans. This broad-scale study investigated samples from 9 locations. They found the genetic differentiation among populations to be twice as high in the maternal mitochondrial lineage compared to the paternal Y-chromosomal data, suggesting males to reduce this differentiation through dispersal.

1.4.3 Social learning after dispersal in orangutan

It is likely that unflanged males use social learning. Due to their long-distance dispersal (Nietlisbach et al., 2012) chances are high that the habitat of their neighbourhood differs from their natal region. While females, as the philopatric sex, will learn the local diet during their infancy, unflanged males will be confronted with a new environment after dispersal requiring them to learn. It remains unclear whether unflanged males use social learning to establish themselves in their new neighbourhood but the results on infants showed that orangutans are capable of social learning (Jaeggi et al., 2010; Schuppli et al., 2016b).

A prerequisite to being able to learn socially is to spend time in association with others. In other species, it has been observed that newly-arrived individuals who spend more time with resident individuals are in a better body condition (Pinter-Wollman et al., 2009). A potential benefit of being well connected is to able to learn from as many different individuals as possible. To allow for social learning through peering, associations should be of tolerant nature such as what is seen in orangutan mothers and their offspring (Jaeggi et al., 2008).

It is known that unflanged males peer (Mörchen, 2017) but the exact function of peering in unflanged males is yet unknown. It remains debated if unflanged males indeed use peering for social learning. One could argue that unflanged males have already learned all essential skills from their mothers during infancy (Schuppli et al., 2016b) and developed ecological competence by reaching the same feeding rates as their mothers (Schuppli et al., 2016a), and are able to build their own nest and range alone. An alternative function of peering would be one of a social function. By imitating infant-like behaviour, unflanged males could seek “permission” to approach to close proximity to females and use this as a way to increase their chances for mating.

To distinguish clearly between the social and the learning function of peering might never be fully possible because most peering probably does have both functions. However, to assess the presence of a social learning function of peering, we can test a series of predictions for different aspects of peering patters, such as role model choice, activity peered at, practising behaviour and the effect of rarity, complexity and time since arrival in the neighbourhood on peering rates. If these patterns are indicative of a social learning function of peering we can infer that peering is used as a tool for social learning in unflanged male orangutans.

1.4.4 Aims of my master thesis

In my master thesis, I focused on two parts: First, in a part based on genetic analyses, I looked into the genetic basis of orangutan dispersal following Nietlisbach and colleagues (2012). I investigated the sex-specific structure of one Sumatran orangutan population by assessing the y-chromosomal and mitochondrial genetic diversity. Second, in a part based on behavioural analyses, I examined the strategies of unflanged males to establish themselves in their new environment after dispersal. To do so, I assessed the social strategies that they might use by looking into association patterns and the

nature of these associations. To evaluate this, I investigated association rates, number of association partners and content of observed interactions. Additionally, I built a social network to examine the unflanged males' position in the local population. Furthermore, I examined whether peering has a social learning function. I did this by assessing unflanged males' role model choice, the activity peered at and the presence of practise behaviour. I also investigated the effects of the frequency of the peered at food items in the local diet and the processing complexity of these items on unflanged males' peering rates. Lastly, I tested whether the time passed since the arrival of an unflanged male in the area effects his peering rate. If peering has a learning function, recently-arrived males are expected to have higher peering rates than already established ones.

1.5 Predictions

My master thesis had two major parts. The first part focused on the genetic basis of dispersal at one orangutan population. The aim was to examine the findings from Nietlisbach et al. (2012) on male-biased dispersal in orangutans by investigating additional data. The second part targeted the investigation of how unflanged males establish themselves in the new neighbourhood after dispersal. I looked into potential social strategies and whether peering has a observational social learning function.

For the first part, focusing on the genetic basis of dispersal, I had the following hypotheses: Males migrate from neighbouring source populations into the investigated population. By doing so, they will bring the mitochondrial haplotypes from these source populations. Hence, **i) I expect a higher mitochondrial haplotypic diversity in male orangutans than in female orangutans at the investigated population.** If the dispersal system of orangutan is male-biased the catchment area for the investigated population is much larger for Y-chromosomal haplotypes than for mitochondrial haplotypes. Therefore, **ii) I expect the Y-chromosomal haplotypic diversity at the investigated population to be higher than the mitochondrial haplotypic diversity.**

For the second part, I investigated unflanged males' strategies after dispersal to establish themselves in their new neighbourhood. In the first section, I concentrate on the social strategies of unflanged males and in the second section, I focus on whether peering has a observational social learning function. My hypotheses are as follows:

To allow for social learning, **iii) I expect unflanged males to be social and well connected** and that **iv) their associations to be of a tolerant nature.** To investigate this, I examined association rates, number of association partners and content of observed interactions. Moreover, I evaluated unflanged males' position in the social network of the local population.

If unflanged males use peering as a tool to learn socially, **v) I expect them to preferentially choose adult females as their peering target**. As the philopatric sex, adult females have spent all their life in the local neighbourhood and, therefore, are the most environmentally competent potential targets. Since unflanged males are adults as well and have had time to learn from their mother throughout infancy, they are already competent in most contexts. Nevertheless, due to the potential ecological difference to their natal neighbourhood, **VI) I expect them to mostly peer in the feeding context.** If peering is a means for social learning, **VII) I expect an increase in practice behaviour after peering.** Because complex feeding techniques require more extensive learning and there are only few peering opportunities for rare food items, **VIII) I expect unflanged males' peering rates to increase with**

complexity of the observed feeding activity and decrease with feeding frequency in the local population, as seen in infants. Rare food items are expected to be preferentially peered at because there are fewer opportunities to learn and learning them might take long as a result. High complexity food, such as tool use items, might be preferentially peered at because they might also take longer to learn. Furthermore, recently arrived males lack more knowledge about the local environment than established males. Hence, **IX) I expect peering rates of unflanged males to be negatively correlated with the time that has passed since their arrival in the neighbourhood.**

2. Material and Methods

2.1 Study Site

The study site Suaq Balimbing (3°42´N, 97°26´E) is located in the primary peat swamp forest of the Gunung Leuser National Park in the province Aceh Selatan, Sumatra, Indonesia. Seventeen years of extensive behavioural observations on Sumatran orangutans have been conducted at this site from 1994 to 1999 and ongoing since 2007. Research activities have resulted in over 20'000 observation hours of more than 170 different followed focal animals. With seven individuals per square kilometre, Suaq Balimbing has the highest density of orangutan currently known (Husson et al. 2009, van Schaik et al. 2016). Compared to Tuanan in Borneo, there is a relatively high number of unflanged males present (Dunkel 2013), resulting in an interesting genetic setting since unflanged males are the dispersing sex and will bring haplotypes from other regions.

The proportion of time the orangutans at Suaq spend in association with conspecifics, as well as the level of social tolerance, is higher than in any other studied population (van Schaik et al., 2009). This is at least partly due to the comparatively high fruit availability in the forest (Husson et al., 2009; Sugardjito et al., 1987), which has lowered food competition and enabled the orangutans to be in closer proximity more often (Reukauf, 2019; Wich et al., 2011)). The frequent associations and increased tolerance may lead to more opportunities for social learning for the unflanged males because they are less often avoided by the local females, as seen in other populations (Scott et al., 2019). These generally high levels of social tolerance and subsequently increased opportunities for social learning make Suaq Balimbing an excellent place to study the strategies of unflanged males.

2.2 Study period

I collected behavioural data at Suaq Balimbing from December 2017 to June 2018, focusing on unflanged males. Due to a delay in the permit process, I was not able to collect genetic samples. Therefore, for the genetic analyses of this thesis, I used samples collected between 2007 and 2010 under the permit 09717/IV/SATS-LN/2010, 07279/IV/SATS-LN/2009, 00961/IV/SATS-LN/2007, 06968/IV/SATS-LN/2005.

For the behavioural portion of the study, I used all the available behavioural data collected from 2007 to August 2018. Whenever I was not able to include this full data set, I stated it in the respective sections.

2.3 Study subjects

For the different sex-age classes of focal individuals, I will use the following terms throughout the thesis: Infants (non-weaned, dependent immatures, aged 0 to ± 8 years), juveniles (weaned immatures, including nulliparous females), adult females (parous females), unflanged males (adult males lacking secondary sexual characteristics), and flanged males (adult males with fully-developed

secondary sexual characteristics; see Utami Atmoko & van Hooff, 2004). Details on which sex-age class was included in which analysis will be given in the respective sections.

2.4 Genetic basis of male-biased dispersal in orangutans

2.4.1. Sample collection

During extensive fieldwork in 2007-2010, samples were collected according to the protocol for "Collection and storage of non-invasive DNA samples from wild primate" (https://www.aim.uzh.ch/de/orangutannetwork/gsp.html). Faecal material was preserved either in alcohol, followed by silica gel desiccation, or RNAlater. Samples were stored in a dry place in the field and were transported to the lab as soon as possible, where samples were stored in a freezer (-8°C). Samples were transferred to Zurich under the Convention on International Trade in Endangered Species from Indonesia (permits 09717/IV/SATS-LN/2010, 07279/IV/SATS-LN/2009, 00961/IV/SATS-LN/2007, 06968/IV/SATS-LN/2005).

2.4.2 DNA Extraction

Most of the samples were already processed by various people of the evolutionary genetics group. However, I extracted the DNA from the faecal samples that had not been extracted previously by using the QIAamp DNA stool Mini Kit (Qiagen), according to the manufacturer's instructions, but applying the following modifications: I added 1.7ml ASL Buffer (instead of 1.6ml), followed by an addition of 0.5µl Proteinase K (20mg/ml) to each sample. The samples were then incubated overnight in an overhead rotator at 37°C. After adding 5µl of proteinase K per sample in the following morning, I continued incubating them for 1 hour to make sure all proteins were completely digested. I then increased the centrifugation step from 1min to 8min after adding the InhibitEX tablet to ensure a pellet was formed and all inhibitors were bound. All further steps were executed by the QIArube robotic workstation (Qiagen). Then I measured the DNA concentrations with the photo spectrometer NanDropR-100 (software v3.3). The extracts were refrigerated until future use.

2.4.3. Y-linked markers

2.4.3.1 Laboratory procedures and data acquisition for Y-haplotypes

To analyse the Y-chromosomal diversity, I used two multiplex reactions (designed by Nietlisbach 2009 in his master thesis, published in Nietlisbach et al., 2010) containing 16 male-specific markers (for details see Appendix Table 1) consisting of nine human-derived microsatellites, six single nucleotides (SNPs) and one insertion-deletion polymorphism (indel). All multiplex PCR reactions were performed in 96 well plates (ABGene super Plate 2400, Applied Biosystems) in a total volume of 8µl per reaction, consisting of 1µl sample, 0.8µl Multiplex master mix (Qiagen), 2.2 µl H_2O, and 0.8µl Primer Mix (for detail on Primer concentrations and amounts used, see Appendix Table 2 and 3). I used an ABI Verity Machine (Veriti^{TM} 96-well thermal cycler for DNA amplification, Applied Biosystems) with conditions presented in Appendix Table 4.

I diluted the 1µl of the PCR product 60 to 80 times with ddH2O, loading it into a 96 well plate (ABGene SuperPlate 2400) with 10µl of HiDi formamide and 0.07µl GenScan 500Liz standard (both Applied Biosystems). Through denaturation of 4 min at 95°C on ABI Veriti Machine. I obtained single-stranded DNA, which I then run on the 3730xl DNA Analyzer. Amplified alleles were analysed using

the GeneMapper software v5.0 (Applied Biosystems) by manually scoring peaks that were subjectively higher than background noise.

Samples of poor quality were run three to four times including one run with 2µl of template (instead of 1µl) and one run with the template diluted 1:6, either leading to an increase in concentration of DNA or a decreased concentration of potential inhibitors in the DNA extracts. Nevertheless, some loci repeatedly did not score well (i.e. DYS502, DYS587, DYS532, DYS630, DYS520). Hence, I increased the primer concentrations of those 1.5- to 2.0-fold.

For the loci that did not show discernible peaks, I carried out a singleplex PCR (for details see Appendix Table 5), using the HotStarTaq® polymerase (Qiagen®). Products were 1:30 diluted with sterile ddH_2O, scored on a 3730 DNA Analyzer (Applied Biosystems TM) and analysed with GeneMapper® Software 5 (Applied Biosystems TM), applying the same criteria as mentioned above. I defined a locus as scored when I could repeat a peak at least twice.

2.4.3.2 Y-chromosomal summary statistics

I statistically analysed 35 samples, including 17 samples previously sequenced by other team members, using the Add-In in GenAlEx (version 6.503, (Peakall and Smouse, 2012, Peakall et al., 2006). I assigned each individual a full Y-haplotype. Additionally, I determined a haplotype, only based on SNPs, henceforth referred to as the 'SNP-haploype'. This facilitated the comparison to the mitochondrial haplotypes, which are only based on SNPs. I calculated haplotype frequencies by dividing the number of individuals of a certain haplotype by the total number of analysed individuals. Following Nei and Tajima (1981), I calculated haplotype diversity (h) and number of effective alleles (N_e). Haplotype diversity is defined as $h = \frac{N}{N-1}(1 - \sum_i x_i^2)$ and Number of effective alleles as $N_e = (1 - \sum_i x_i^2)$. For both equations is x_i the haplotype frequency of each haplotype and N the sample size.

2.4.4. Laboratory procedures and data acquisition for mtDNA-haplotypes

To determine the mtDNA-haplotypes I analysed the hypervariable region1 (HVR1) by sequencing a 410bp long sequence, using primers DLF (5'-CCA GYC TTG TAA CCT GAA AAT GAA G-3'; Nater et al. 2011) and D5 (5'-TGT GCG GGA TAT TGA TTT CAC-3', Warren et al., 2001). PCR master mix setup and PCR conditions are described in Appendix Table 6 and Appendix Table 7. After visually examining the quality of the PCR product by doing gel electrophoresis, I ran a cycle sequencing PCR (details on master mix in Appendix Table 8 and conditions in Appendix Table 9) using the primer DLF. The products were cleaned according to the cycle sequencing clean up protocol (Appendix Protocol 2) and subsequently sequenced on a 3730 DNA Analyzer (Applied Biosystems™). I examined the resulting electropherograms on Sequence Analysis 5.3.1 (Applied Biosystems ™), added unambiguous missing peak calls and then aligned the sequences against the reference sequence of already existing haplotypes of the Suaq population in Ugene (version 1.32.0m Okonechnikov et al., 2012). According to this alignment, I assigned haplotypes to different individuals.

2.4.5 Haplotype networks

To visually assess relationships of haplotypes, I constructed a median-joining haplotype networks (Bandelt et al., 1999) using the software Network (version 5.0.1.1) and Network publisher (Version 2.1.2.5, fluxus-engineering.com). The epsilon value of the haplotype network represents a weighted genetic distance measure. For my network I used a value of 0. To control for different likelihood of

transversions and transitions, I weighted Transversions 3 times as much as Transitions (according to Fluxus Technology, 2015). Since the software Networks only generates networks for samples with three and more different haplotypes, I only assed the Y-chromosomal Haplotype network.

2.4.6 Study subjects

For the genetic analyses, I focused on adult females, unflanged males and flanged males (for details see Appendix Table 10). Whenever possible, I selected samples that had already been autosomally genotyped in previous studies (Nietlisbach et al., 2010; also: Rianti et al., 2015). Because this was only the case for few samples, I also included samples of individuals that had not been autosomally genotyped, but behavioural data suggest a constant presence in the research area. I excluded samples if I was not able to score more than 4 loci after two repetitions of the Y-chromosomal PCR-reactions. During the acquisition for mtDNA-haplotypes I excluded samples when PCR reactions had not produced a product after the second repetition.

I matched the assigned identities of the samples with the ones of the field data by comparing the photos of the dates, when the sample was collected, with the ID photos to ensure that I did not include individuals twice. However, there is still a slight chance that some of the individuals were included more than once since I did not have autosomal data on most of the included individuals.

2.5 Behavioural part

2.5.1 Data collection

2.5.1.1 Activity data

Whenever possible focal animals were followed from their morning nest to their evening nest. Data were collected according to the standardized methods of the department of Anthropology of the University of Zürich[1]. The behavioural data collection during these focal animal follows included instantaneous scan sampling of the focal animal at two minutes' intervals recoding the focal's activity, i.e. Social Activity, Feeding, Moving, Resting (definitions are listed in the Appendix Table 11), and ad libitum data to describe the details and contexts of the observed behaviours (for details Appendix Table 12 and Table 13). For each 'feeding event', defined as a scan during which the focal animal was recorded to be feeding, the food species and part of the plant eaten (i.e. fruit, flower, leaf, bark, pith or vegetation) were noted. Throughout this thesis I refer to the combination of species and plant part as the 'food item'.

2.5.1.2 Association data

To assess opportunities for social learning, I relied on the association data. Associations were defined as individuals present within a 50m radius of the focal individual. Dependent offspring were not counted as an association partner. The distance of each association member to the focal animal was assessed at two minute intervals and divided into the following classes: 0, <2, <5, <10 or <50m. Start and end time of an association were noted, as well as pauses (where the association partners were >50m apart). Based on these data, total association times for each dyad of focal animals were calculated. Furthermore, all observed social interactions during these associations were described in detail in the ad libitum data, including the direction of the interaction, content of the interaction and who initiated it and who ended it. Data on associations and distances were available from 2007

[1] described in detail on https://www.aim.uzh.ch/de/orangutannetwork/sfm.html

onwards for all sex-age classes of focal individuals. Data on social interactions were available for all follows during which at least one individual of the unflanged male sex-age class was present.

2.5.2 Study subjects

The main focus of my thesis was unflanged males and, depending on the analysis, additional adult classes were focused on. For each unflanged male, an approximate date of arrival at the Suaq Balimbing study area was determined via the date of the first photographic evidence of the individual recorded by the research team at Suaq Balimbing. I used two measures of observation time: "focal follow time," which refers to the sum of the hours that an individual was followed as a focal animal and "association time," which refers to the hours that an individual was in association with another focal individual, but was not subject of a focal follow itself. The calculated sum of focal follow time and the association time resulted in the "observation time" for an individual (see Appendix Table 14 and Appendix Figure 1 for details on individuals).

2.5.3. Measures of social learning

To investigate the tools unflanged male orangutans use to establish themselves in their new environment after dispersal I looked into social strategies which allow for non-observational forms of social learning and I investigated observational forms of social learning. Therefore, I split the analysis into two parts: In the first part, I focused on social strategies by assessing the sociality and positions in the populations' social network of unflanged males. These overall measures of associations and social tolerance were used as proxies for opportunities for non-observational forms of social learning. In the second part, I investigated the potential role of observational learning by looking at opportunities and pattern of measures of observational social learning.

2.5.3.1 Sociability

To assess the sociality of unflanged males I calculated the average number of hourly association partners by dividing the number of association partners per follow by the total follow duration. Furthermore, I computed association rates for each adult individual by dividing the time the individual had spent in association with each association partner, by the total duration of the follow. To avoid biases caused by proportionally high numbers of association partners respectively association rates caused by short follow durations, I only included nest to nest follows.

Having established how much time unflanged males spend with others, I also looked into the nature of the associations, i.e. what kind of social interactions they contained. The nature of associations likely affects learning opportunities and might vary greatly even if individuals spent similar amounts if time with each other. Associations can be of a positive or negative nature; whereby positive associations would enhance the opportunity for social learning. To assess the nature of social interactions I only had follows where unflanged males were focal animals available. I categorized the interactions during the associations of these follows as either positive or negative. Both categories were then subdivided according to their intensity into three states of expression: low, medium and high (details in Table 2).

Table 2: State of expression of social interactions. *Social interactions were either positive or negative and were subdivided into three levels of intensity (low, medium and high).*

State of expression	*Positive*	*negative*
Low	Social watch	Displacement
Medium	Feeding tolerance, coordinated moving	Non-sexual agonistic interactions, such as chasing, biting
High	Peering, begging, Co-Feeding	Sexual agonistic interactions

2.5.3.2. Social Networks

In order to construct a social network of the Suaq Balimbing population, I used all association data collected from 2013 to August 2018. Following Carne et al. 2013 I computed the dyadic association index (DAI): DAI= $\frac{AB}{A+B-AB}$. Whereas AB is defined as the time two individuals have spent together divided by the observation time of each (A + B) minus their overlap (AB). I only calculated DAIs for adult age sex-class dyads with a minimum of 20 hours of summed observation time.

There are different ways of investigating the position of certain individuals in a social network. I investigated Betweenness centrality, Closeness centrality, Eigen centrality (overview in Figure 2) and weighted degree. Betweenness centrality is the number of these shortest paths that pass through the vertex. Eigen Centrality is regarded as a ranking measure where every node gets assigned a relative score based on their connections to other well-connected nodes. Closeness centrality captures the average distance between a node and every other node in the network. A low closeness centrality means that an individual is directly connected, or just a few steps away, from most others in the network. Individuals in peripheral locations have high closeness scores, indicating the higher number of steps they need to take to connect to distant others in the network. Therefore, Closeness centrality was my measure of choice to evaluate the unflanged males' position in the network, since unflanged males are expected to be well connected.

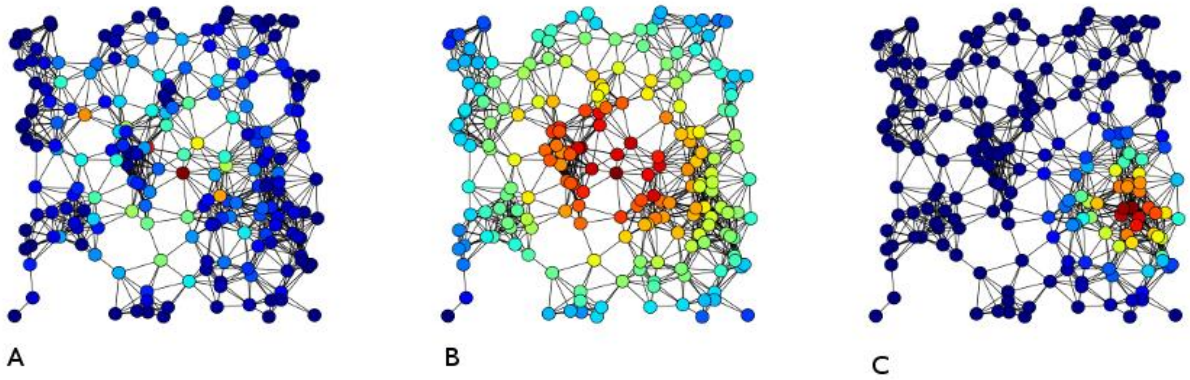


Figure 2: Examples of centrality. *A) Betweenness centrality. B) Closeness centrality. C) Eigen Centrality. Graphs by Tapiocozzo - Own work, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=39064835*

2.5.3.3 observational learning

As a measure of observational social learning, I used peering, which 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). Peering events were recorded ad libitum for focal individuals and association partners aiming at all occurrence records of the behaviour. For every peering event, details on the following parameters were noted: the name of the 'peerer' (i.e. the individual peering), and the 'peering target' (i.e. the peered at individuals), the activity performed by the peering target and in case of peering in the feeding context, the food item.

For some of my analysis, I had to correct for the opportunity each unflanged male had to observe a certain sex-age class. I calculated this opportunity as the proportion of time unflanged males spent with each sex-age class by dividing the daily association time unflanged males spent with each sex-age class by the absolute focal follow time of the respective follow, hereafter, this rate is referred to as the 'opportunity to observe a certain sex-age class' (for details see Appendix Table 15).

To correct for the opportunities unflanged males had to observe certain activities, I calculated the proportion of time the adult females at Suaq spent on feeding, nesting, social activities and others (i.e. moving, resting). For females' activity proportions can be calculated most reliable because most of the collected data were on females. Further, females are the resident individuals and therefore their activity proportions can be seen as an approximation of the overall frequency of an activity in the local population. I divided the time a certain activity was observed in the adult females by their follow time, henceforth referred to as 'activity proportion of resident individuals' (for details see Appendix Table 16).

In the context of food peering, to calculate the opportunity unflanged males had to observe certain food item being consumed, I assessed the 'frequency of a food item' in the diets of the resident individuals at Suaq by computing population wide frequencies of these food items based on 132'280 feeding events from over 4'400 hours of feeding data on 20 females (Ehmann, 2019).

To investigate unflanged males choice of peering targets, I calculated the proportion of peering events each unflanged male directed at each sex-age class and corrected for the 'opportunity to observe a certain sex-age class'. Also, I calculated the proportion of peering events directed at certain activities for each unflanged male and corrected for the 'activity proportion of resident individuals' to assess their preference for certain activities. I only included individuals that had a minimum of 10 peering events recorded to obtain meaningful proportions.

In order to examine practising behaviour, I compared the presence or absence of any forms of attempts to feed on the same food item as the peering target one hour before and one hour after the peering event. I included all individuals for which I had a least three peering events recorded. I then compared the proportion of peering events in which the peerer fed on the same item as the peering target before the peering event with the proportion of peering events in which the peerer fed on the same item as the peering target after.

Furthermore, I calculated peering rates as peering events per hour of observation time. To be able to investigate the effect of time since arrival on peering behaviour, I calculated these rates per unflanged male per year corrected for the respective opportunity in each analysis (consisting of 'food item frequencies,' 'activity proportion of resident individuals' and 'opportunity to observe a certain sex-age class').

Also, I split the unflanged males into two groups: 'recently-arrived males' up to their fourth year in the neighbourhood and 'established males' from their fourth year onwards. For these groups, I pooled all

peering events of all individuals and calculated proportions of peering events directed at each sex-age class corrected for the 'opportunity to observe a certain sex-age class' as well as proportions for peering events directed at certain activities corrected for 'activity proportion of resident individuals'.

2.5.4 Statistical Analysis

Analyses and plots were done in the R Programming language, R 3.4.1 (R development Core Team, 2011) using the base package for all bar and boxplots plots. To visualize the social network, I used the program Gephi (Bastian et al. 2009).

For comparison of means, I first checked for normal distribution using a Shapiro test. If the data were normally distributed, I either used a student's T-test or, in the case of multiple groups, an ANVOA. If the data were not normally distributed, I used the Kruskal-Wallis test from the stats package. For comparison of frequencies, I used a Chi-square test from the package survey (Lumley, 2004; Lumley, 2019). I calculated closeness centrality by using the closeness function of the Igraph package (Csardi and Nepusz, 2016) to the analyse the network data.

To assess whether peering is used as a tool for social learning, I investigated whether rarity and complexity of observed activities have an influence on peering behaviour of unflanged males. I used a linear mixed effects models (LMM) of the "lmer" function to assess the effect of rarity, represented here as the effect of food item frequencies, on the food peering rates. In a second step, I added complexity, measured as the number of steps, a food item needed before it can be ingested, as a fixed effect. As a means to evaluate the effect of time already spent in the population on peering rates, I utilised the rarity model and added 'time since arrival' in years as a fixed effect to the model. To visualize the effect of time since arrival, I plotted the residual peering rates (corrected for the rarity effect) over time since arrival.

3. Results

3.1 Genetic basis of male-biased dispersal

3.1.1 Y-Haplotypes

To investigate the Y-chromosomal haplotypic diversity in the population, I analysed a dataset of 27 males ('full haplotypes', 18 Y-linked loci consisting of six SNPs, one indel and eleven microsatellites). Additionally, I assessed Y-chromosomal haplotypic diversity based on SNP-Haplotypes only. There were eleven full Y-haplotypes and four different SNP-haplotypes (Table 3 & Table 4). The analysis of effective number of haplotypes (N_e) in the population resulted in a value of 6.58 and populations' haplotype diversity (h) was calculated to be 0.85. I repeated the analysis of these two measures for only SNP-haplotypes and found a N_e of 2.02 and h resulted in 0.50.

I found three SNP-loci and three microsatellite-loci to be polymorphic. Polymorphic microsatellite loci showed more different alleles per loci than polymorphic SNP-loci. More details on that can be found in Appendix Table 17 and Table 18.

For each full Y-haplotype, I calculated the frequency in the sampled population (Table 5 and Figure 3). The frequencies ranged from 0.037 to 0.222. There were only three frequent haplotypes – the other eight haplotypes only occurred one to two times.

Table 3: Overview of Haplotypes. *For SNP-Loci and the Indel-Locus, the bases (A, C, G or T) are reported. For Microsatellite-Loci, I reported the number of repetitions of DNA motifs. If the base or the number of repeats was the same as in the first haplotype, It is marked as a* ***"."****. Haplotype names h-o were assigned according to pre-existing haplotypes in the database. Haplotypes p-s were newly described.*

	SNPs						*InD*	*Microsatellites*										
Haplotype	DBY13	SMCY12_26	SMCY12_337	DYS630	DYIS577	SMCY14	DYS630	DYS502	DYS532	DYS645	Y6C2	DYS556	DYS577	DYS502	DYS510	DYS561	DYS587	DYS630
h	G	C	A	G	G	C	G	3	11	5	5	8	7	10	12	10	13	14
i	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15
k	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13	.	.	13
l	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13	.	.	15
m	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14	.	.	13
n	.	G	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	13
o	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11	9	.	13
p	.	.	.	.	C	.	.	.	.	.	.	.	.	.	11	.	.	13
q	.	.	.	.	C	.	.	.	.	.	.	.	.	.	11	11	.	.
r	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	11	.	.
s	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.		.	15

***Table 4: SNP-Haploypes**. SNP-Haplotype I and III were assigned according to pre-existing SNP-Haplotypes in the data base, IV was newly described.*

SNP_Haplot.	DBY13	SMCY12_26	SMCY12_337	DYS630	DYS577	SMCY14
I	G	C	A	G	C	C
II	.	.	.	.	G	.
III	.	G	.	.	G	.
IV	.	.	C	.	G	.

***Table 5: Y-Haplotype Frequencies.** Number of individuals divided by total number of individuals.*

Haplytype	Number of individuals	Frequency
H	6	0.222
I	6	0.222
K	1	0.037
L	1	0.037
M	2	0.074
N	1	0.037
O	2	0.074
P	1	0.037
Q	1	0.037
R	1	0.037
S	5	0.185

***Figure 3: Y-Haplotype diversity**. The Pie chart shows the numbers of individuals assigned to the different full Y-Haplotypes.*

3.1.2 mitochondrial Haplotypes

To investigate the mitochondrial diversity, I analysed the sequences of the hypervariable region 1 in 31 males and 14 females. I only included adults that were not knowingly descendants of other included individuals. Because many females in the investigated population are known to be related, many females were excluded (Figure 4A). I have illustrated this in Figure 4B, where I included all individuals that were haplotyped. In total, I found 2 haplotypes. The number of effective haplotypes N_e was calculated to be 1.59 and the analysis of the haplotype diversity *h* resulted in 0.37.

I also compared the mitochondrial diversity of males with the mitochondrial diversity of females. The most common mitochondrial haplotype was the same for both females and males. However, my analysis resulted in more effective alleles and a higher haplotype diversity for females (N_e=1.69, h=0.41, Figure 5B) than for males (N_e=1.63, h=0.390, Figure 5A).

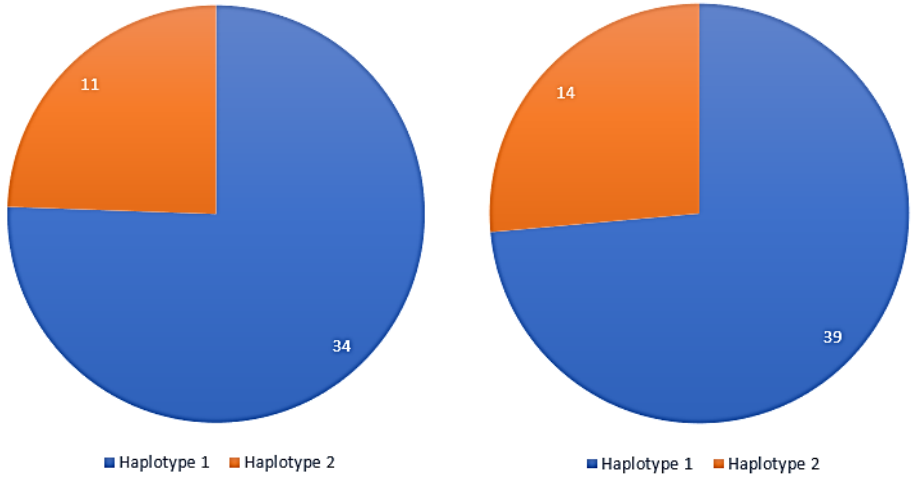


Figure 4: *A) Distribution mtDNA-Haplotypes without descendants. B) Distribution mtDNA Haplotypes including descendants.*

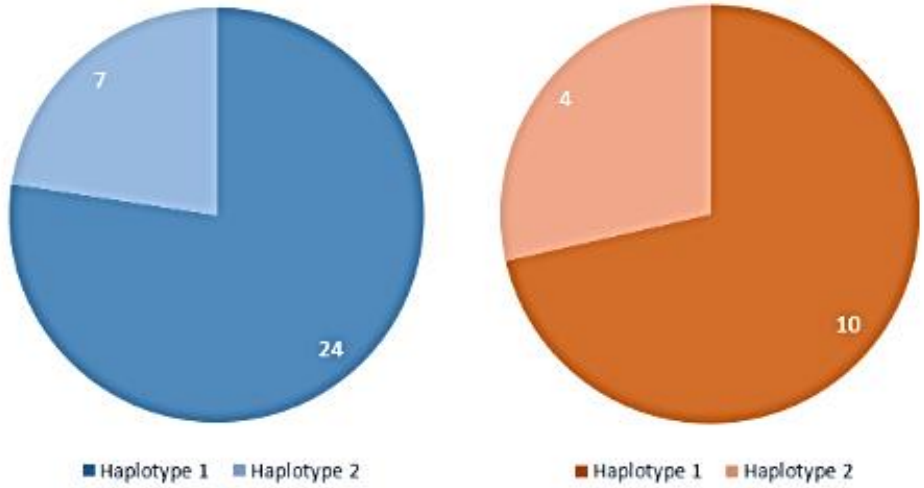


Figure 5*: A) Distribution mtDNA-Haplotypes male; B) distribution mtDNA Haplotypes females*

3.1.3 Haplotype networks

I constructed a Median-Joining network to visually asses the relation between the Y-Haplotypes. The three most frequent haplotypes (I, S and H) were only separated by one mutation. Most other haplotypes seem to be many steps away from each other (Figure 6).

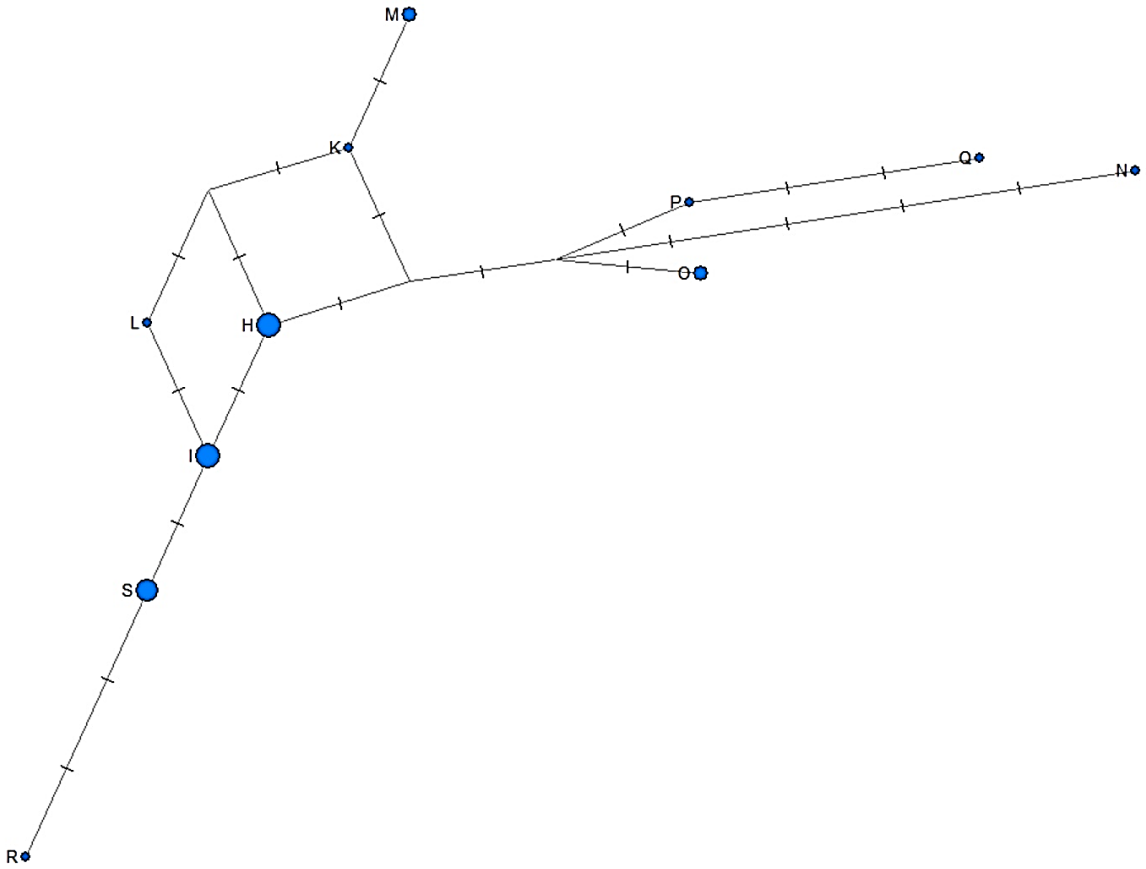


Figure 6: Median-Joining Network Y Haploytpes. *The haplotypes are shown as nodes. The number of vertical lines on the edges connecting the nodes indicates how many mutation steps happened between two haplotypes. The size of the node indicates the haplotypes' frequency*

3.2 Strategies of unflanged males to establish themselves in their new social and physical environment

First, I explored the social strategies unflanged males use to establish themselves in their new host population. By assessing different measures of their sociality, I examined the potential presence of non-observational social learning. Second, I investigated the potential role of peering as a tool for observational social learning by investigating role model choice, preferred activity to be peered at as well as practising behaviour. Furthermore, I explored the effect of rarity and complexity on the peering rates as well as the effect of time since arrival.

3.2.1. Social strategies

3.2.1.1 Association Rates and association partners

To measure the level of sociability, I compared the association rates and numbers of association partners of unflanged males to the ones of adult females and flanged males. I included all individuals that were followed at least three times resulting in 16 adult females, 20 unflanged males and 13 flanged males. Unflanged males' association rates were significantly higher than the ones of flanged males (ANOVA; $p > 0.05$) but did not significantly differ from the association rates of adult females (Table 6, Figure 7). Moreover, the average hourly number of association partners of unflanged males significantly differed from the ones of flanged males (ANOVA, $p > 0.05$) but did not differ from the ones of females (Table 7, Figure 8).

3.2.1.2 Social network

I constructed a network, using the Dyadic association index (DAI) as the edge weight to assess unflanged males' positions in the social network. I included all unflanged males, adult females and flanged males of which I had more than 20 hours of observation available. This allowed me to include a total of 65 individuals consisting of 37 unflanged males, 12 females and 16 flanged males. All these individuals together had 285 dyadic associations (Figure 7).

To investigate how well unflanged males are connected, I used the measure of closeness centrality. Unflanged males were found to have the lowest closeness centrality score (mean = 255.66, sd = 75.22) of the adult sex-age classes. This means that they are very well connected to other well-connected individuals. Compared to the ones of adult females (mean = 341.86, sd = 114.10), their scores was significantly lower (t-test, $p < 0.05$), but did not significantly differ from flanged males (mean = 288.10, sd = 48.75) (Figure 9). Also, the closeness centrality from females did not differ significantly from the ones from flanged males.

To investigate how the DAI is affected by the follow effort, I plotted the DAI against the total time of observation for a dyad, meaning the sum of the observation time for both dyad-members and fitted a general linear model (Table 6). The DAI did not seem to be normally distributed for dyads with little observation time (when sum of both observation times <500 hours) and only stabilized at around 500 observation hours (Figure 10). I tried various ways to control for the effect of follow effort on DAI but unfortunately, none of them was ideal. I further investigated this in Appendix "Further assessment of the social network" (Appendix Figure 2-4).

Table 6: GLMM with DAI as a dependent variable. *Estimates, standard error, t-values and p-values are reported for fixed effect.*

	Estimate	*Std.Error*	*T value*	*P value*
Intercept	0.000678	0.0002501	2.711	< 0.01
I(1/(TotalObservation)	0.9381592	0.0714460	13.131	<0.001

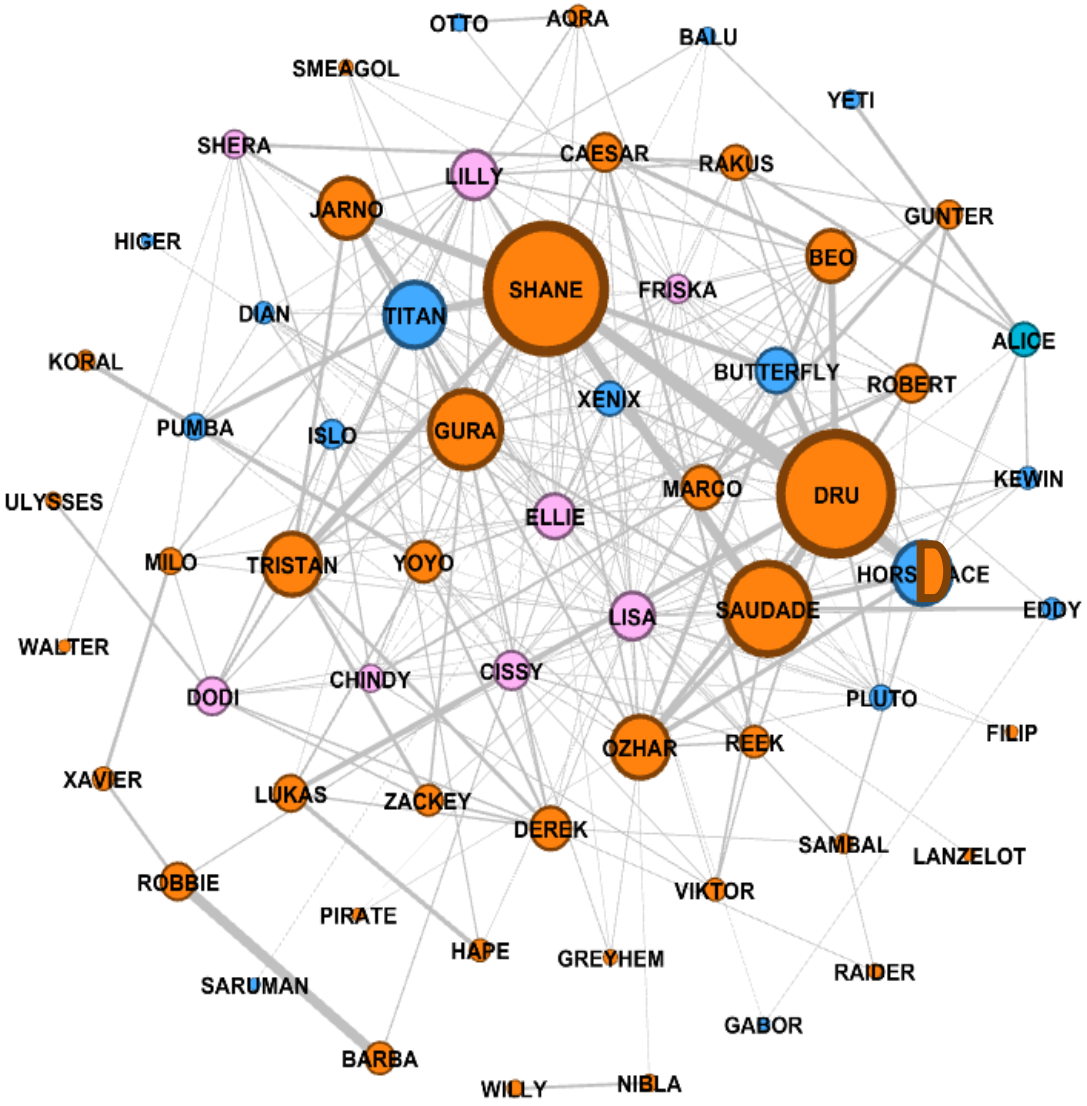


Figure 7: Social network of Suaq population*. As an edge weight the dyadic association index (DAI) was used. Node size indicates the weighted degree of each node. Pink colour relates to female individuals, blue to flanged males and orange to unflanged males*

***Table 7: Time spent in association**. Hourly association rates of the adult age-sex classes.*

Sex-age class	*Mean*	*sd*
Unflanged males	0.649	0.682
Females	0.624	0.537
Flanged male	0.153	0.193

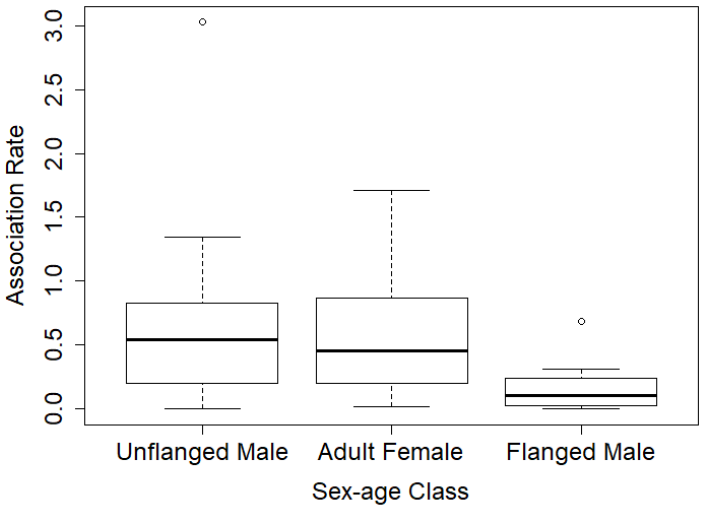


***Figure 8: Time spent in association**. Hourly association rates of the adult age-sex classes*

***Table 8: Numbers of association partners.** Hourly numbers of association partners of adult sex-age classes*

Sex-age class	*Mean*	*sd*
Unflanged males	0.649	0.682
Females	0.624	0.537
Flanged male	0.153	0.193

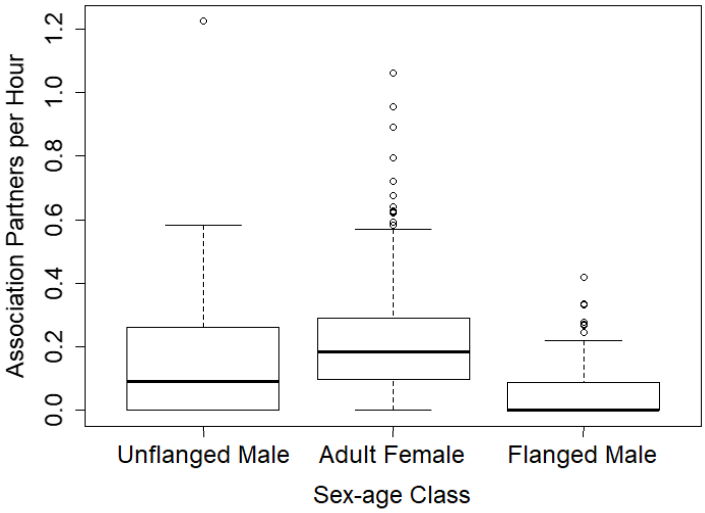


***Figure 9: Number of association partners.** Hourly numbers of association partners of adult sex-age classes.*

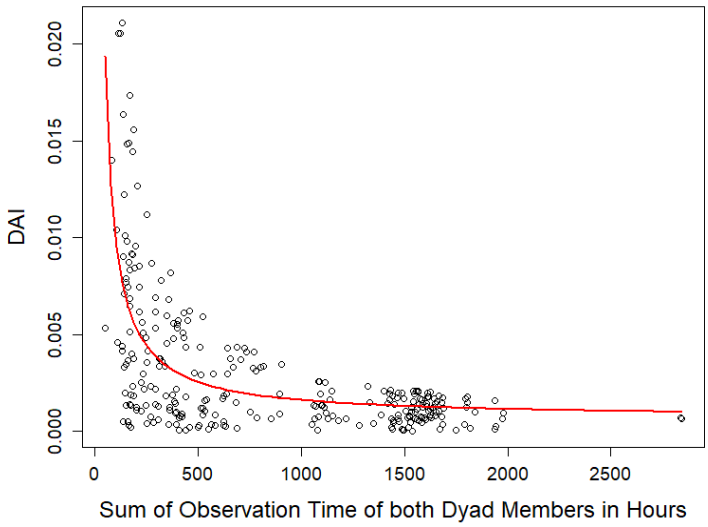


***Figure 10: Dyadic association index dependent on time**. Red line shows fitted model*

3.2.1.3 type of social interactions during associations

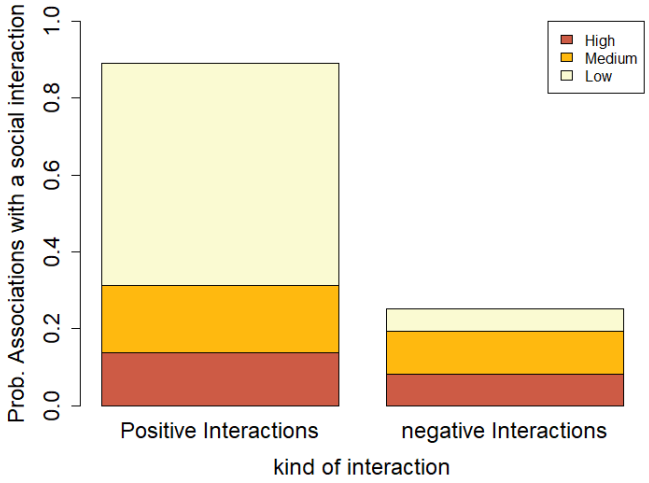
I investigated the nature of interactions during associations by looking into the presence and absence of positive or negative social interactions in 211 focal follows of unflanged males. I found that in 89,1% (N=188) of all unflanged males focal follows with associations positive social interactions were observed. Negative social interactions have been noted in only 24,1% (N=53) of the follows (Table 9, Figure 11).

Table 9: Proportions of social interactions. *Proportion calculated for each nature and intensity of social interaction.*

Type of interaction	*Proportion of follows*
Highly positive	0.14
Medium positive	0.18
Low positive	0.57
Highly negative	0.08
Medium negative	0.11
Low negative	0.06

.

Figure 11: Social interactions during unflanged male follows. *Percent of follows containing a positive or negative social interaction*



3.2.2 Peering as a tool for social learning

To investigate whether unflanged males use peering as a tool for social learning I analysed 270 peering events of 20 unflanged males.

3.2.2.1 Choice of Peering target

In order to investigate unflanged males' choice of peering target, I first computed the absolute numbers of peering events of unflanged males towards the different sex-age classes. Unflanged males directed 211 of their peering events at adult females. 15 of the peering events were directed towards juveniles and 15 were directed towards other unflanged males. No peering event was recorded towards flanged males (Figure 6 A).

In a second step, I calculated for each unflanged male relative proportions of peering events directed at different sex-age classes, corrected for the opportunity they had to peer at the different sex-age classes ("opportunity to observe a certain sex-age class"). Because I only included unflanged males that had at least ten peering events reported (see methods), I could only include eight unflanged males. The proportions of peering events unflanged males directed at the different sex-age classes differed significantly [ANOVA: $F(3, 28) = 8.99$, $p < 0.001$]. Post hoc comparisons using the Tukey HSD test indicated the mean proportion of peering events directed at females (mean = 0.62, sd = 0.34) was significantly higher than the mean proportion of peering events directed at juveniles (mean = 0.16 , sd = 0.26), unflanged males (mean = 0.22 , sd = 0.25) and flanged males (mean = 0.00 , sd = 0.00). The

peering proportions directed at other sex-age classes did not significantly differ from each other (Fig. 6B).

3.2.2.2 Activity of interest

To investigate unflanged males' interest in different activities, as first step, I looked at how many peering events were directed at which activity. In absolute numbers, of the 270 peering events by unflanged males 211 were observed in the feeding context, 5 in the nesting context and 6 in a social context. 14 peering events were observed in another context such as resting or moving (Fig. 6C). In a second step, I investigated the relative proportions of peering events directed at certain activities corrected for the opportunity they had to peer at these activities ('activity proportion of resident individuals'). Again, I excluded all unflanged males that did not reach the minimum of 10 observed peering events, resulting in 8 unflanged males. I found that peering proportions in the feeding context were significantly higher compared to peering proportions in nesting or other contexts (Kruskal-Wallis, p-value > 0.05), but not to peering in a social context (Fig. 6D).

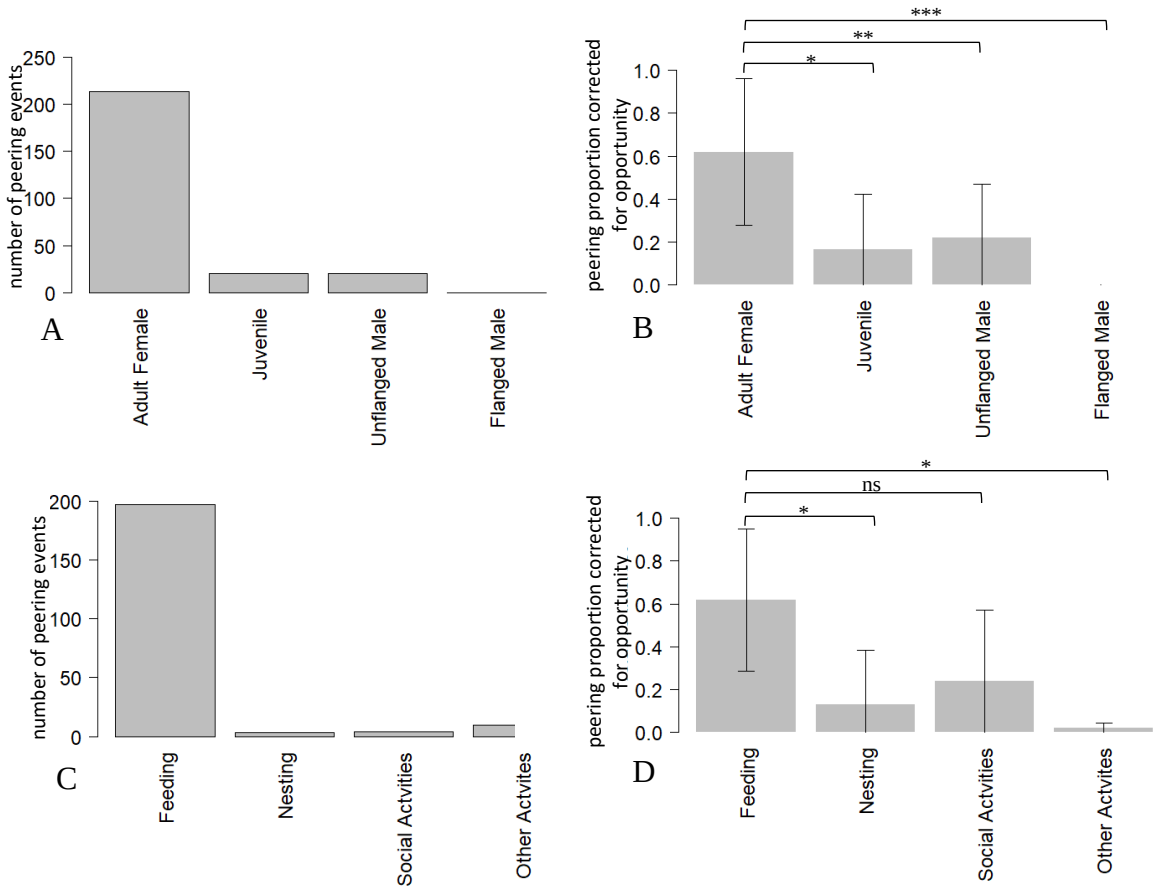


Figure 12: Role model choice and preferred peered at activity. *A) Absolute number of peering events unflanged males directed towards each age-sex class. B) Proportion of peering events directed to each sex-age class corrected for opportunity. C) Aboslute numbers of peering events in a certain peering context. D) Proportion of peering events in a certain context corrected for opportunity*

3.2.2.3 Peering practise cycle

To investigate whether unflanged males used peering as a tool for social learning, I examined whether unflanged males practise the observed behaviour after peering events. To do so, I examined the presence or absence of interaction with the same food item a peering target was feeding on one hour before and one hour after the peering event. I also did this for infants and juveniles from whom we know that they use peering as a tool to socially learn from others. Hence, if in infants and juveniles the interaction rate after peering is significantly higher, it provides us with an indication that this approach might demonstrate the presence of a peering practise cycle. On the contrary, adult females most likely do not use peering to socially learn anymore and therefore we expect to see no difference in the interaction rate before and after peering and can use them as a negative control. To analyse this, I used 48 food peering events of 8 different unflanged males for which we had information on whether an individual was feeding on the same species one hour before and one hour after the peering event. For adult females, I included 49 food peering events of 4 individuals, for juveniles 100 peering events of 7 different individuals and for infants 2'192 peering events of 17 different individuals. I found a significant increase in practice behaviour after peering in infants and for juveniles. Moreover, in unflanged males and adult females, the interaction after was increased. However, this increase did not reach statistical significance (Table 10, Figure 13).

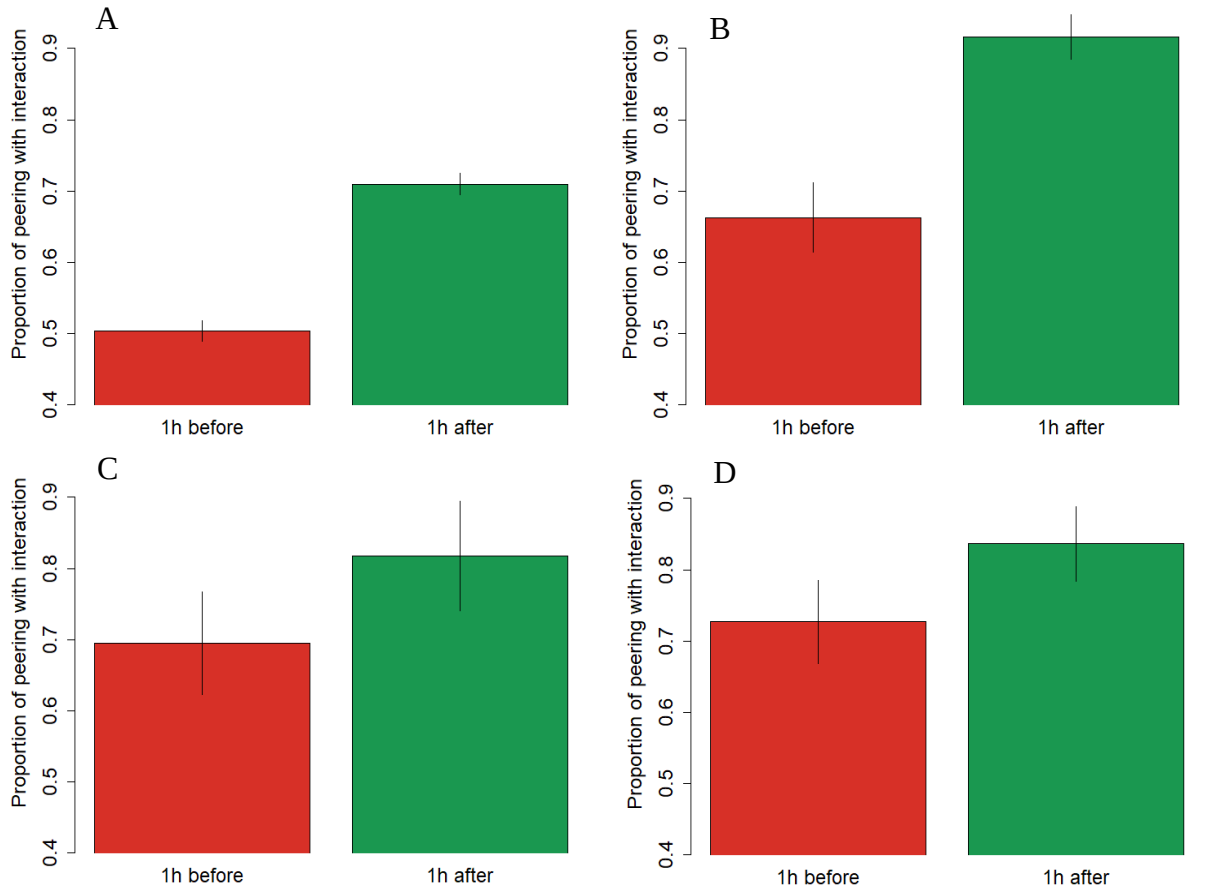


Figure 13: Peering practise cycle. *Proportion of interaction with the same food item as the peering target one hour before and one hour after the peering event for A) infants, B) juveniles, C) unflanged males and D) adult females*

Table 10: Practice before and after peering. *Proportion of peering events where feeding on the same species as peering target was observed in the hour before respectively after*

Sex-age class	*Proportion Before*	*Proportion after*	*T-test before vs. after*
Infants	0.5	0.7	< 0.001
Juveniles	0.67	0.87	< 0.01
Adult females	0.7	0.8	0.381
Unflanged males	0.71	0.82	0.312

3.2.2.4 Do unflanged males indeed learn when they are peering?

If peering is used for social learning, we expect peering rates to decrease with complexity and rarity of the observed activity. Therefore, for food peering, I investigated the effect of the frequency and complexity of the peered at food item on peering rates. I first investigated the rarity effect by approximating the frequency of the food item in the population's repertoire. Since most food items are rare and only some are very frequent, I used a logarithmic scale for this. I only included identified unflanged males that had at least 10 observation hours per year ($N_{Unfl.Male}$=14, $N_{Peering\ events}$=165). I found a strong negative effect of the food item frequency on the peering per opportunity, which consists of the 'opportunity to observe a certain sex-age class', the 'activity proportion of resident individuals' and the 'frequency of a food item' (GLMM, p-value < 0.001) (Figure 14A). To examine the complexity effect, I added processing steps (defined as the number of steps a food item requires before it can be consumed, see Schuppli et al. 2016), as a fixed effect to the model (Table 11). Complexity had no significant effect on peering rates (Figure 14B). Therefore, we can conclude that food frequency had an effect on the peering per opportunity while complexity did not influence the peering frequency.

Table 11: GLMM with logarithm of 'peering per opportunity' as dependent variable*. I reported effects, estimates, standard error and p-values.*

	Type of effect	*Estimate*	*Std.Error*	*P-value*
Intercept	-	-0.21	0.39	0.588
Log(Food Frequency)	Fixed	-1.02	0.04	<0.001
Processing steps	Fixed	-0.01	0.06	0.818
Individual	Random	-	-	-

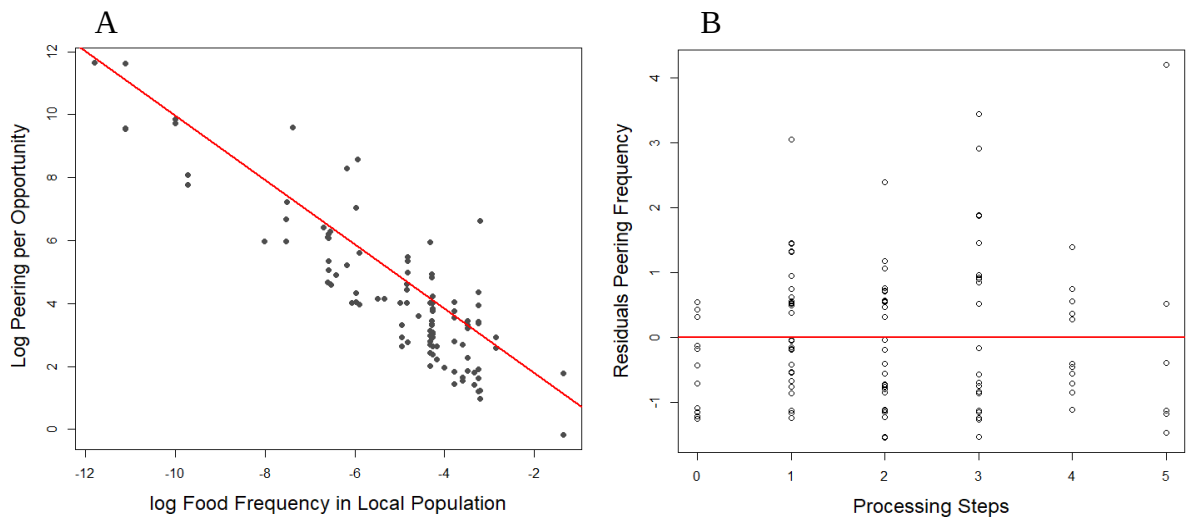


Figure 14: Rarity and complexity effect. *A) Effect of food frequency in population on peering corrected for opportunity. B) Effect of peering steps on peering frequency plotted as residuals of food peering effect.*

3.2.2.5 Do new unflanged males peer more often?

To investigate whether newly arrived unflanged males peer more often than already established unflanged males, I analysed the effect of time since arrival on the peering rate. This resulted in a negative correlation of peering rates with years-since-arrival, meaning that recently arrived unflanged males do peer more than the ones that were there for longer (GLMM, p-value <0.001). One could argue that not the time since arrival, but the actual age of the unflanged males did play a role, assuming that unflanged males are younger when they arrived. Younger individuals are expected to peer more often. Since we did not have any estimates of their age, I compared it to two females from which we had data since infancy. Supposing that unflanged males leave their natal area when they are about 12 years old, I computed the peering rates of the females from 12 years old onwards for each year. The general linear mixed model with age as a fixed factor and ID as a random factor did not show a significant effect of age on the peering rate.

Table 12: GLMM with logarithm of Peering Per Opportunity as dependent variable. *I reported effects, estimates, standard error and p-values.*

	Type of effect	*Estimate*	*Std.Error*	*P-value*
Intercept	-	1.09	0.44	<0.05
Log(Food Frequency)	Fixed	-1.02	0.03	<0.001
Years since arrival	Fixed	-0.34	0.06	<0.001
Individual	Random	-	-	-

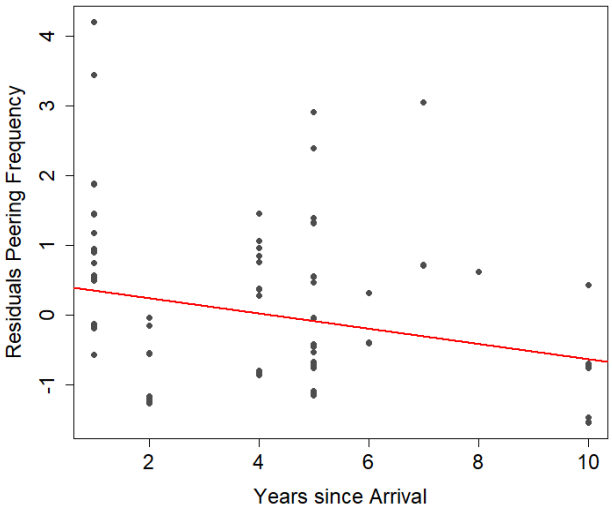


Figure 15: Effect of time since arrival on peering frequency. *Residuals of rarity effect plotted against years since arrival of unflanged males.*

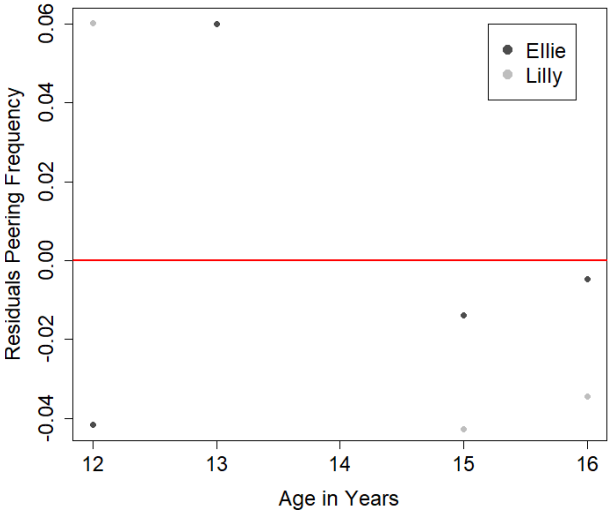


Figure 15: Age effect on peering. *Residuals of rarity effect plotted against age of two females.*

Based on these findings on the effects of time since arrival on peering rates, I re-analysed the first results concerning peering target and contexts. Then I performed a Chi-Square test to check whether the groups differed in their preference for females as peering targets respectively feeding as a peering context. I compared the proportions of all peering events of the class 'recently-arrived males' to the proportions of all peering events of the 'established males', resulting in no difference in the choice of peering target sex-age class between the groups of males, but a significant difference in the proportion of peering feeding context. Recently-arrived males peered more in a feeding context (150 out of 164 peering events) than established males (81 out of 92 peering events, Chi-square: p-value > 0.001, Figure 16).

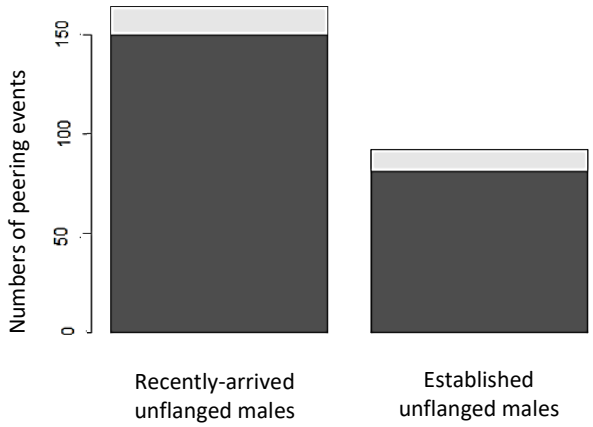


Figure 16: Proportion of Food Peering. *Dark grey shows the number of Food peering events for each class. The light grey shows peering in all other context.*

4. Discussion

The aim of this master thesis was to first investigate the genetic basis of the dispersal strategies of orangutans and also to identify the strategies of unflanged Sumatran orangutan to cope with a new environment after dispersal. Unflanged males are expected to come up with strategies to deal with the challenges they are facing in their new neighbourhood after dispersal. I expected them to use social strategies and to also learn to establish themselves in the new area.

4.1. Genetic basis of male-biased dispersal in orangutans

In the first part of my master thesis, I looked into the sex-specific marker system of Y-chromosomal DNA and mitochondrial DNA. I investigated a multiplex system for the Y-chromosomal DNA consisting of SNPs and microsatellites. I found more full haplotypes than SNP-haplotype. The diversity of the full haplotypes was mainly based on the diversity of the microsatellites. This can be explained by the higher mutation rate of microsatellites compared to SNPs (Joblin et al. 2003). In general, it is problematic to combine microsatellites and SNPs in a Y-chromosomal haplotype, but due to the difficulty of developing Y-specific genetic markers, we only have little genetic data on the paternal line (reviewed in Greminger et al., 2010). Hence, including microsatellites provides us with the chance to find variation in the first place.

Next, I found two mitochondrial haplotypes represented in both males and females. My hypothesis of male orangutan showing a higher mitochondrial haplotypic diversity than females was therefore not supported. From earlier autosomal research and backed by behavioural research, we know that two main families exist in the research area represented in two maternal mitochondrial haplotypes (Nater et al., 2011). A third group of orangutans could not be autosomally assigned to either of the families, but had the same haplotype as family 1 (unpublished data). Most incoming males also had haplotype 1. Since the mitochondrial haplotype is inherited by the mother, this could mean that family 1 maternal ancestor immigrated, just like the immigrant males. Support for this theory can be found in the generally bolder behaviour of family 1 (pers. Communication with C. Schuppli) since boldness is an indicator of dispersal tendencies in other species (Cote et al., 2010; Fraser et al., 2001). We lack autosomal data from males to investigate this further. If they were more closely related to family 1 than 2, this would strongly support my assumption. Autosomal data on females of other close-by population might shed a light on this.

I used different techniques to assess mitochondrial and Y-chromosomal diversity. I only targeted loci on the Y-chromosome that are known to be polymorphic, while I sequenced a 415bp pair-long region for mitochondrial DNA. Hence, I cannot directly compare the results of both analyses. However, both analyses represent the same effective population size, which is one-fourth of the autosomal population size (Jorde et al., 2000). Assuming that SNPs in the HVR on the mitochondrial DNA have a similar mutation rate than the SNPs on the Y-chromosomal DNA, my finding of four Y-chromosomal SNP-haplotypes compared to two mitochondrial haplotypes supports a slightly male-biased dispersal.

Compared to other populations (i.e. Tuanan and Sabangau in Borneo; Fluck 2019), the mitochondrial diversity at Suaq Balimbing was found to be unexpectedly low. Nater and colleagues (2017) showed in their study on the new species *Pongo tapanuliensis* that the best-supported colonization scenario suggested an ancestral population most likely situated south of Lake Toba on Sumatra. The earliest split in the genus *Pongo* was estimated to have happened 3.38 MA years ago. The split occurred between the lineages leading to *P. abelii* and *P. tapanuliensis.* The colonization

event leading to *P.pygmaeus* was estimated to have happened 674 kya. This means that *P.abelii* is a much older species than their Bornean sister species. We would therefore expect them to be more diverse than *P.pygmaeus*. Nater et al. (2013) has investigated diversity of the hyper-variable region I of Sumatran orangutans from seven different regions and found a haplotypic diversity reaching from 0.27 to 0.95. Only one region showed a smaller diversity than Suaq, indicating that Suaq has most likely experienced a recent bottleneck.

Despite Suaq being known to have the highest density of orangutan (Husson et al. 2009, van Schaik et al. 2016), this does not tell us anything about the extent of the population. Small populations are prone to genetic drift reducing their diversity (Willi et al., 2007). Suaq, located at the edge of a offshoots of the Nation park Gunung Leuser (Appendix Figure 5), was believed to be well connected to the rest of the national park (Singleton and van Schaik, 2001). However, my results indicate a low mitochondrial diversity, raising the question of whether or not this is true. In other great apes, a significant loss of mitochondrial diversity as a result of human activities negatively impacting peripheral populations has been observed (Valk et al., 2018). Although Suaq is situated in the protected national park, adjacent forest areas located outside the park experience severe habitat loss due to deforestation. Wich et al. (2016) predicted a potential population size decrease of roughly 31% by 2030. Sites with the highest density of orangutans, such as Suaq, should therefore be prioritized for conservation (Husson et al., 2008). I conclude that my concerning findings on the low mitochondrial diversity should be backed up with autosomal data on the Suaq orangutans.

4.2. Strategies unflanged males use to establish themselves in a new neighbourhood

In the second part of my master thesis, I investigated the strategies unflanged males used to establish themselves in a new social and physical environment after dispersal. I expected them to use social strategies to be well connected and tolerated by resident individuals. Despite peering potentially having functions other than social learning, I evaluated whether peering is a means for social learning.

In terms of social strategies, I predicted that unflanged males would be highly social and well connected. To assess how social unflanged males were, I compared their association rates and average association partners to the ones of other sex-age classes. I found that unflanged males had significantly higher association rates than flanged males and similar association rates to adult females. In terms of average association partners, there was a significantly higher number for unflanged than for flanged males, but no significant difference to females. These results suggest that unflanged males were as social as adult females. However, females usually settle close to their mothers home range (Singleton et al., 2009), and therefore have their maternal family cluster around them with whom they develop relationships from an early age. Conversely, unflanged males were confronted with unfamiliar and unrelated individuals. These findings suggest that unflanged males actively sought associations and probably used behavioural strategies to earn tolerance from the resident individuals. In other primate species, grooming has been shown to be used for this purpose (white-crested Gibbons: Guan et al., 2013; Bonobos: Sakamaki et al., 2015). Orangutans, as a semi-solitary living species with minimal body contact between adult individuals, might have other behaviours that do not require body contact. In a follow-up project, one could try to pin down what behavioural strategies unflanged males use.

In terms of the nature of social interactions, I found that most of the unflanged males' associations had positive social interactions, whereas negative social interactions were observed in

only about one third of the interactions. While highly social interactions (i.e. peering, begging and co-feeding) were observed rather infrequently (14% of all positive interactions), I found numerous associations to have medium-to-low social interactions (i.e. deeding tolerance, social watch and coordinated moving, 75% of all positive interactions). Unflanged males might have used positive social behaviours to increase the tolerance of resident individuals. By being accepted in association for extended periods of time, unflanged males increased their opportunities for social learning – this included the non-observational forms, like eavesdropping, which presumably worked from a larger range of association distances. Observational forms, like peering, required to be tolerated in a closer proximity of a role model, which was more easily achieved if the association is of tolerant nature, in general.

To further investigate unflanged males' sociability, I analysed their position in the social network of the population. I analysed their closeness centrality, which is the average length of the shortest path between the node and all other nodes in the graph. Closeness centrality thus expresses how many steps away an individual is from all the other individuals in the network (Dijkstra, 1959). It has been shown to be a good predictor for success in terms of fitness (div. animal taxas: Brent, 2015) and knowledge acquisition (primates: Senior et al., 2016; humans: Pratiwi and Suzuki, 2017). My results showed that unflanged males had significantly lower closeness centrality values than adult females and flanged males, which means they are close to a large number of individuals and therefore in the position to access knowledge from many individuals in the population.

I also computed other centrality measures, such as Eigen centrality and weighted degree. Eigen centrality reflects the level of connectedness to other vertices, which are, in turn, connected to many others (Newman, 2006.). The largest values of Eigen centrality will thus be obtained by individuals in large cliques. Weighted degree is based on the number of edges for a node, reflected in the weight of each edge – it is the sum of all edges of a node. Both measures seemed to be higher, but not significantly different, in unflanged males than in other sex-age classes. These patterns suggest that unflanged males were well connected, but this could be a result of the bias in follow effort for the different sex-age classes.

During the network analysis, I realized that the edge weight I used in my analyses was strongly negatively correlated with follow effort. Dyads with a small total observation time had a significantly increased dyadic association index (DAI), whereby stabilization occurred at around 500 hours of observation time. In general, males were followed less often than females at Suaq, due to the main focus of past research projects being on females and their dependent offspring. This resulted in a higher estimated DAI for male-male dyads than for male-female dyads. To control for the effect of follow effort on DAI, I first approximated the effect with a non-linear function in the data. The residual DAI (controlled for observation time) was then used as a new measure of the association strength. However, the obtained residual values showed a very small variance (see appendix for results) and did not allow for further analyses. As an alternative way to control for follow effort, I partitioned the data into yearly subsets for all age-sex classes, expecting those data to be less biased due to more similar observation times. However, the data followed the same bias-pattern as the five-year pooled data.

Because of these limitations, aside from DAI, I also used another edge weight known as the Simple Ratio index (SRI). The SRI is the probability that two individuals have been observed together, given that one has been seen (Cairns & Schwager, 1987). However, the SRI can only be calculated based on direct associations and none of the indirect associations could be included, meaning that if two individuals were in association with the focal animal at the same time, I could not calculate their dyadic relation. This reduced my sample size drastically and made further analyses impossible.

With the help of the social network, one could ultimately analyse an individual's set of learned skills as a function of their social connectedness. So far, the network-based diffusion analysis (NBDA) has mainly focused on the social transmission of innovations (methods described in Hoppitt, 2017; applied in Wild et al., 2019). In orangutans, this could be extended to not just innovation, but all socially-learned skills that are not population-wide universals, such as unique nest building techniques (Russon et al., 2007), tool use (Sanz et al., 2013, Schaik and Knott, 2001) and call types (Lameira et al., 2013). Furthermore, because diet repertoires are socially-learned in orangutans (Schuppli and van Schaik, 2019) diet repertoires could also be included in these analyses (Bastian et al., 2010; Russon et al., 2004). If skills are socially transmitted, one would expect that individuals with high similarity in their skill sets would show a higher degree of connectedness, as has been suggested for other species (Hobaiter et al., 2014). Social network analysis would thus allow us to infer social transmission of knowledge without the direct observation of social learning. However, this analysis would require large quantities of data on an individual orangutan level. Unfortunately, I did not extract this type of repertoire data from the extensive notes taken during follows due to time constraints. However, once we have found a method to control for the bias in DAI and the repertoire data is extracted, this idea should be revisited.

To investigate if peering is used as a tool for observational learning by unflanged males, I tested several predictions: First, I predicted that unflanged males peer at the most knowledgeable individuals in the area, namely adult females who have spent their whole life in the local area (Schuppli et al., in preparation). I indeed found that unflanged males peered mostly towards adult females. However, this pattern could also be explained by an alternative scenario: if peering had a social function, and was used by the unflanged males as means for increasing their chances of gaining access to females. A striking feature in the mating system of orangutans is the occurrence of forced matings (Fox 2002, Utami et al. 2009). While aggression before mating and sexual cohesion can be observed in other primate species (Soltis et al., 1997; van Schaik et al. 2004), in orangutans, the strength of the resistance of females towards mating with certain males is enormous (Knott et al., 2009) Therefore, unflanged males might use peering - an infant-like behaviour - as a submissive signal to show their harmlessness. This may ultimately allow them to approach adult females.

Second, because they might lack knowledge on the local diet, I expected unflanged males to peer mostly in the feeding context. Unflanged males are adults and thus have learnt most routine skills from their mothers as immatures (Schuppli et al., 2016b). Therefore, they have most likely already reached competence in building nests and other location-independent activities. However, because local ecologies differ even between populations in close proximity, after dispersal, unflanged males might lack some knowledge on the local food species (Bastian et al., 2010). Consistent with this prediction, I found that food peering was the most commonly peered-at activity by unflanged males, even after controlling for opportunities to peer by controlling for the frequencies of all behaviours.

Aside from food peering, unflanged males showed high rates of peering at social interactions between associated conspecifics. To disentangle this further, I split the unflanged males into two groups: recently-arrived (<4 years in the area) and already-established males (>4 years in the area). I predicted that recently-arrived males would do more food peering than established males, because they might still lack knowledge of the local diet. Consistent with this prediction, my results evidenced that recently-arrived males peered more often in the feeding context than established males. This suggests that the high number of peering on social interaction was driven by locally-established unflanged males who have presumably reached local ecological competence in feeding. From that, we

can infer that peering by adults might have functions other than social learning. Peering is potentially a means to gain tolerance and access to mating opportunities for established males.

Furthermore, I investigated the peering practise cycles of unflanged males. Based on the results on infant learning in orangutans (Ehmann, 2019), I expected unflanged males to do some form of practising of the observed activity after peering. To investigate this, I looked into if there was an increase in interactions with a food species after peering at a target consuming this food species. This was the case, but not on a significant level. Only infants and juveniles showed significant differences in interaction rates. Though, because we could only use focal follow peering events, there were only a small fraction of all peering events going into this analysis for unflanged male. I did not find significant support for my hypothesis, but this might also be due to the limited data set.

Next, I looked into the effects of rarity and complexity of the food item on peering rates. Based on results on immature orangutans (Schuppli et al., 2016b), peering rates were expected to decrease with increasing frequency of the food item in the local diet (rarity effect) and increase with increasing complexity (complexity effect). In terms of rarity, as predicted, I found a strong decrease in peering rates with increasing frequency of the peered-at food item in the local diet. However, this result must be interpreted with caution because of the method I used to control for the opportunity unflanged males had to peer at the different food items, which was partly based on the overall frequency of the food item in the local diet. A better way to control for the opportunity to peer would be to use the actual frequency of each peered-at food item in the diets of the unflanged males' association partners during the time an unflanged male was present. However, because we did not have nearly enough simultaneous follows to compute the actual frequencies, using the food frequency in the population was the best alternative. Furthermore, food items that are rarely consumed in Suaq are not necessarily rare at the neighbourhoods where unflanged males come from. Therefore, it would be highly interesting to add the frequencies of the food items in the unflanged males origin populations to the model.

I did not find any effect from the complexity of the food item on unflanged males' peering rates. Unlike than infants, unflanged males did not peer more often for food that took more steps to process or for complex feeding techniques in general (i.e. techniques involving tool use). While the food repertoires of orangutans seem to vary on a relatively small spatial scale (Bastian et al., 2010). To date, we do not know much about the variation of tool use by orangutans in neighbouring areas of Suaq. Thus far, variation of tool use has only been investigated on a larger spatial scale (Fox et al., 2004). If tool use is spread throughout the areas around Suaq, unflanged males most likely already learnt these techniques from their mothers, which would explain my findings.

My last prediction to test the use of peering as a tool for social learning was that peering rates were negatively correlated with the time that passed since the arrival of unflanged males in the neighbourhood, assuming that recently-arrived unflanged males lack more local knowledge than males that had already established themselves in the area. In support of this prediction, I found that recently-arrived unflanged males had significantly higher peering rates than established males. However, one could argue that peering rates also correlate with the age of unflanged males in that younger individuals would peer more often than older individuals. Because newly arrived males are most likely younger than established males, it is important to investigate the potential age effect on adult orangutans' peering rates. Therefore, I investigated the peering rates of two adult females of which we had peering data available from the age of 12, which is the age we expect unflanged males to approximately be when they arrive in Suaq. I did not find any effect of age on the female's peering rates. This suggests that, rather than age, a lack of local knowledge caused increased peering rates in

recently-arrived unflanged males. All in all, this set of results on unflanged males' peering behaviour strongly supports the hypothesis that they use peering as a tool for social learning.

Overall, I found strong evidence that unflanged males use social strategies to establish themselves in their new environment after dispersal. My results showed that unflanged males had a high sociality and were well connected, presumably because they use strategies to earn tolerance from resident individuals. This high social tolerance paved the way for non-observational and observational forms of social learning. The sum of my findings on unflanged males' peering behaviour indicates that peering was used as a tool to socially learn from resident individuals. These results are a first step to shine a light on the learning behaviour of adult orangutans. While some studies have focused on *if* wild great apes learn after dispersal (Luncz et al., 2015; Luncz and Boesch, 2014), my findings, in addition to strongly supporting the presence of social learning after dispersal, might contribute to a better understanding on *how* great apes learn after dispersal. In fact, also in humans adult learning is still puzzling (Summary on adult learning in Illeris, 2018), but given our fast-changing world, becomes more and more important.

Furthermore, the comprehension of the knowledge transmission process in adult orangutan might provide crucial insight for orangutan conservation. Increasing habitat destruction leads to the need to translocate individuals to a better, more suitable habitat. In fact, in Sumatra, more than 200 orangutans have been translocated from destroyed habitat to nature reserves (Wich and Marshall, 2016). Translocated orangutans are confronted with a new environment just as unflanged males are after dispersal. The knowledge on preferred role models might suggest that releasing translocated individuals close to knowledgeable conspecifics could be beneficial. It could increase the speed on which a translocated individual learns the local diet and eventually lead to an increase in survival rate.

5. Acknowledgments

I am thankful for the guidance and supervision of Michael Krützen and Caroline Schuppli. I would like to thank them to have given me the opportunity to do this thesis. Caroline's exceptional engagement in supervising me has encouraged me immensely. The time in the field has become a memory for life that I would not want to miss. A big thank you goes to Puji Rianti. She did not just make me feel home in Indonesia, she also was a great support for all tasks related to administrative permit acquisition. I also want to thank Carel van Schaik and Mara van Noordwijk for fruitful discussions and expertise-based comments every time I presented my work.

Furthermore, I would like to thank A.H. Schultz-Stiftung for their financial support. I gratefully acknowledge the Indonesian Institute of Science (LIPI), the Indonesian State Ministry for Research and Technology (RISTEK), Departamen Dalam Negri, the local government in South Aceh, the Sumatran orangutan conservation Program (SOCP) and Taman Nasional Gunung Leuser (TNGL) in Medan for their permission to conduct this research. I also thank the Department of Biology, Bogor Agriculture University (IPB) for their collaboration and support during my stay there.

I would also like to thank all assistants, students and volunteers, who collected data at Suaq Balimbing. Especially Natasha, Belinda and Helvi, with whom I shared many laughs and Bea and Josh, who always accompanied me in the field through stormy and sunny days. They were not only the best co-researcher, emotional supporters, R-teachers, proof-readers and conference-buddies I could wish for, they also became good friends. Same is true for my officemates Svenja, Ramona and Haley.

Further, I am grateful for Aurora and Ayu, who let me stay in their house in Bogor and introduced me to spicy food. Many members of the anthropological institute supported me during my thesis: I am grateful for Livias help in the lab, Sams support in R-related problems over a cup of coffee, Allies

help in coding to disentangle the association data, Lucios' time on discussing network-biases and all other institute members who made my time here as enjoyable as it was.

A huge thanks goes my brother Marco for checking for comprehensibility and to Raleigh Grysko for last-minute proofreading. Last but not least, I want to thank my friends and family. Especially my mother, on whose support I can count on no matter what and my father who had always encouraged me to reach for my dreams.

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7. Appendix

Table 1: Overview of human derived orangutan specific Y-chromosomal primers. *Designed by (Nietlisbach, 2009) to obtain the Y-chromosomal haplotypes of the male individuals.*

Locus amplicon [repeat] length	Primer Name	Label	Primer sequence (PIG-tails in lower case letters)	PYMP
DYS502 112.5 [2; 9] - 118.5 [2; 11]	DYS502new-F_FAM	6-FAM	CCTGGAAGTGTAGATCCCTCAA	63
	DYS502new_A-R		gtttGTACCCCAGATCTTAAAATATGATGATA	
	DYS502new_G-R		gtttgtCCCCAGATCTTAAAATATGATGATG	
Y6C2 124 [5] - 127 [6]	Y6C2new-F_FAM	6-FAM	CTTCTCCTTCTTCCTATTCTTCATCT	63
	Y6C2new-R		gtttCAATAGTTTGGGGAAATAAGACAATG	
DYS577 148 [5; C] - 158.5 [7; G]	DYS577new-F	6-FAM	CCACTAACCCCATGCATATTAT	63
	DYS577new_C-R		gtttGAGAGGTTGAGGCTGCAGTAAG	
	DYS577new_G-R		gtttgtGAGAGGTTGAGGCTGCAGTAAC	
DBY13 171 [C] - 173 [G]	DBY13new-F_FAM	6-FAM	GGAAACTAAAATATGACATTGTAATTTG	63
	DBY13new_C-R		gtttATTTTTTTATTGTGATGCATACAGC	
	DBY13new_G-R		gtttgtATTTTTTTATTGTGATGCATACAGG	
DYS645 186 [5] - 196 [7]	DYS645new-F_FAM	6-FAM	GTACTAATTTTATTTCTTATGGCGTAGA	63
	DYS645new-R		gtttACACATGGCACCTGACACTG	
DYS587 201 [12] - 235 [19]	DYS587new-F_FAM	6-FAM	AAAATTACCTTCTTTGGAAAGTAGTATT	63
	DYS587new-R		gtttGTTATTTCTGAGCAGGGTTTCTAAG	
DYS532 115 [7] - 130.5 [11]	DYS532new-F_NED	NED	AGCAGGATTCCCTCTAAAAATATCA	63
	DYS532new-R		gTTTCTCCCTCCCTCCCTCTC	
DYS630 147 [G; 12] - 198 [Del; 23] 152 - 191	DYS630new-F_PET	PET	AGCAAGACTCCACCTCAAAAAGA	63 & 64
	DYS630new-R		gtttGCTGTGAGTTCCATAAATTTCTTCC	
	DYS630new_G-R		gttTGAGTTCCATAAATTTCTTCCTTCC	63 & 64
	DYS630new_T-R		gtttgTGAGTTCCATAAATTTCTTCCTTCT	
DYS510 120 [8] - 144 [13]	DYS510new-F_PET	PET	GAAAGATAGATCAACAAGGTAGAAACAA	64
	DYS510new-R		gtttCATCCATCCATCCATCCATCT	
SMCY12_26 87 [G] - 89 [C]	SMCY12_26-F_FAM	6-FAM	AAGGGTCACCACAGAAATACTTAG	64
	SMCY12_26_C-R		gtttgtCAGGTGGGGCGTAGTCTC	
	SMCY12_26_G-R		gtttCAGGTGGGGCGTAGTCTG	
SMCY12_337 95 [C] - 97 [A]	SMCY12_337-F_FAM	6-FAM	GTTACAGGTATACATGCACCTTTTT	64
	SMCY12_337_A-R		gtttgtGTGTGGCTTCTTTACTCTGTCA	
	SMCY12_337_C-R		gtttGTGTGGCTTCTTTACTCTGTCC	
SMCY14 119[T] - 121 [C]	SMCY14new-F_FAM	6-FAM	ATGGGGAAAAGATGAGTTCTGA	64
	SMCY14new_A-R		gtttGTCTGGCATCCTAATGCCT	
	SMCY14new_G-R		gtttgtGTCTGGCATCCTAATGCCC	
DYS556 118.5 [5] - 130.5 [8]	DYS556new-F_FAM	6-FAM	TTACAAAACTAACATAAAGACCAAACAG	64
	DYS556new-R		gtttGAAGCATTGAGTATAGTATAAAGTTGGT	
DYS561 152 [10] - 168 [14]	DYS561new-F_FAM	6-FAM	CCTGATGCCATCTGAAAATTAA	
	DYS561new-R		gtttACAACTGCACTCCAGCTTAGG	
DYS470 220 - 227	DYS470-F_FAM	6-FAM	GGTCCTTCAGGAACCAGTTG	64
	DYS470-R		gttTGGCTGTAAAACAAATATCAGCA	

Appendix PCR PYMP 64/63

Table 2: Primer mix and Master mix set up PYMP 64. *Per multiplex PCR reaction one µl DNA template, 0.8 µl of the primer mix, 4 µl of multiplex master mix and 2.2 µl of ddH2O is used*

PYMP64: PCR set up *Primer Mix*	*Conc. [µM]*	*Primer Mix [µl]*	*Final Conc. in PCR [µM]*	*Volume in PCR [µl]*
DYS630new-F_PET	100	1.5	0.15	0.015
DYS630new_G-R	100	2	0.2	0.02
DYS630new_T-R	100	2	0.2	0.02
DYS510new-F_PET	100	3	0.3	0.03
DYS510new-R	100	4	0.4	0.04
SMCY12_26-F_FAM	100	1.5	0.15	0.015
SMCY12_26_C-R	100	2	0.2	0.02
SMCY12_26_G-R	100	2	0.2	0.02
SMCY12_337-F_FAM	100	1.5	0.15	0.015
SMCY12_337_A-R	100	2	0.2	0.02
SMCY12_337_C-R	100	2	0.2	0.02
SMCY14new-F_FAM	100	1.5	0.15	0.015
SMCY14new_A-R	100	2	0.2	0.02
SMCY14new_G-R	100	2	0.2	0.02
DYS556new-F_FAM	100	3	0.3	0.03
DYS556new-R	100	4	0.4	0.04
DYS561new-F_FAM	100	3	0.3	0.03
DYS561new-R	100	4	0.4	0.04
DYS470-F_FAM	100	3	0.3	0.03
DYS470-F-R	100	4	0.4	0.04
ddH₂O [µl]		50		
Primer Mix Volume		100		
DNA Template				**1**
Primer Mix	10		1	**0.8**
Multiplex Master mix	2		1	**4**
ddH₂O				**2.2**
Final Volume				**8**

Table 3: Primer mix and Master mix set up PYMP63. *Per multiplex PCR reaction one µl DNA template, 0.8 µl of the primer mix, 4 µl of multiplex master mix and 2.2 µl of ddH2O is used.*

PYMP63: PCR set up *Primer Mix*	*Conc. [µM]*	*Primer Mix [µl]*	*Final Conc. in PCR [µM]*	*Volume in PCR [µl]*
DYS502new-F_FAM	100	1	0.1	0.01
DYS502new-F_A-R	100	1.4	0.14	0.014
DYS502new-F_G-R	100	1.4	0.14	0.014
Y6C2new-F_FAM	100	1	0.1	0.01
Y6C2new-R	100	1.4	0.14	0.014
DYS577new-F	100	3	0.3	0.03
DYS577new-C-R	100	4	0.4	0.04
DYS577new-G-R	100	4	0.4	0.04
DBY13new-F_FAM	100	3	0.3	0.03
DBY13new_C-R	100	4	0.4	0.04
DBY13new_G-R	100	4	0.4	0.04
DYS645new-F_FAM	100	1.5	0.15	0.015
DYS645new-R	100	2	0.2	0.02
DYS587new-F_FAM	100	3	0.3	0.03
DYS587new-R	100	4	0.4	0.04
DYS532new-F_NED	100	1	0.1	0.01
DYS532new-R	100	1.4	0.14	0.014
DYS630new-F_PET	100	1.5	0.15	0.015
DYS630new-R	100	2	0.2	0.02
ddH₂O [µl]		55.4		
Primer Mix Volume		100		
DNA Template				**1**
Primer Mix	10		1	**0.8**
Multiplex Master mix	2		1	**4**
ddH₂O				**2.2**
Final Volume				**8**

***Table 4: PCR Protocol for the multiplex Y-chromosomal PCR**. T_a corresponds to the annealing temperature which is set to 63° or 64° degrees.*

Multiplex PCR profile	***Temperature [°C]***	***Time [min:sec]***	***Cycles***
Initial Denaturation	95	15:00	1
Denaturation	94	00:30	
Annealing	(T_a+4)-0.5 / cycle	01:30	8
Extension	72	01:00	
Denaturation	94	00:30	
Annealing	Ta	01:30	40
Extension	72	01:00	
Final Extension	60	30:00	1

***Table 5: Master Mix for the singleplex PCR.** Depending on locus, other primer concentrations were used.*

Singleple: PCR set up	***Conc. [µM]***	***Final Conc. in PCR***		***Volume in PCR [µl]***
DNA Template				1
Primer_F	10	0.2	[µM]	x
Primer_R	10	0.15	[µM]	x
(Primer_R2)	10	0.15	[µM]	x
dNTPs	10	0.1	[mM]	0.1
MgCl2	25	0.3125	[mM]	0.125
Buffer (with MgCl2)	10	1	[µl]	1
Polymerase [u/µl]	2.5	0.1	u	0.05
ddH2O				10-rest
Final Volume				10

Appendix mtDNA HVRI Sequencing

Table 6: Master mix set up HVRI. *For the first PCR for the mtDNA HVRI sequencing.*

mtDNA sequencing first PCR set up	*Conc.*	*Final Conc. in PCR*		*Volume in PCR [µl]*
DNA Template				1
Primer DLF_wobble_F	10	0.1	[µM]	0.2
Primer D5_R	10	0.1	[mM]	0.2
AmpliTaq Gold Master Mix	2	1	[mM]	10
ddH_2O				8.6
Final Volume				20

Table 7: PCR Protocol HVRI. *For the first PCR of the mtDNA HVRI sequencing.*

mtDNA sequencing first PCR set up	*Temperature [°C]*	*Time [min:sec]*	*Cycles*
Initial Denaturation	95	15:00	1
Denaturation	94	00:30	45
Annealing	58	00:30	
Extension	72	00:30	
Final Extension	72	10:00	1

Table 8: Master mix set up for the second PCR HVRI. *Cycle sequencing for the mtDNA HVRI sequencing.*

Cycle sequencing PCR set up	*Conc.*	*Final Conc. in PCR*		*Volume in PCR [µl]*
PCR product				1
Primer DLF_wobble_F	10	0.1	[µM]	0.4
5x CS Buffer	5		[µM]	1.85
BrilliantDye™	2.5	1	[µM]	0.3
ddH_2O				6.45
Final Volume				10

Table 9: PCR Protocol for the second PCR HVRI*. Cycle sequencing of the mtDNA HVRI sequencing.*

Cycle sequencing PCR profile:	*Temperature [°C]*	*Time [min:sec]*	*Cycles*
Initial Denaturation	95	45s	1
Denaturation	95	30 sec	30
Annealing	52	20 sec	
Extension	60	2 min	
Final Extension	12	∞	

Appendix mtDNA Sequencing

***Protocol 1: Lab Protocol for the HVR I**. Amplification and subsequent Cycle sequencing of the mtDNA HVR I.*

Day 1
1. Prepare the PCR according to the protocol.
2. After PCR run a 1.5% agarose gel with 1 microliter of the PCR product (20 min. 140 V)
(Agarose-Gel: 0.75 g of Agarose and 50ml TBE buffer into a beaker, microwave it for 90 seconds, pour the gel into the chamber)

Day 2
1. Prepare the cycle sequencing Master Mix according to the protocol. Brilliant dye is light sensitive!
2. 9 microliters of the Master Mix into a new plate.
3. Dilute the PCR product between 5 and 10 times in a dilution plate. Add 1 microliter of the diluted samples to the Master Mix in the new plate.
4. Close the plate with a grey knobbed seal, vortex and centrifuge.
5. Let run the cycle sequencing protocol on the PCR machine.
6. Follow the Cycle sequencing protocol.

Appendix Cycle – Sequencing clean – up protocol

***Protocol 2: Cycle sequencing clean-up protocol**. Lab instruction to do the clean-up after Cycle sequencing*

For half a plate

- Mix in ($MgSO_4$ labelled) bath
    - 1500 µl ddH_2O
    - 3500 µl EtOH (100%)
    - 1 µl $MgSO_4$
    - Mix all with pipette tip
- Add 75 µl of the mix to each sample.
- Put a rubber lid on (without holes), cover with something hard (pipette tip holder), and vortex it (holding the plate and the hard top with both hands, so that it does not spill)
- Quickly spin it down. Balance the centrifuge precisely (balance it on scale by adding water to the opposite plate).
- Leave the samples in the dark in the centrifuge for 15 minutes
- Centrifuge at 3000 RCF for 30 minutes
- Turn plate and discard the fluid, on paper towel or in the sink
- Put it upside down on a new paper towel and centrifuge at 50 RCF for 15 sec, then 700 RCF for 1 minute
- Incubate at room temperature for 2 – 3 minutes (step back, to not inhale pellet)
- Add 30 µl ddH_2O to each row
- Centrifuge for 20 sec
- Put rubber lid with holes on (check that there are no bleach crystals in holes) and put it in the white and black box
- Add label. Write number down and prepare file on memory stick
- Take samples to Eliane 55L78

***Table 10: Study subjects of genetic part**. All extracts from faecal samples collected at Suaq Balimbing.*

Inventory Number	*Storage solution*	*Field Individual ID*	*Sex*	*Age*	*Y-Haplotype*	*Mt-Haplotype*
2246	Silca	Robert	Male	Unflanged	r	1
4324	Silica	Hotma	Male	Flanged	NA	1
4326	Silica	Arno	Male	Flanged	NA	2
4356	Silica	Payung	Male	Juvenile	NA	1
4364	Silica	Nata	Male	infant	NA	2
4672	RNA Later	Cissy	Female	Mother	-	1
4673	EtOH	Frisca	Female	Mother	-	2
4675	RNA Later	UNK	Male	Unflanged	N	NA
4678	RNA Later	Xenix	Male	Unflanged	I	1
4682	RNA Later	Astra	Male	Flanged	K	1
4690	Silica	Elly	Female	Juvenile	-	2
4691	RNA Later	Fredy	Male	Infant	L	2
4702	RNA Later	Guntur	Male	Juvenile	NA	1
4704	RNA Later	Halte	Female	Mother	-	2
4712	RNA Later	Jimmy	Male	Unflanged	NA	1
4716	RNA Later	Karma	Female	Mother	-	2
4724	Silica	Lilly	Female	Juvenile	-	1
4730	RNA Later	Mamba	Male	Half-Flanged	H	1
4733	Silica	Metty	Female	Mother	-	1
4734	RNA Later	Negi	Male	Flanged	H	1
4736	RNA Later	Otto	male	Flanged	M	NA
4744	RNA Later	Simpson	male	Flanged	H	NA
4746	RNA Later	Sumo	male	Flanged	I	NA
4751	EtOH	Vincent	Male	Unflanged	I	1
4752	RNA Later	Kombek	Male	Flanged	I	1
4753	EtOH	Chick	Female	Mother	-	1
4754	EtOH	Chindy	Female	Infant	-	1
4755	EtOH	Chuck	Male	Infant	NA	1
4756	EtOH	Heiger	Male	Flanged	H	1
4757	EtOH	Intai	Female	Mother	-	1
4758	EtOH	Leo	Male	Unflanged	I	NA
5505	EtOH	Astra	Male	Flanged	NA	1
5507	EtOH	Sumo	Male	Flanged	NA	1
5521	EtOH	Hans	Male	Unflanged	NA	1
5547	EtOH	Aqra	male	Unflanged	S	1
5548	EtOH	Rakus	male	Unflanged	P	NA
5549	EtOH	Dian	Male	Flanged	I	1
5550	EtOH	Robbi	Male	Unflanged	H	2
5554	EtOH	Yoyo	Male	Unflanged	S	1
5556	EtOH	Dodi	Female	Mother	-	1
5557	EtOH	Lisa	Female	Mother	-	1
5561	EtOH	Nuk	Male	Infant	S	1
5565	EtOH	Diddy	Male	Infant	NA	1
5567	EtOH	Precilla	Female	Mother	-	1
5569	EtOH	Gura	Male	Unflanged	O	1
5579	EtOH	Eddy	Male	Flanged	NA	1
5580	EtOH	Alice	Female	Mother	-	1
5581	EtOH	Tina	Female	Mother	-	2
5583	EtOH	Shera	Female	Mother	-	1
5591	Silica	Rakus(guess)	Male	Unflanged	NA	1
5602	Silica	Flanged male	Male	Flanged	S	1
6030	Silica	Flanged male	Male	Flanged	H	1
6035	Silica	Saruman	Male	Flanged	Q	1

Study Subjects Behaviour

ACTIVITY DEFINITIONS

Table 11: Activity definitions. *From orangutan network https://www.aim.uzh.ch/de/orangutannetwork/gsp.html.*

„Activity	*Short name*	*Description*
Move	M	all locomotion, usually between trees/patches, if within patch movement should last for more than five seconds and not be simultaneously with feeding
	Mq	quadrupedal walking on horizontal substrate
	Mb	Brachiating
	Mt	Treesway
Rest	R	sit, lie, stand, hang for more than 5 seconds, not doing anything else
	Rs	sit or lie on nest (= sarang)
Feed	F	processing, gathering, ingesting food items, some movement (less than 5 seconds duration) within a patch consistent with these goals may be included
	Ffr	feed on fruit note ripe/unripe in item column (if clearly feeding on seeds, OK to make new subcategory F sd)
	Fsd	feed on seeds (still note ripe/unripe in item column)
	Ffl	feed on flowers; note details in item column
	Fyl	feed on young leaves
	Flv	feed on mature leaves
	Fveg	feed on other vegetative plant parts, note details in item column
	Fins	feed on insects, note kind in item column
	F bk	feed on bark
	Foth	feed on something else, describe in item column
	Fw	drink water, note from where in item column and how: directly with mouth, drip from hand, drip from leaves, cupped hand etc.
	TF	Only for young offspring: trying out food / tasting without really eating; add same items as for F
Suckle	D	only for immatures: drink milk from mother
Nest	N	build nest; always note special features (roofs, repair old nest, etc.) - use checklist for night nest (+ nest-list for mother-offspring)
Social	Soc	all social interactions. Write kind in item column (sex, agonistic, groom, long call or display if directed at other orangutan); give details in sosial column, including how interaction ended
Social Play	SP	social play with a partner; write kind in item column (wrestle, chase); note details in sosial column and include position (on/above nest, hanging, upside down, etc.) (Remember appropriate approach/leave entries)
Auto play	APO APM	Solitary object play: “nonfunctional” manipulation of objects Solitary movement play: repetitive movement such as twirling, swinging etc
Cling	C	only for immatures: being carried clinging to the mother’s body, note whether mother supports offspring with arm or leg in item column (Note that Cling is not an exclusive category and may be used in combination with other compatible activities; see #6 Rules for Mother-Offspring)

If in doubt use hierarchy Soc > M > F > R”

Social interactions

***Table 12: List of agonistic behaviours**. Behaviours that are negative against other individuals.*

behaviour	*description*
unprovoked retreat/submission	in response to a 'neutral" approach, other one shows signs of fear (submissive mips) and retreats
active displacement	fast approach, may include touch or enter into nest resulting in retreat of the approached individual
chase	pursuit over more than 10 m or into other tree
flee	fast retreat from other individual
flee towards	approach and stay close to more dominant individual after third individual approached/threatened
bite	"
slap	"
pull	"
push	"
fight	whole body wrestle
display	sway, drop (or throw) branches; push over dead tree trunks; make clear whether directed at other orangutans or at observers

***Table 13: List of other social behaviours.** Other social behaviours might require a higher level of social tolerance.*

kiss	*mouth to mouth touch ("smell")*
embrace	at least one arm touches shoulder/back of other individual
groom	skin/hair care (with fingers while looking at this) of other individual; describe details: which body part, wound
Social watch	close attention to action of other e.g. feeding, manipulating, tool-use; describe details and distance (appropriate approach/leave checklist should also be filled out)
look away	look away from ("ignore") other's action at close range
bridge	form a bridge between trees to let smaller individual transfer
beg	outstretched hand to other, with or without vocalization
Social play	Two individuals playing with each other

Table 14: Study subjects behavioural part. *Date first seen is the date an individual was photographical reported in the study area for the first time. Follow time relates to focal follow time, Observation time is the sum of follow time and time an individual was observed in association with another focal animal, when it was not focal itself.*

Orangutan name	*Sex-Age Class*	*Date First seen*	*Follow time*	*Observation time*	*Number peering events*
Aqra	Unflanged Male	04.04.2013	97.1	216.1	0
Barba	Unflanged Male	09.08.2011	0	79.0	0
Beo	Unflanged Male	05.09.2016	38.7	170.7	37
Caesar	Unflanged Male	04.08.2016	89.4	165.6	56
Derek	Unflanged Male	26.03.2013	25.6	147.6	3
Dru	Unflanged Male	04.11.2013	31.6	193.0	22
Greyhem	Unflanged Male	23.03.2017	0	148.0	1
Gura	Unflanged Male	15.05.2008	245.7	328.7	35
Hape	Unflanged Male	04.09.2016	7.2	133.2	0
Horseface	Unflanged Male	01.01.2014	79.8	223.1	19
Jarno	Unflanged Male	28.05.2008	5.9	63.9	0
Koral	Unflanged Male	04.06.2013	0	111.0	0
Lanzelot	Unflanged Male	07.10.2017	0	78.0	0
Lukas	Unflanged Male	02.06.2018	10.8	18.5	0
Marco	Unflanged Male	12.08.2017	40.2	107.2	3
Milo	Unflanged Male	12.11.2008	41.4	194.4	1
Momok	Unflanged Male	13.04.2018	12.2	14.3	0
Nibla	Unflanged Male	17.11.2010	11.3	41.3	0
Ozhar	Unflanged Male	27.01.2017	10.7	97.7	0
Rakus	Unflanged Male	19.03.2009	53.6	196.6	6
Reek	Unflanged Male	15.12.2014	13.4	118.4	17
Robbie	Unflanged Male	09.08.2011	0	51.0	0
Robert	Unflanged Male	26.06.2013	48.0	58.9	3
Sambal	Unflanged Male	16.11.2013	12.4	148.4	4
Saudade	Unflanged Male	08.11.2013	24.9	60.9	15
Shane	Unflanged Male	05.06.2013	19.2	56.2	3
Smeagol	Unflanged Male	05.02.2011	26.3	121.6	3
Tristan	Unflanged Male	21.11.2013	0	112.0	0
Tom	Unflanged Male	05.04.2015	0	22.0	2
Ulysses	Unflanged Male	28.08.2007	16.3	112,3	0
Viktor	Unflanged Male	02.11.2013	0	52.0	9
Walter	Unflanged Male	17.12.2010	0	6.0	0
Willy	Unflanged Male	01.09.2007	0	15.0	0
Yoyo	Unflanged Male	17.11.2011	35.1	133.1	1
Zackey	Unflanged Male	09.05.2018	0	146.0	1

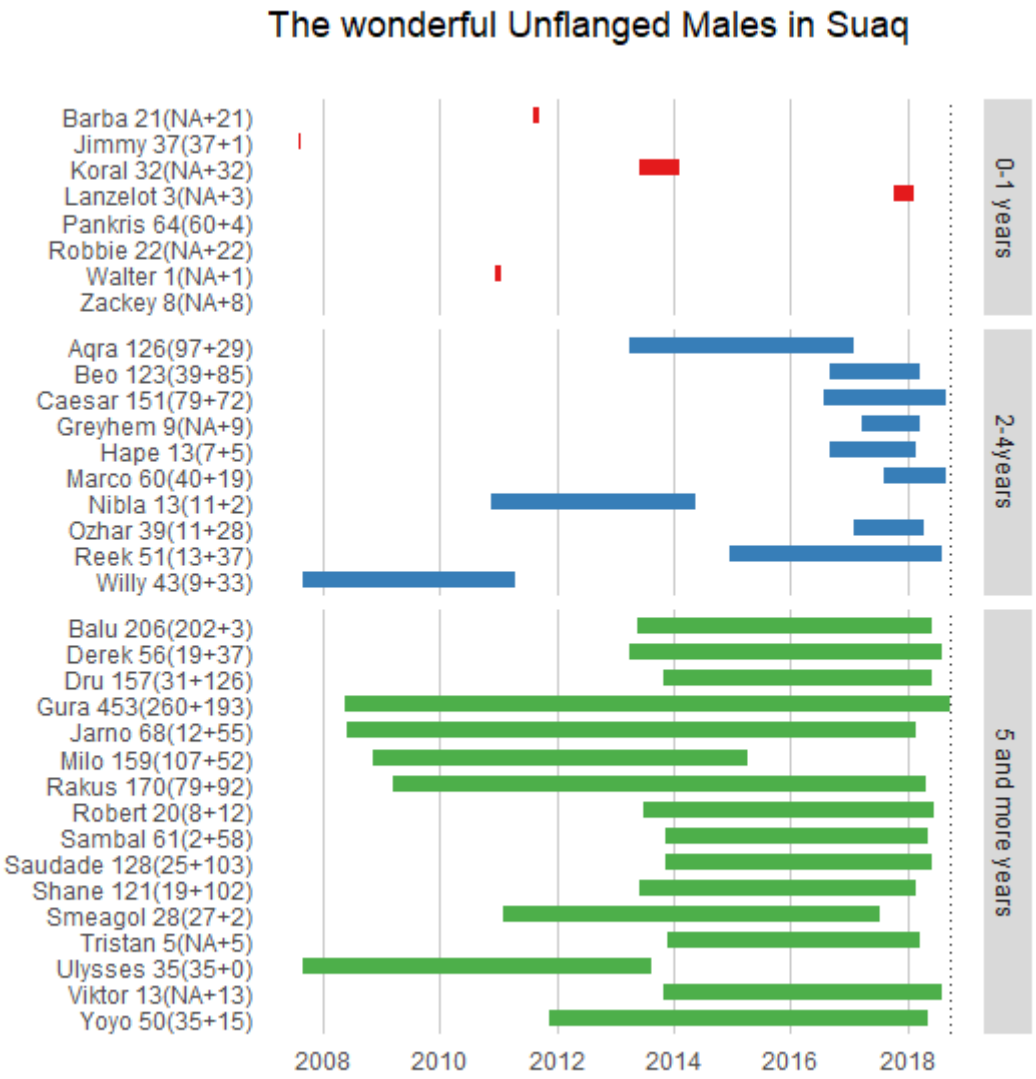

Figure 1: Presence table of unflanged males at Suaq. *Bars reach from date of first report to date of last report of each unflanged male. In brackets number of focal follow hours + number of association hours.*

Peering opportunities

***Table 15: Association with unflanged males**.in this thesis this is used as 'Opportunity to observe a certain sex-age class.'*

Associating Sex age class	*Prop. of unflanged follow time*
Adult female	0.11
Unflanged male	0.1
Flanged male	0.03
Juvenile	0.04
infant	0.1

***Table 16: Activity proportions of females**. This is used to correct for 'activity proportion of resident individuals.'.*

Activity	*Proportion of time*
Feeding	0.49
Nesting	0.02
Other	0.46
Social	0.01

Polymorphic Loci

***Table 17: Locus of non-variable Locis.** Here I reported the number of individuals that where not variable at certain loci.*

Loci	*N*
DBY13	32
SMCY12_26	34
SMCY14	34
DYS502	33
DYS532	33
DYS645	29
Y6C2	35
DYS556	32
DYS503	33
DYS587	29

***Table 18: Overview variable Loci.** I reported number of individuals, number of alleles, locus diversity and unbiased diversity.*

	Locus	*N*	*N_{Allele}*	*N_e*	*h*	*uh*
SNPs	SMCY12_337	34	2	1.545	0.353	0.363
	DYS577	31	2	1.067	0.062	0.065
microsatellites	DYS577	31	2	1.067	0.62	0.065
	DYS510	30	4	1.915	0.478	0.494
	DYS561	33	3	1.283	0.220	0.227
	DYS630	35	3	2.910	0.656	0.676

Further assessment of the social network

To asses unflanged males' position in the social network I investigated additional measures of the social network such as Betweenness Centrality, Eigen-centrality and weighted degree. Even though unflanged males seemed to have a higher eigen centrality and a higher weighted degree there were no significant differences between all sex-age classes.

To bypass the bias of the DAI, my edge weight, due to the differences in follow effort, I took the residuals from the General linear mixed model presented in 3.2.1.2 Table x and continued with those as my new edge weight. These values showed a smaller variation than my initial edge weight, however they still were influenced by the observation time (Figure x). Nevertheless, I re-calculated all network parameters using the residuals as my edge weight. This resulted in no significant differences of the sex-age classes.

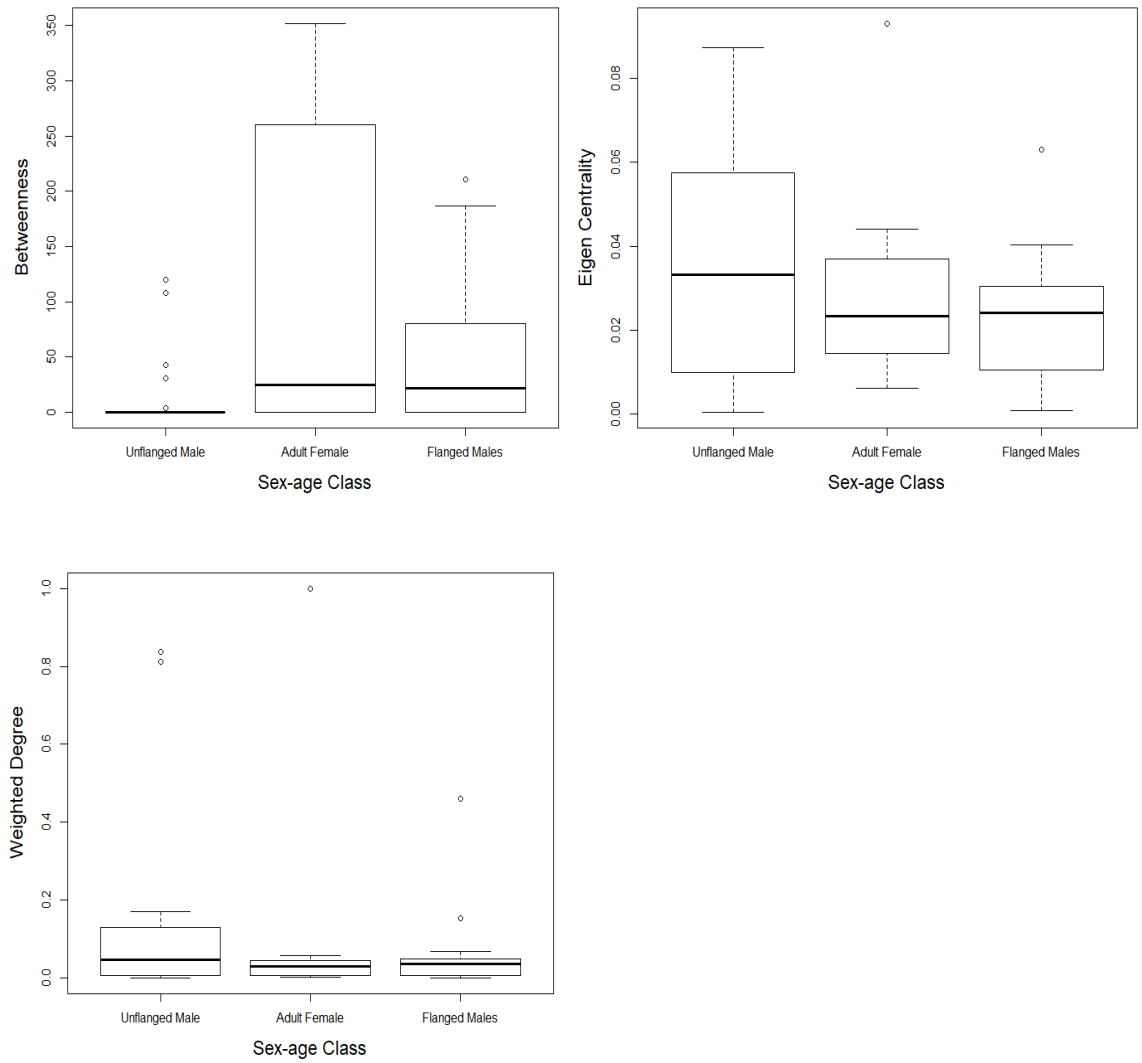

Figure 2: Additional measures of social network parameters. *A) Betweenness Centrality. B) Eigen centrality. C) Weighted degree.*

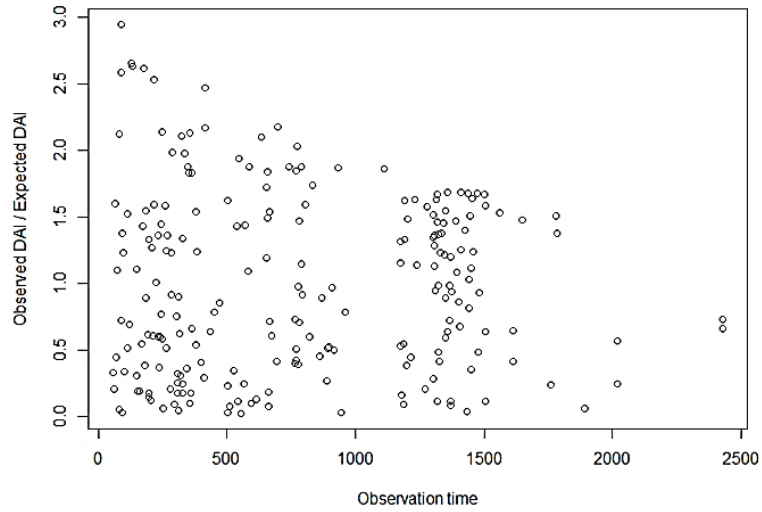

Figure 3: Residuals of GLMM with DAI as dependent variable. *Residuals still were influenced by the observation time.*

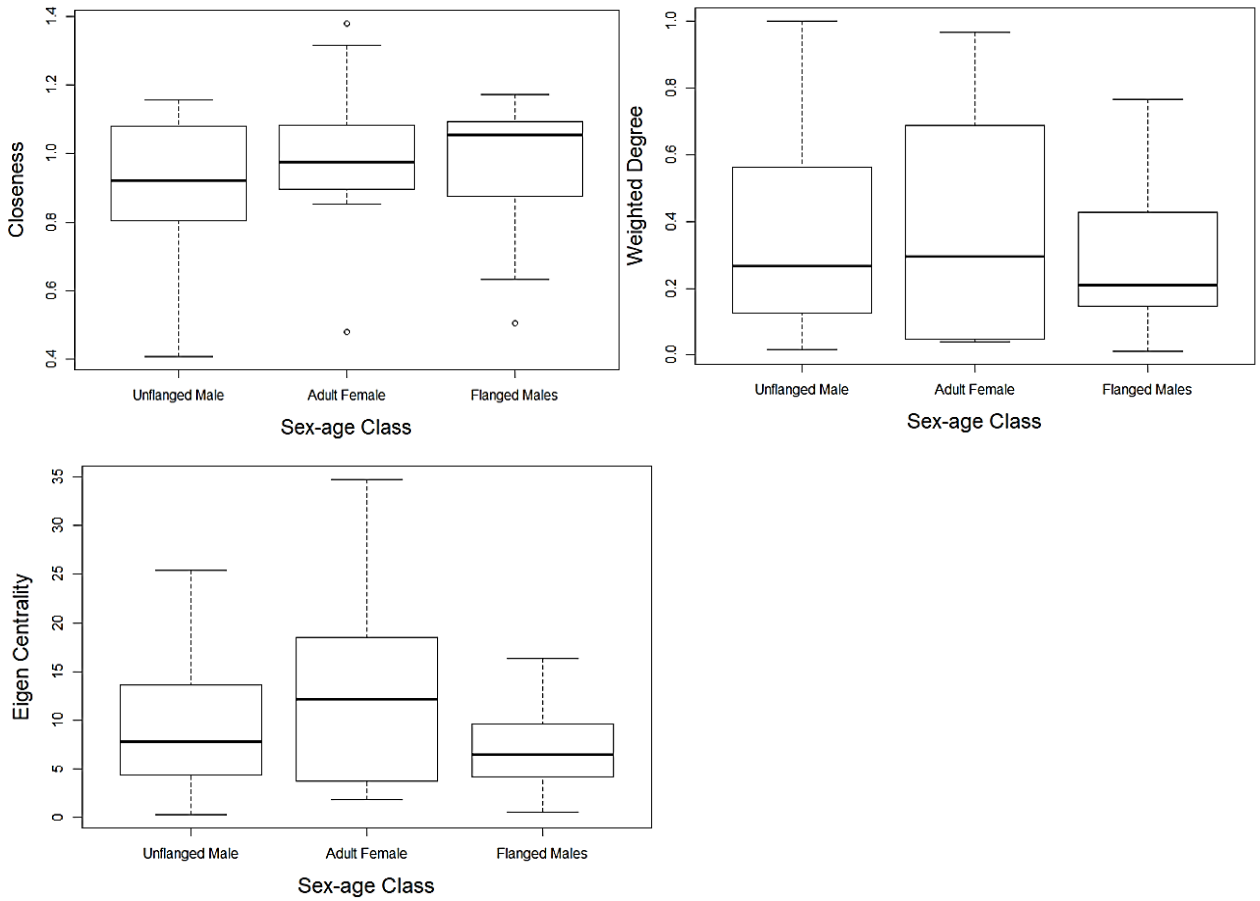

Figure 4: Social network parameters based on residuals. *Re-calculation of all above mentioned centrality measures.*

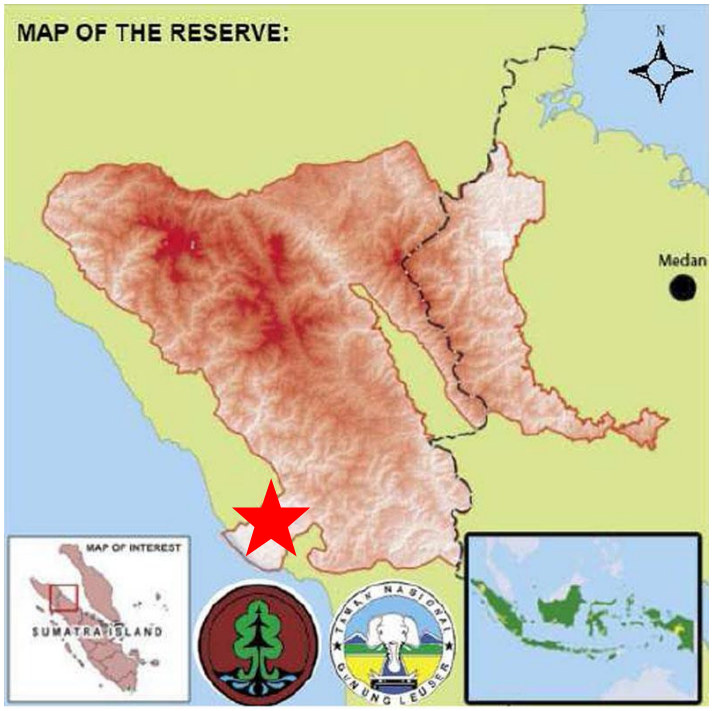

Figure 5: Map of the National Park Gunung Leuser. *Star indicates the approximate location of Suaq Balimbing. Map source: unesco.org*