MSc in Human Evolution and Behaviour Dissertation

COMING OF AGE IN THE TREES. THE DEVELOPMENT OF INDEPENDENCE IN BORNEAN ORANG-UTANS IN CENTRAL KALIMANTAN

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ABSTRACT

Bornean orang-utans are semi-solitary primates with the longest dependency period among the great apes. Understanding of how the activity budgets of mothers and offspring change during this period is limited. This study draws on data from twelve wild Central Bornean orang-utans in The Sabangau Forest in Central Kalimantan. Six habituated mother orang-utans, each with one dependent offspring, were followed for up to 16 hours each day, and their behaviour, including feeding, playing, travelling, resting and socialising, along with measurements of mother-offspring proximity were recorded every 5-min, over a period of approximately five years. Rather than seeking to analyse all of the different behaviours observed, this study focuses on two of them. The first is feeding, because self-feeding is key to independence. The second is proximity between mother and offspring, because before independent offspring can live outside of the mother's range they must first separate from her. Levels of offspring feeding and mother-offspring proximity were significantly related to age. There was a non-significant tendency between mother feeding and offspring age. There are some suggestive trends for sex differences in dependent offspring orang-utans. Data collected from a larger number of individuals, over a longer period of time, would increase the study's power.

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INTRODUCTION

Overcoming the challenges involved in raising individuals who can survive long enough to reproduce and pass on genetic traits is central to a species' propagation and evolutionary success (Darwin 1871). In mammals, the length and intensity of post-weaning parental care is an important factor, which varies greatly. For example, rabbits, *Leoporidae*, are born altricial, that is relatively undeveloped, and in large litters. Parental care persists for a short period of time before the offspring are weaned and become independent. Gorillas, *Gorilla gorilla*, on the other hand, are born relatively precocious, that is developed, and in small litters of one and sometimes two offspring. Weaning occurs at about four years, and parental care subsists for a few years after this (Galdikas & Wood 1990). Even within a species, the extent of parental care varies. In Humans, *Homo sapiens*, geographical location, social, and financial influences all play a role (Main 1990). In non-human animals, food availability and resource distribution are likewise influential.

Rates of reproduction also vary across species, depending on ecological and biological constraints. These variations can be understood as different strategies designed to achieve the maximum relative fitness (Klopfer 1981, Pianka 1970, Wilson & MacArthur 1967). R strategists have large numbers of offspring at regular intervals, as their intrinsic rate of natural increase allows, whereas K strategists have low numbers of offspring less often, limited by the carrying capacity of their niche. R and K strategies are relative terms of reference, and no species falls clearly into one of the two categories (Fisher 1930). Humans, for instance, have small litters, usually one infant, born relatively precocious; at first glance a typical K-strategist. However, because the encephelization quotient in humans is so high, that is brain size relative to body size, a fully developed human brain would not fit through its mother's birth canal. Therefore a new-born human, although precocious in many ways, still has significant further development to undergo, postnatally. This would indicate that *H. sapiens* might be closer to the r end of the r-K continuum than their small litter size suggests.

Environment, namely tropical or temperate, is correlated to both reproductive strategy, that is r or K selection, and the level of parental care. It has been predicted that, in the relatively constant climate of the tropics, where external events are less often the cause of deaths, those individuals who die prematurely do so because they are less fit than their peers. In these areas, K selection will be favoured. In temperate zones, where random events, which kill off individuals regardless of their competitive ability, are more regular, mortality is less connected to phenotype. In these areas r-selection will be favoured (Dobzhansky 1950). So in a tropical dwelling species that favours K-selection, such as the Bornean orang-utan, *Pongo pygmaeus*, one would expect a small clutch, and a prolonged period of parental investment, with offspring being born relatively precocious, but with significant further development to undergo postnatally. The time during which the offspring is dependent on parental care after birth is known as the dependency period. By the end of this period, Bornean orang-utans must have acquired a wide range of knowledge and skills, one of the most basic of which is the ability to feed themselves. In addition, given their post-dependency solitary lifestyle, they must have physically distanced themselves from their mother, with female offspring moving to a neighbouring range and males even further afield (Morrogh-Bernard 2011). This study focuses on how these two factors -feeding and proximity between mother and offspring- vary over time, in an attempt to better understand how Bornean orang-utans come of age.

The Dependency Period

The length of dependency is influenced by a number of factors: resource availability in the given environment, rate of reproduction, timing of life history events, stage of development at birth, and the social structure surrounding a new member of a group of animals. In primates, the dependency period is often prolonged, but in some species gregariousness (sociality) means that alloparenting (when an individual who is not the parent acts in a parental role) and other advantages of being social, may reduce the load on the biological mother, allowing her to have another offspring, while the current one is still dependent (van Adrichem et al. 2006). This implies that we can also expect the length of dependency to increase the more solitary individuals of a species are.

In orang-utans, *Pongo spp*., a semi-solitary genus of great ape, a mother's young will depend on her for resources and guidance for a period of six to eight years (Galdikas & Wood 1990, van Adrichem et al. 2006, Wich et al. 2004). This period of dependency dictates an inter birth interval of equal length, and is the longest of all of the great apes (Tab. 1). At the end of this dependency period, a mother either has another infant or reverts to the semi-solitary state in which she existed before having an offspring, where social interactions are rare and short-lived. In mothers with male offspring and mothers with female offspring this may have different implications. Female orang-utans will acquire a home range adjacent to that of their mother when they reach independence (Morrogh-Bernard 2009). Therefore, the mother will likely still encounter and socialise with her daughter occasionally. Male offspring will venture far away from the natal range that they share with their mother, and when independent will very likely not encounter their mother at all. What is not known, and what this study, in part, seeks to throw some light on, is whether these different male and female endpoints are presaged by different parenting styles, and whether transitioning towards independence varies between male and female offspring.

There is a paradox inherent in the drawn out life-history of Bornean orang-utans. For six to eight years, an individual of a species that is usually solitary, lives in constant proximity to another growing and developing individual, who makes increasing demands of food and space. Proximately, it would be more efficient to detach from an offspring, who is a drain on time and resources, but ultimately a high level of parental investment will mean that the offspring will live longer and pass on parental genes (Darwin 1871, Klopfer 1981). A shift from dependence to independence most likely coincides with a threshold of the carrying capacity of the environment being crossed, necessitating that a portion of the inhabitants (here, the offspring) find a new range and niche. The prolonged period of time during which a mother shares her limited resources with her offspring must be important to development, otherwise the costly investment would not be made. There are two main hypotheses for why this period of time is so important in orang-utan development, and why it exists.

Table 1: Great Ape inter birth interval (Galdikas & Wood 1990). Estimates based on populations of gorillas in Virunga, Rwanda, chimpanzees in Gombe, Tanzania, orang-utans in Tanjung Puting, Indonesia and Ganji humans in Papua New Guinea.

Species	Inter-birth interval (years)
Gorilla	3.8
Chimpanzee	5.6
Orang-utan	7.7
Human	3.6

The solitary lifestyle hypothesis

The solitary lifestyle hypothesis considers the semi solitary social structure of orang-utans as an adaptation to patched resources and a dictator of the long dependency period of immature orang-utans (Van Noordwijk & Van Schaik 2005). According to the solitary lifestyle hypothesis, a mother cannot associate with more than one offspring at a time because she cannot provide enough resources to simultaneously support a second offspring. Therefore a mother must prepare one offspring entirely for independence before having another. As this offspring grows, he or she begins to make a demand on the mother that is comparable to two offspring and at a certain point the mother becomes unable to support him or her. The large offspring must break away, or be forced away, from the mother, allowing her to have another smaller infant that she can realistically support into maturity. In orang-utans, weaning coincides with the end of the dependency period at six to eight years. Interestingly, a mother begins to impose independence on an offspring when she is already pregnant, rather than imposing independence and then attempting to become pregnant (van Adrichem et al. 2006). The late weaning of orang-utan offspring may exist as a mechanism to prevent a mother conceiving until her offspring is able to nutritionally provide for itself.

The development of skills hypothesis

The development of skills hypothesis considers the possibility that the reason that the dyad remains together for as long as eight years is in order to allow the offspring the necessary time to acquire and develop the skills that will ensure his or her survival, when independent (Galdikas & Wood 1990, Van Noordwijk & Van Schaik 2005). In an environment where resources are patchily available and vulnerable to seasonal change, a long dependency period allows an offspring sufficient opportunity to observe the mother using the skills that he or she will need when they are independent to forage, build nests and travel in a variety of seasonal conditions. In the case of Bornean orang-utans, offspring must, for example, learn to distinguish between the over 400 species of fruits, flowers, leaves and shoots, eggs, invertebrates, honey, bark and epiphytes that are edible from those that are not (Ciszek & Schommer 2009). Unsurprisingly, this takes some time. According to the development of skills hypothesis, the multi-year lactation, and late weaning of orang-utans (van Noordwijk et al. 2013) is therefore simply a by-product of the need for the offspring to be around the mother for a sufficient period to acquire these essential skills.

While the solitary lifestyle hypothesis is concerned primarily with the consequences of a resource poor environment on reproductive strategy and parental investment, and the development of skills hypothesis on the time it takes for the offspring to learn what it needs to survive, neither hypothesis discounts the other. Indeed the two hypotheses are compatible, and it can be difficult distinguish which of the two possibilities a given set of data may support (van Adrichem et al. 2006).

Feeding

The ability to feed oneself is paramount to being independent because without sufficient calorific intake life is unsustainable. Foraging nutritious food is therefore an essential skill that individuals must acquire by the end of the dependency period (see Development of Skills Hypothesis, above). Bornean orang-utans infants (0-2 years) rarely forage independently. Instead they learn how to forage by following their mother's lead, eating the foods she locates, observing the skills she uses, and imitating them (Jaeggi et al. 2010). After two years of age, the offspring's movements become more independent of the mother, and they begin to practise the foraging skills they have learned, and continue to learn, through observation of the mother. By eight years of age they will need to have learned how to forage independently. This prolonged period of association between mother and offspring, in combination with the use of extractive foraging techniques, facilitates observational learning (Galef & Giraldeau 2001). For example, immature orang-utans have frequently been observed biting open a piece of dead wood, and then carefully examining it for termites. Observational data from one hour before and after a termite-feeding bout by a mother was analysed to compare the amount of time the offspring spent manipulating dead, i.e. potentially termite rich, wood during this time. Offspring were significantly more likely to manipulate dead wood in the hour after they observed their mothers foraging for termites (Jaeggi et al. 2010). There is similar evidence with nest building (Prasetyo et al. 2009). Whether initiated by the mother or by the offspring themselves, this apparent practicing of skills, especially in foraging, suggests that the skills acquired and perfected during the dependency period prepare the offspring for independence. Likewise, one would expect the proportion of the activity budget spent feeding to increase throughout the dependency period, until it reaches that of an adult, a level which differs between males and females (Wich et al. 2004, Galdikas 1988). The mother's feeding behaviour also changes when she has an offspring. The proportion of the activity budget that she spends feeding decreases in the few days after she has given birth (Mitani 1989). In bottlenose dolphins, *Tursiops truncates*, we see the mother's rate of feeding decrease up to the point when the offspring is weaned, and then continue to decrease as the offspring begins to feed independently (Kastelein et al. 2002).

Proximity

By definition, being solitary requires having physical distance between yourself and other individuals. The amount of space required is dependent on the size of the organisms in question and the carrying capacity of the environment. Given these constraints, to be solitary an individual needs enough space to allow little to no interaction with other parties. Therefore, a proxy for evidence of immature orang-utans becoming solitary and independent may be a reduction in mother-offspring proximity, as

measured by an increase in the time mother and offspring spend at some distance from each other. The changes that occur in mother and offspring proximity, as the offspring develops both socially and physically have been explored in captive chimpanzees, *Pan trogladytes*, and Bornean orang-utans, *Pongo pygmaeus*. In both species, infants remain in physical contact with their mothers nearly all the time for the first four months of their lives. In orang-utans, the contact time between mother and offspring begins to decrease in the fifth month, to 55 %. In chimpanzees close physical proximity only begins to decrease in frequency in the seventh month, to 83 % of observation time (Miller & Nadler 1981). This suggests that the relatively long inter birth interval of orang-utans may not be a result of slow offspring development, but a product of how much they learn and adapt to become successful mature orang-utans (Jaeggi et al. 2010, Van Noordwijk & Van Schaik 2005). The early break from close contact between mother and offspring may well be a precursor to the solitary nature of mature orang-utans. The disparity between the timing of this break in orang-utans and chimpanzees may be explained as follows. Orang-utans are semi-solitary when independent; chimpanzees remain very social in independence, living in large polygynous groups. The development of social play and solitary play in both species seems to reflect this: young orang-utans appear to play more solitarily (on their own) as they age, whereas chimpanzees tend to play more socially as they grow older (Fig. 1). This suggests that the development of a solitary or social nature develops early in individuals, at an age before their sociality will directly affect their reproductive success and ability to mate successfully. It is worth noting that in the lab-based study (Fig. 1) (Miller & Nadler 1981), all of the focal orang-utans infants were males. This may or may not be a source of bias, depending on whether dependent males and females display significantly different social behaviour. Given that, ultimately, males and females adopt different ranging behaviours this is an interesting possibility.

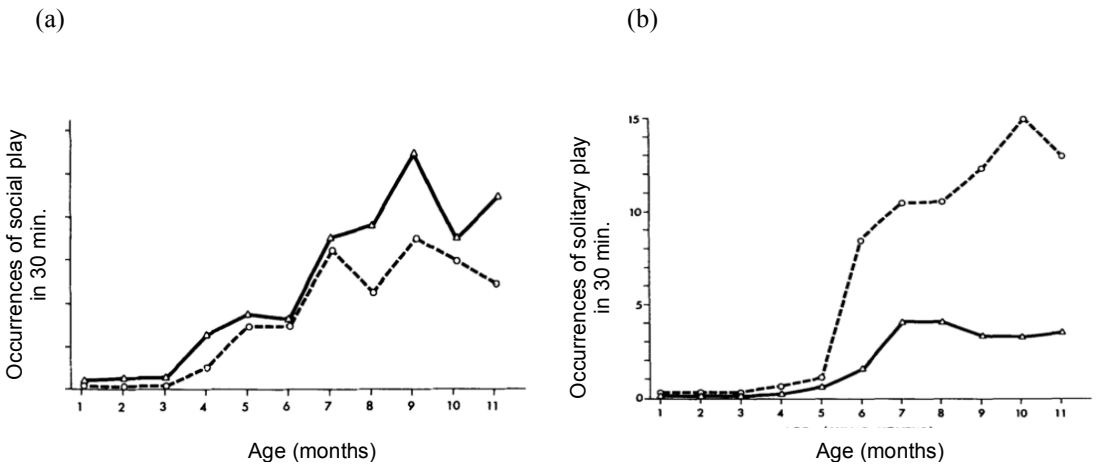


Figure 1: Rates of play in captive chimpanzees and captive orang-utans (Miller & Nadler 1981).
--------- = orang-utans, ———— = chimpanzees.

(a) Frequency of social play in orang-utans and chimpanzees.
(b) Frequency of solitary play in orang-utans and chimpanzees.

The "sphere of exploration"

It has been established that proximity between mother and child is strongly correlated with offspring's age across various species. The average distance between mother and offspring increases as the offspring ages, as does the average "sphere of exploration" (Thomas & Taber 1984: 1081; Boinski & Fragaszy 1989, Hinde & Atkinson 1970, Thomas & Taber 1984, van Adrichem et al. 2006, Van Noordwijk & Van Schaik 2005). Age may also correlate with proximity when performing certain behaviours. Depending on the behaviour, a decrease in proximity may indicate a rise in confidence levels (the infant's, the mother's, or both), or attainment of an age at which the independent performance of an activity is prioritised above close proximity of mother and infant. For example, an experiment examining bottlenose dolphins', *Tursiops spp.*, mother-infant proximity was studied under two different conditions (Mann & Smuts 1999). One was an area where dolphins were not provisioned by humans and had to hunt and forage for food independently. The other was in an area in which humans provisioned them. In areas with no provisioning, younger offspring spent significantly more time in closer proximity to their mother than in provisioned areas. In the provisioned areas, mothers stayed in shallow water close to those provisioning them, while allowing infants to venture further away, into deeper water. This suggests that the ease of finding and eating food has an effect on mother-infant proximity, although it may also be that the presence of humans, who could potentially provide protection from predators of the dolphins, influences the proximity of the mother and offspring.

The study of spatial relationships in southern right whales, *Eubalaena australis*, reveals a positive correlation between body size and average distance between mother and offspring. This finding highlights the importance of present and potential body size of the offspring and the significance of physical growth in the developmental period. Physical growth is correlated with both age and sex, and it therefore follows that distance between mother and offspring will be too (Thomas & Taber 1984). The older a whale calf, the more they seem to instigate and maintain close proximity to their mothers, becoming less dependent on being retrieved maternally. A proximity quotient, a value calculated to represent distance as well as who was responsible for creating or closing distance between a mother and offspring, was calculated for these whale calves (Thomas & Taber 1984). Examining the dynamics of which dyad member creates distance and proximity is revealing of changing pressures on developing offspring. In yellow baboons, *Papio cynocephatus*, and rhesus macaques, *Macaca mulatta,* the initial state is that infants create distance between themselves and their mothers, and mothers are responsible for decreasing that distance. Later the roles are reversed (Hinde & Atkinson 1970, Hinde & White 1974). This highlights something not yet directly considered: the process of weaning conflict. It has been found in several studies, involving multiple species, that the mother is the one, of the mother-offspring pair, who initiates independence by rejecting attempts by the offspring to suckle (Hinde & White 1974, Nash 1978, Rosenblum 1971, Struhsaker 1971). In whale calves "the mother's decreased rate of approaching her calf may be the factor that causes the final separation" (Thomas & Taber 1984: 1081). Similarly, between day 20 and 30 after birth, a mother tarsier, *Tarsius bancanus*, begins to create distance between herself and her offspring. This is attributed to the mother creating periods of no contact in order to test the infant's reaction and therefore gauge his or her readiness for independence (Roberts 1994). As in whale calves, the responsibility for maintaining

proximity, or lack thereof, shifts from mother to infant in tarsiers, which are solitary primates (Roberts 1994). The consideration of proximity, in relation to the frequency of suckling and weaning, is therefore of great interest and could indicate important events in the approach to independence undergone by dependent individuals.

METHODS

Study Species: Bornean Orang-utans

Taxonomy

The subfamily, *Ponginae*, to which orang-utans belong, split from the African great ape lineage between 15.7 and 19.3 million years ago (mya). There are two extant species of orang-utans: *Pongo pygmaeus* and *Pongo albelii*. The two species diverged about 0.4 mya, and a low level of gene flow between the species exists today. The Bornean orang-utan falls into three subspecies; North-west Bornean orang-utan, *Pongo pygmaeus pygmaeus*, in Sarawak and northern West Kalimantan; Central Bornean orang-utan, *Pongo pygmaeus wurmbii*, in southern West and Central Kalimantan; North-east Bornean orang-utan, *Pongo pygmaeus morio*, in East Kalimantan and Sabah. *Pongo pygmaeus wurmbii* is the focal subspecies of this study (Ancrenaz et al. 2008, Brandon-Jones et al. 2004, Cawthon Lang 2005, Wilson & Reeder 2005).

Biogeography

Sumatran orang-utans*, Pongo abelii*, and Bornean orang-utans*, Pongo pygmaeus,* are found on the Indonesian and Malaysian islands of Sumatra and Borneo, primarily in peat swamp forests and mixed dipterocarp forests (Morrogh-Bernard 2009). A history of over 100 years of *Pongo* fossil discovery has revealed the biogeographic range of orang-utans as far back as the Early Pleistocene (2.5-0.8 mya), when orang-utans spread over a considerably larger area than they do at present. Prehistoric *Pongo*, including *Lufengpithecus, Sivapithecus* and *Gigantopithecus,* occupied areas across the Indomalayan region, including south China, Vietnam, Laos, Cambodia, Thailand, Peninsular Malaysia, Sumatra, Borneo and Java (Fig. 2) (Tshen 2016).

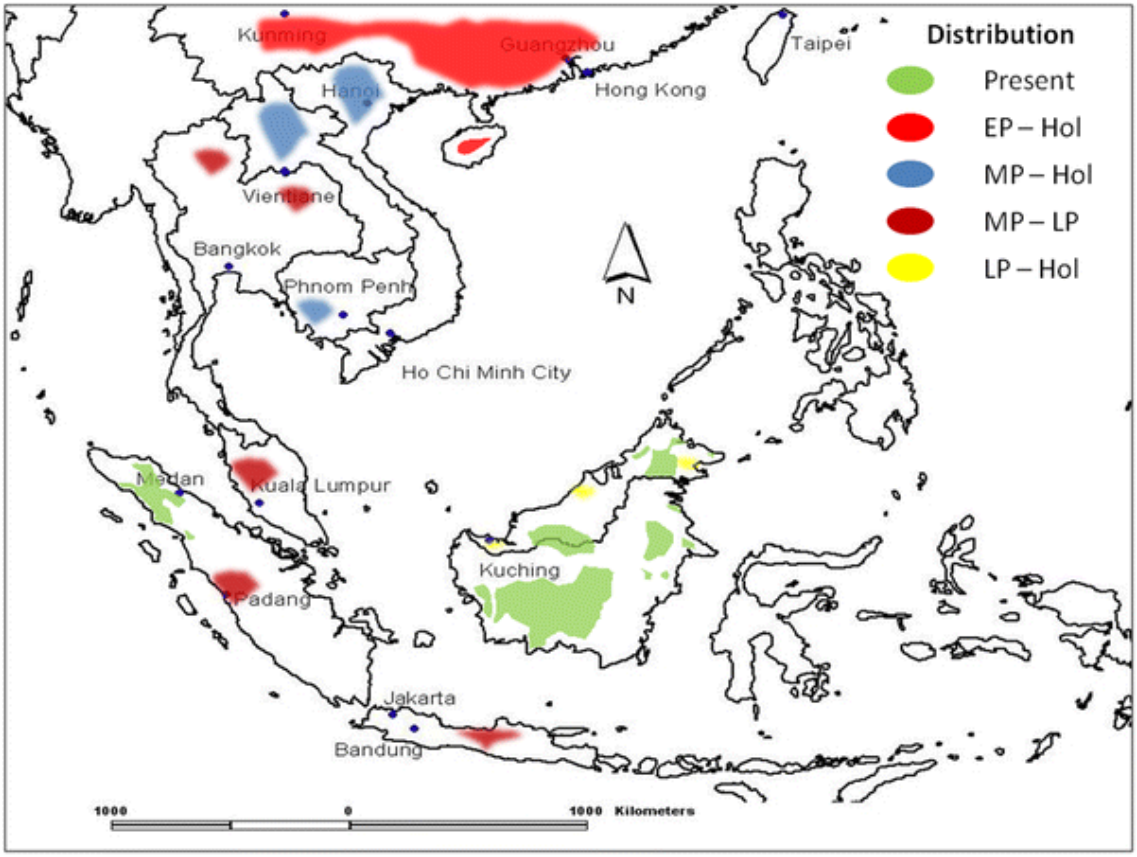


Figure 2: Temporal and geographical distributions of fossil and living *Pongo* across south-east Asia region from Early Pleistocene until present. *EP*-Early Pleistocene (2.6- 0.8 mya), *MP*-Middle Pleistocene (0.8-0.125 mya), *LP*-Late Pleistocene (~0.125 mya), *Hol*-Holocene (~0.01 mya). Image and caption taken from Tshen 2016.

Ecology

Orang-utans are the largest extant arboreal mammals. Spending most of their time in the trees, orang-utans do occasionally come down to the ground: to feed, to travel in areas of low tree density (Loken et al. 2013) or to travel more efficiently where trees may not be strong enough to support their weight,. They also come to the forest floor to escape the midday heat, or indeed to play. (On a particularly hot day, in Jun 15 SK observed a mother and her infant performing forward-rolls on the forest floor). Bornean orang-utans are more terrestrial than their Sumatran relatives, probably in part due to the fact that they have very few ground dwelling predators, and can therefore safely travel along the forest floor. In contrast, Sumatran orang-utans face predation from the Sumatran tiger*, Panthera tigris sumatrae*, and so must avoid spending prolonged periods of time on the ground (Cawthon Lang 2005, Galdikas 1988).

Bornean orang-utans eat over 500 species of plants (Ancrenaz et al. 2008). Their diet primarily consists of fruits. They also feed on flowers, leaves and shoots, invertebrates, eggs, honey, bark and epiphytes (Ciszek and Schommer 2009). They source water from tree holes, to supplement water from the fruit and leaves they consume. Tool use to catch live food, such as fish and slow lorises, has been observed (Bleiman 2008, Hardus et al.2012). Practical use of natural resources for other purposes has been observed: using leaves to wipe off faeces, using a pad of leaves to hold a spiny fruit, creating an

"umbrella" and a fly swatter from leaves, using a stick as a backscratcher (Parker et al. 1999, Rogers & Kaplan 1994, van Schaik & Knott 2001).

Life history

Young orang-utans are in constant contact with their mother for the first fourth months of their lives (Miller & Nadler 1981). By the age of two years independent travelling is developed, and at around four years partial weaning occurs. The offspring will remain dependent on its mother for roughly another four years, undergoing behavioural changes during this time (Tab. 2). In orang-utans, females are philopatric meaning that while independent males will disperse from their natal range, female will remain in, or in this case close to, their natal ranges, adopting a range adjacent to and perhaps partially overlapping that of her mothers (Morrogh-Bernard 2009). The Bornean orang-utan has an average lifespan of 35–45 years in the wild (Locke et al. 2011). Female orang-utans reach menarche between 5.8 and 11 years, earlier in females with more body fat. Giving birth for the first time around 14-15 years old, females experience a similar gestation time to humans: approximately nine months, with menopause being recorded in some captive individuals at about 48 (Rogers & Kaplan 1994). Males reach full size at about 15 years, but this is highly flexible due to the phenomenon of arrested development (Emery Thompson et al. 2012) (see Sexual Dimorphism, below).

Table 2: Age, class and features of maturing orang-utans (Cawthon Lang 2005).

Age (years)	Class	Features
0-2	Infant	Suckling. Completely dependent on mother. Always carried by mother. Sleeps in the same nest as mother.
2-5	Juvenile	Climbing and swinging independently. Beginning to take short trips away from mother to explore. Beginning to sleep in own nest by the end of this period. Common form of independent play is practicing building nests. Reduced suckling. Independent feeding developing.
5-8	Adolescent	Frequent, but reduced, contact with mother. Individuals seek out peers. Trips away from mother may become extended, lasting a few days at a time.

Social structure

Orang-utans are semi-solitary, a unique social structure among great apes, with Bornean orang-utans being more solitary than Sumatran orang-utans. But perhaps it is more accurate to refer to them as "solitary but social" (Galdikas 1984). Mature individuals range alone, occasionally participating in transitory social groups: females with other females for feeding bouts, juvenile males with juvenile males in search of food and females, or male and female in mating consortship (Mitani et al. 1991, Utami et al. 2002, te Boekhorst et al. 1990). The primary group of interest in this dissertation is that of mother and dependent offspring, who range within discrete home ranges, overlapping other female ranges (likely those of female relatives) and existing as one of multiple female ranges within the territory of a dominant flanged male. The flanged male will roam his territory, mating with females that reside within it. Females mate with him preferentially, while unflanged males roaming this area must forcefully mate with females to have a chance of reproducing (Emery Thompson et al. 2012). Adult males do not have any contact with their offspring as they are constantly on the move, and parental care falls to the mother and other female relatives (Blaffer Hrdy 1999, Galdikas 1984, Munn & Fernandez 1997, Singleton & van Schaik 2002, van Schaik & van Hooff 1996). This unique social structure is tied to body size and diet, with a central motivation being sourcing and eating sufficient food to achieve and maintain body size and condition. This is particularly important for dominant males, if they are to uphold their position (Delgado & van Schaik 2000).

Sexual dimorphism

Bornean orang-utans display sexually dimorphic features such as mature body size, timing of maturity, ranging patterns and distances, and mating strategies (Wich et al. 2004, Galdikas 1988). A female reaches her full size around ten years. A male will likely reach his full size at 15 years, but this is hugely plastic, due to his ability to arrest his development, developing secondary sexual characteristics (cheek pads/flanges, throat sac, larger body size) when and only when the ecological situation is appropriate (Emery Thompson et al. 2012, Rogers & Kaplan 1994, Utami et al. 2002, Van Schaik & Knott 2001 2001). Skull length, body size, facial features as well as muscle volume are all traits displaying significant sexual dimorphism in orang-utans. Attaining and maintaining this dimorphism may well necessitate different levels and forms of feeding, locomotion and other activities (Zihlman 1997).

Adult male and female orang-utans also diverge in the time that they spend feeding; male orang-utans spend proportionately less time eating leaves and bark and more time foraging for and eating termites than female orang-utans (Galdikas 1988). When mature, male orang-utans are also more solitary in nature than females. It has been suggested that males are more active in infancy than females, but when mature spend more time resting (Campbell & Eaton 1999). It has been observed that, as they grow older, male orang-utans spend less time socialising and making physical contact with other individuals (Poole 1987). Females, on the other hand, often play with and groom other individuals into adulthood. It is important to remember that in Poole's study sociality between individuals was facilitated, and would not occur in wild, that is semi-solitary, orang-utans. Sociality increases the "stimulus component" of the orang-utan's environment (Poole 1987: 315), with social interaction being

an important part of development. Therefore, patterns of sociality (how often individuals socialise and with whom) may be expected to vary in mother and offspring, as well as with offspring age and sex.

Nesting

Orang-utans sleep in nests. Depending on the body mass of an individual, which is strongly correlated with both age and sex, the nest may be built high in the trees, in the case of females, infants, and small males, or on the ground for large flanged males (pers. comm.). In infancy a mother will build a nest for her and her offspring to share. This can be a day nest, built for use as short as ten minutes and as long as three or four hours, or a night nest, used to sleep in for the entire night. A juvenile will begin to build nests as a form of independent play (Tab. 2), practicing for adolescence, when they begin to nest and sleep separately from their mother (Munn & Fernandez 1997, Rijksen 1978).

Anthropogenic influence

Only one archaeological site tentatively provides supportive evidence that humans may pre-historically have hunted orang-utans for consumption: the Nguom rock shelter, Vietnam (Harrison 2000). The distribution of *Pongo* was, in the past, more widespread than it is currently (Fig. 2), and anthropogenic factors, like hunting and habitat destruction, are likely to have had an affect on this decline. Today, anthropogenic factors are largely to blame for the continuing decline of the species, with orang-utans being hunted largely for the pet trade, with mothers often being shot in order to gain access to an infant. However, habitat destruction remains the primary threat to these great apes, with humans creating forest fires, logging illegally and clearing vast forest spaces to plant palm oil fields. The anthropogenic influence on orang-utan habitat can affect orang-utan behaviour. For example, in the Wehea Forest of East Kalimantan, orang-utans are found to travel along the ground more often than previously thought. It has been suggested that the ability of orang-utans to move terrestrially may increase their ability to adapt to forest fragmentation and cross open spaces created by gaps in the canopy (Loken et al. 2013).

Data Collection

This research was carried out as part of the *Orang-utan Tropical Peatland Project* (OuTrop) multi-disciplinary research project in collaboration with the *Center for International Cooperation in Sustainable Management of Tropical Peatland* (CIMTROP). Between May 15 and Sep 15, SK (Fig. 3) was the primary researcher collecting behavioural data, in the field. Previous field experience in the tropics collecting and analysing data on baboon crop raiding behaviour equipped SK with the necessary understanding and skills to be a reliable observer, data collector, and data analyst. Other researchers in the team were very practiced, all having extensive experience collecting behavioural data on orang-utans and receiving regular training on data collection and input methods. In addition to assisting SK over five months, the team collected data from Sep 09 to Apr 15. All the data collected between Sep 09 and Sep 15 were used in this dissertation.



Figure 3: Primary researcher, Sophie Kirklin (SK), in the field observing orang-utans. Photo taken by Ben Thomas.

Study site

Field-work took place in The Sabangau Forest, Central Kalimantan, 20km south-west of the provincial capital Palangkaraya. An area of 5,780 km^2 makes up *The Natural Laboratory for the Study of Peat-Swamp Forests* (21° 18' 58.21" S, 113° 54' 26.94" E) (Fig. 4). Researchers were based at a wooden camp at the edge of the forest (Fig. 5). With peat deposits reaching depths of 15m, The Sabangau Forest is one of the largest terrestrial carbon stores in the world. There are three distinct peat-swamp forest sub-types of varied structure and composition: mixed swamp forest, low pole forest, and tall interior forest. Research was conducted in the mixed-swamp forest habitat, which supports a large proportion of the orang-utan population (Morrogh-Bernard et al. 2003). SK's arrival in the forest in May 15 coincided with the peat swamp terrain beginning to dry at the end of the wet season. The following five months saw fruit shortages in the forest and, as a result, focal orang-utans were seen deviating quite far from their expected home ranges, in search of sustenance. In late Aug 15 fires began to burn across Borneo and the density of smoke prevented researchers from observing the orang-utans (see Discussion for more information). All forest research was suspended from Sep 15. The section of mixed-swamp forest in which orang-utans were observed measures 3 km x 3 km (cf. Fig. 4) Within this space there is a constructed grid system of transects, some marked by a pathway of raised wooden planks and others by trails cleared by a railway system implemented when the forest was selectively logged from 1973 to 2005 (Fig. 6). This grid was used to contextualize and record orang-utan ranges and nest locations within the forest. In addition, during the logging concession, canals were cut into the peat to remove logs from the forest. The canals lead to leaching of the peat, with water leaving the terrain and draining into the nearby Sabangau River. The drying of the peat makes the land more vulnerable to catching fire, exacerbating the problem of habitat destruction by forest fires. As part of OuTrop's on-going work, dams are being built across these canals in an attempt to restore the

capacity of the peat to retain water. Despite these problems, the forest currently remains unfragmented, containing the largest continuous population of orang-utans in the world. It supports a huge variety of biodiversity, including but not limited to the Bornean orang-utan, *Pongo pygmaeus*, agile gibbon, *Hylobates agilis*, maroon langur, *Presbytis rubicunda*, sun-bear, *Helarctos malayanus*, leopard cat, *Felis bangalensis*, and marbled cat, *Felis marmorata* (Morrogh-Bernard 2003) (Fig. 7).

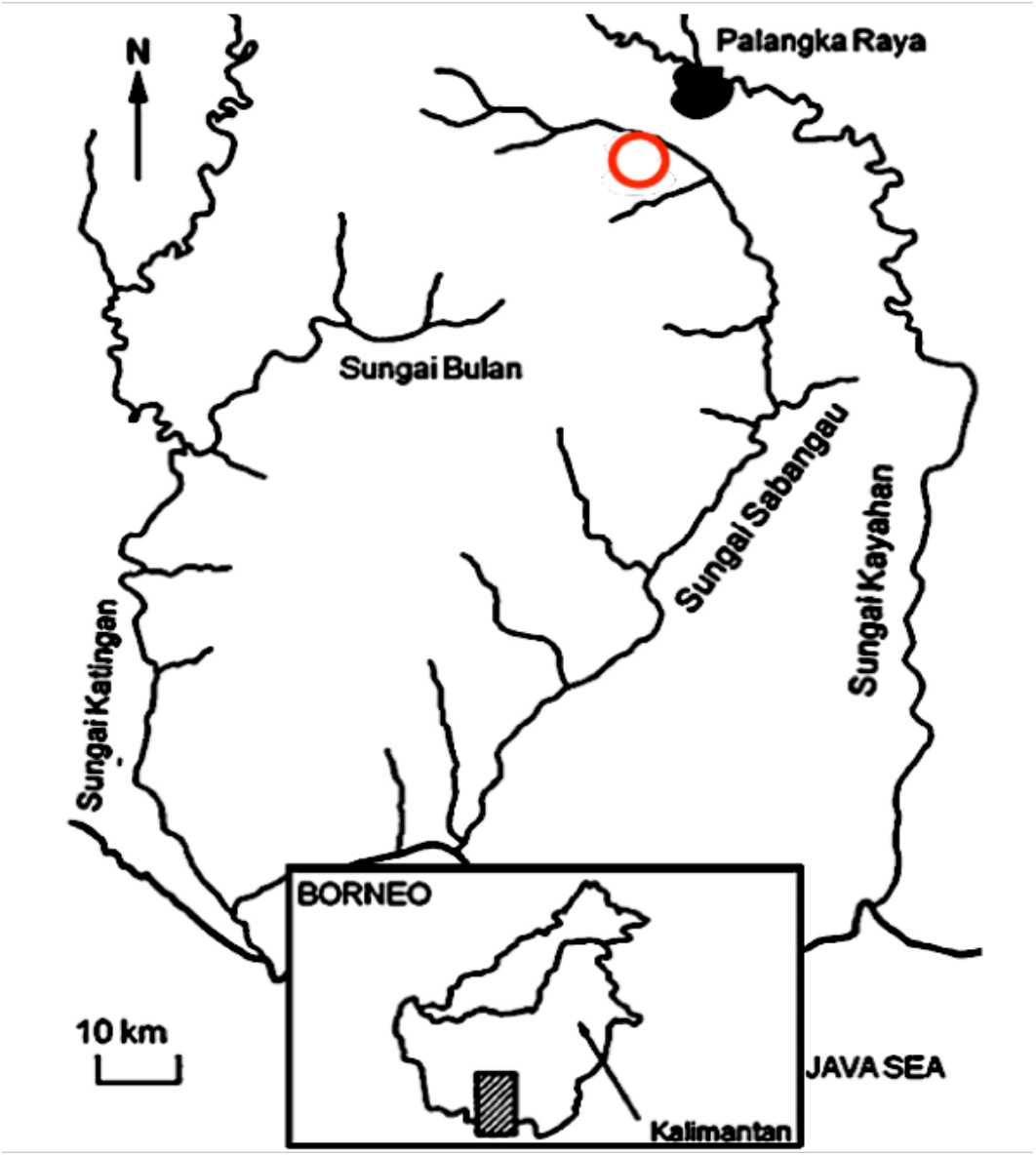


Figure 4: The Sabangau Forest in Kalimantan. 'O' marks the study area (adapted from Cheyne & Macdonald, 2011).



Figure 5: An aerial view of base camp.



Figure 6: A section of the railway constructed for the logging concession (1973-2005) leading into basecamp. The railway continues into the forest for 3 km.

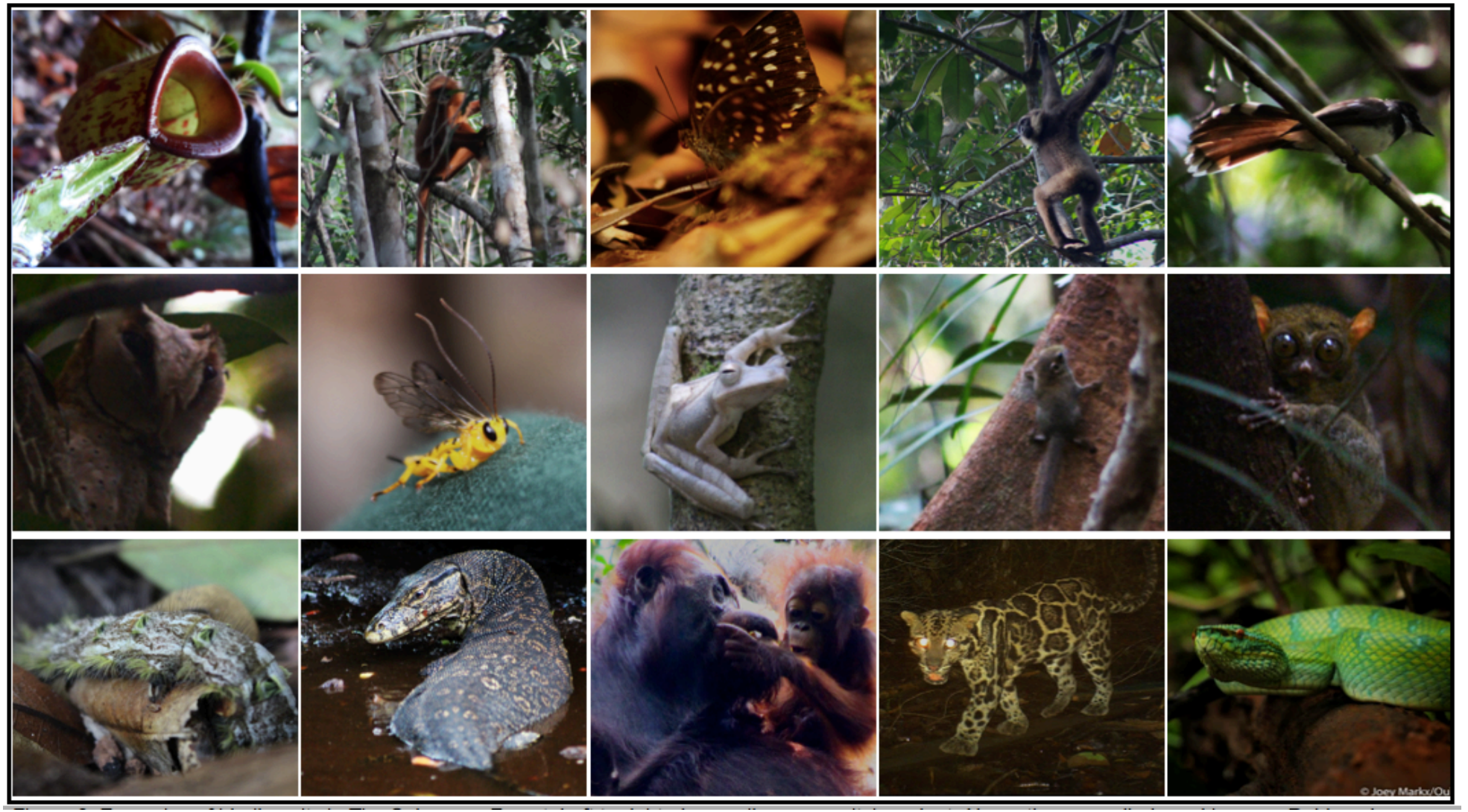


Figure 7: Examples of biodiversity in The Sabangau Forest. Left to right, descending rows: pitcher plant, *Nepenthes ampullaria*; red langur, *Rubicunda rubida*; butterfly, *Lexius pardalis*; agile gibbon, *Hylobates agilis*; bird-unidentified; oriental barn owl, *Phodius badius*; insect-unidentified; collettes tree frog, *Polypedates colletti*; pygmy squirrel, *Nannosciurus melanotis*; western tarsier, *Cephalopachus bancanua*; hairy catapillar-unidentified; water monitor lizard, *Varanus salvator*; Bornean orang-utan, *Pongo pygmaeus wurmbii*-photos taken by Sophie Kirklin; clouded leopard, *Neofelis nebulosa*-photo courtesy of OuTrop; Wagler's pit viper, *Tropidolaemus wagleri*-photo taken by Joey Marx on behalf of OuTrop.

Orang-utan observation

Orang-utan mothers with dependent offspring, below eight years old, were followed whenever found. The process of finding an orang-utan to follow consisted of splitting up the team of two to four researchers, and pre-determining a route for each person to travel within the target orang-utan's home range. Each researcher walked slowly and quietly along the assigned route, stopping regularly to detect signs of an orang-utan. Orang-utans spend much of the time resting and making very little noise (pers. obs.). Therefore, searching for a focal individual to follow can be a difficult task. Once found, individuals were only followed if they were either a mother or a dependent offspring. An exception to this rule was when independent adolescent females, who are still in intermittent close proximity with their mother, were followed as a way of locating the mother. When located, female individuals were identified, a task simplified by using their offspring's age and sex as reference points. Identifications were always confirmed in situ by a second researcher. Photographs were taken if there was any doubt, and these were later compared to existing records. A mother and her dependent offspring are henceforth referred to as a dyad (Tab. 4). Mother-offspring dyads were followed to their night nest, and researchers were at the nest the next morning, by the time the orang-utans woke up (usually around 04:45), to continue the follow. Focal orang-utans (a mother and her dependent offspring) were followed for at least five days, if possible, from "nest-to-nest". From the start of a follow, marked by a focal individual sitting up in the previous night's nest, to the end of the follow, marked by a focal individual lying down in a nest to be used until the following morning, data were recorded instantaneously at 5-min intervals. All data collected for one individual between the hours of 00:00 and 23:59 on the same day, whether it represents a follow from nest-to-nest or only a few hours, is collectively denoted as a 'follow day'.

Two researchers were responsible for data collection on each follow day. Researcher 1 was responsible for recording the location every 5-min using a handheld Garmin GPS system. At each data point researcher 1 also recorded: the primary and secondary behaviour of the mother, species being eaten (if applicable), the size of the party (focal individual plus other independent orang-utans present) and the focal's proximity to other party members. Researcher 2 was responsible for observation of the dependent offspring's behaviours. Every 5-min, researcher 2 recorded: the primary and secondary behaviour of the offspring, species being eaten (if applicable), and proximity of the offspring to the mother. Timers carried by each researcher were always synchronized, and set to beep at 5-min intervals, ensuring that both researchers collected their observations simultaneously. Activities were recorded on observation sheets, using codes detailed on a behavioural ethogram (Tab. 3). The above detailed data collection procedures were based on standardized guidelines designed at the *Leakey Foundation Orang-utan Compared Workshop* held in San Anselmo, California in 2002, and the OuTrop protocol.

Table 3: A selection of ethogram codes corresponding to primary activities and secondary activities. Both primary and secondary behaviours were recorded at each instantaneous data point.

Primary Activity	Ethogram code	Secondary Activity	Ethogram Code
Feeding	F	Feeding on Invertebrates	IV
		Feeding on the pith of ripe fruit	Fr/pi
Resting	R	Sitting on tree	Si/tr
		Lying down in nest	Ld/n
Travelling	T	Clambering	Cla
		Brachiating	Br

Sample size

Data were collected from twelve focal individuals. Six were mothers and six were their dependent offspring (Tab. 4), of varying ages spanning just under 2, 000 days (Fig. 8). All six mothers were habituated before data collection began, although some individuals were observed more than others because of a higher level of habituation and home ranges that are relatively close to camp, resulting in them being found relatively often. Although researchers attempted to prevent the distribution of follows across individuals from becoming too unbalanced, opportunistic following resulted in more data existing on Indy and her offspring Icarus, and Feb and her offspring Fio. The sample size in this study is longitudinally large, with 4, 565 hours of useable data for mothers, and 1, 533 hours of useable data for offspring. However cross-sectionally the sample size is small, with only six mothers and six offspring. Therefore, individual variations must and will be controlled for. It should be also be noted that within the within the distribution of age of study offspring (cf. Fig. 8) there is an outlying datum. In this case, an outlier in Chuck's age tells us that data was collected on him at around 250 days old, and then not resumed for a considerable amount of time, probably due to not being able to find him.

Table 4: Sample of twelve individuals, consisting of six mothers and their dependent offspring. Mother details are in bold and capitals, with their offspring's details listed below them.

Individual	Estimated birth	Birth Order	Sex
CLEOPATRA			**FEMALE**
Chuck	Jul 2012	2	Male
FEB			**FEMALE**
Fio	Apr 2010	1	Male
GRACIA			**FEMALE**
Gretel	Jun 2010	2	Female
INDY			**FEMALE**
Icarus	Aug 2012	1	Male
INDAH			**FEMALE**
Ima	Apr 2014	3	Female
TERESIA			**FEMALE**
Trevor	Nov 2011	2	Male

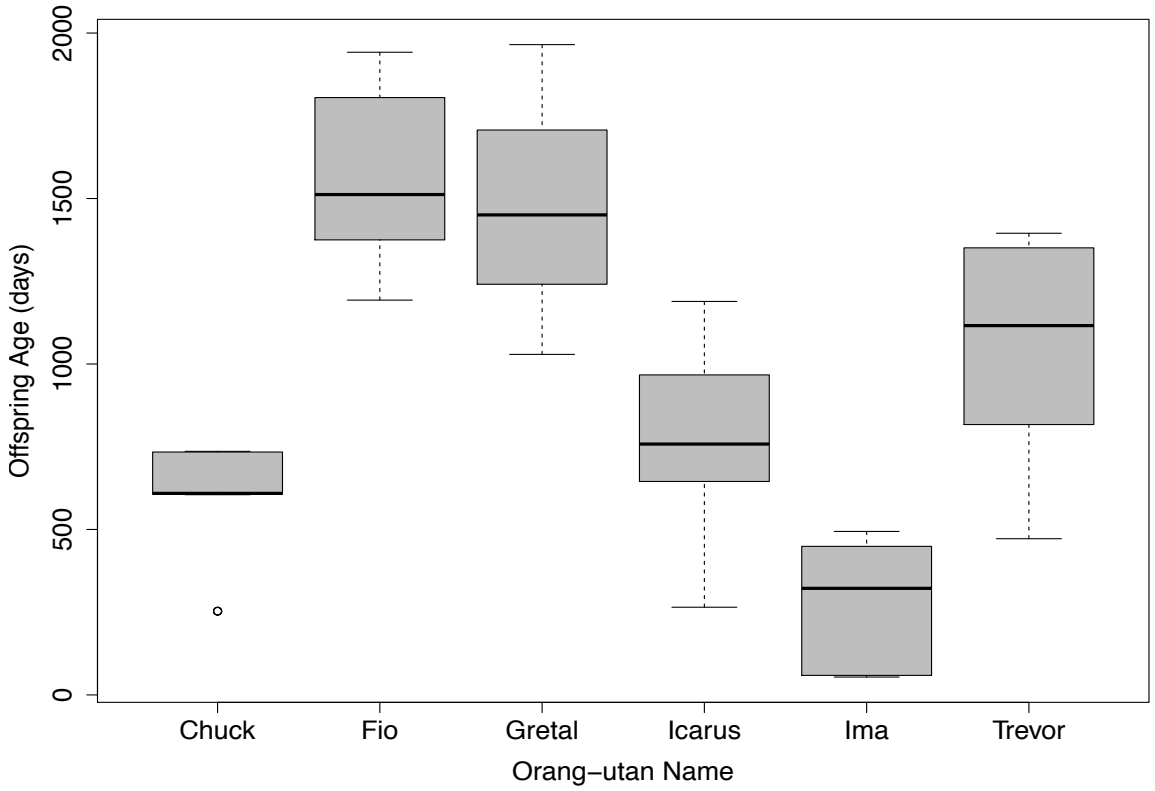


Figure 8: Distribution of ages of study offspring. ^{O} shows an outlying datum.

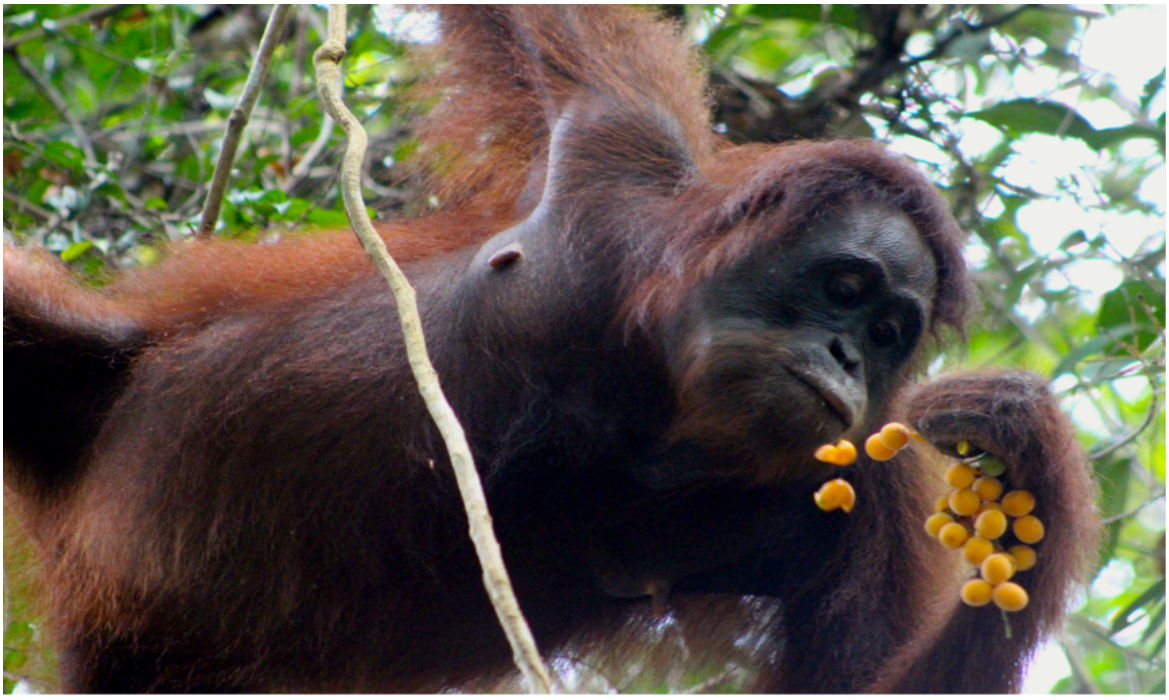
Definitions

Presented in this dissertation are patterns of development of feeding and co-feeding. Below are the definitions used in this study, which are taken from the Standard Operating Procedures of OuTrop (OuTrop, 2015: 29).

“Feeding (F) - When the orang-utan is actively eating, reaching for food, processing or preparing food items. Includes drinking and travelling within a patch [“One individual food tree/liana/termite log/insect nest/patch of fungi etc. in which the individual is feeding”]”. Feeding behaviour in a mother in this study denotes independent feeding behaviour; in an offspring feeding behaviour denotes either independent feeding or feeding alongside another orang-utan (Fig. 9).

“Co-Feeding (CF) – [When an independent individual is] feeding in the same patch as another independent individual who feeds on the same food species”. For a mother orang-utan, who is an independent adult, co-feeding is a behaviour recorded fairly regularly (Fig. 10). By definition, co-feeding is not a possible status for offspring, because they are not independent. This distinction has however proved problematic in the field, with a number of mis-recordings of co-feeding in offspring. A decision was therefore made to treat all incidences misreported as offspring co-feeding as incidences of offspring feeding. For the sake of this study it is important to remember that for mothers we can distinguish between independent feeding and co-feeding, whereas for offspring we cannot.

(a)



(b)

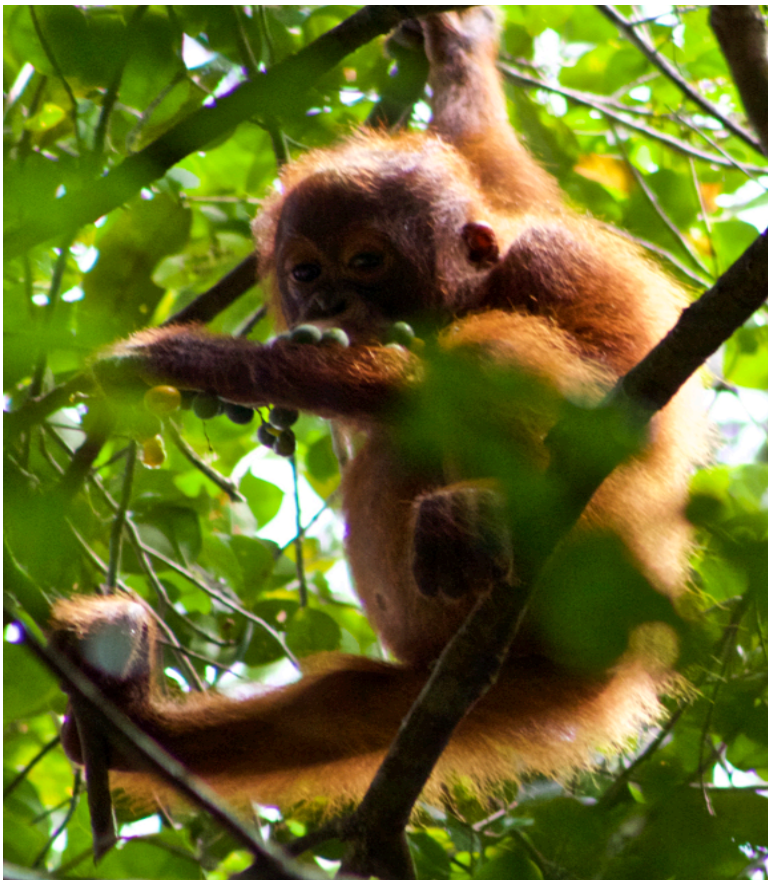


Figure 9: Examples of independent feeding, on Liana Kuning, *Menispermaceae*. (a) Adult female Feb. (b) Fio, Feb's son, age 62 months. Photos taken by Sophie Kirklin, Jun 15.

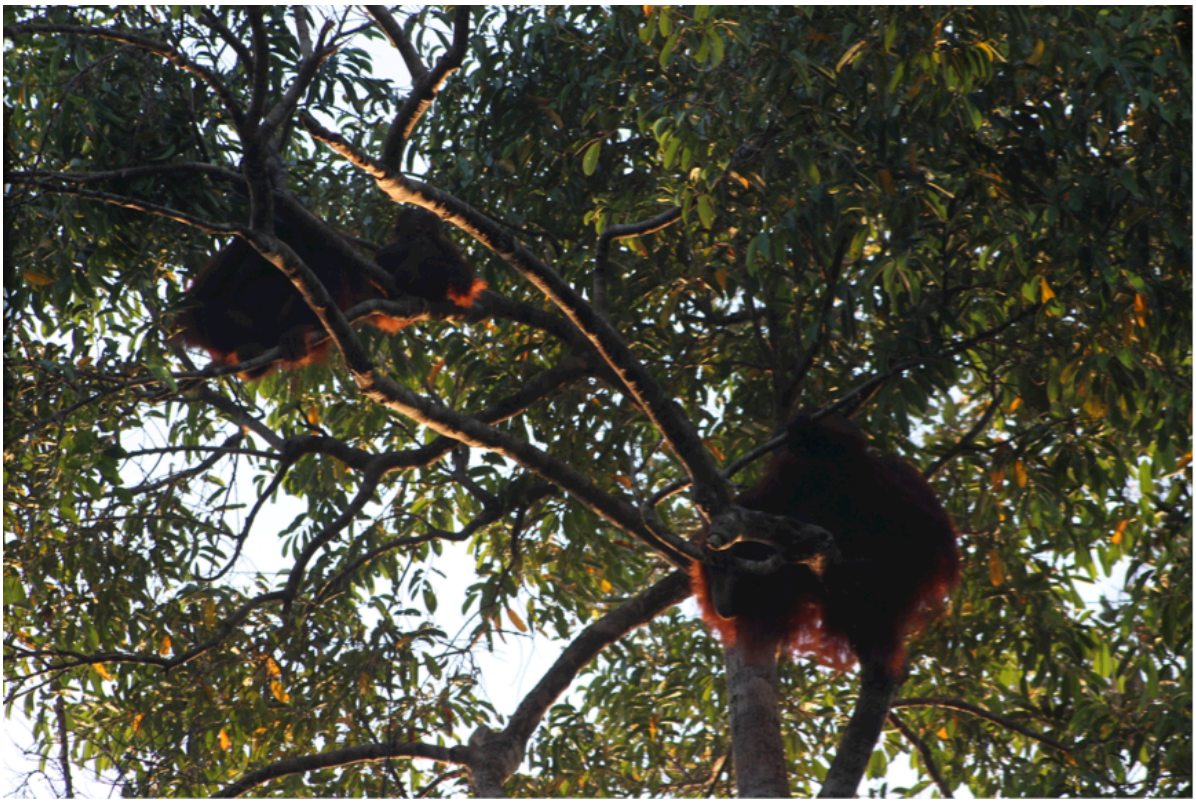


Figure 10: Adult female Indah (left) co-feeding with a male orang-utan (right). Indah is sitting next to her 16-month-old infant, Ima (Ima's behaviour is recorded as feeding in this instance). Photo taken by Sophie Kirklin, Aug 15.

Data Analysis

Preparation

Data collection on adult orang-utans began before data collection on offspring, so there are data points where mother behaviour is recorded with no corresponding offspring behaviour. Therefore, the mother dataset contains all of the data available, including some data on mother behaviour prior to infant birth. A separate offspring dataset contains only data points where a mother activity and an offspring activity are recorded simultaneously. There are no instances in the data where offspring behaviour is recorded without corresponding mother behaviour. A variable denoting the focal's age in days and in years (in the case of the offspring dataset), and the age of the focal's offspring in days and in years (in the case of the mother dataset) was created. In this data the estimated birth of an infant is only given as a month, and so all offspring birthdays were assigned as the 15th day of the month. For example, Chuck was born in Jul 12, and so his exact birthday was assigned as the 15 Jul 12. In regards to data collected on the 01 Aug 12, the "offspring's age in days" variable for Chuck will be 17.

Data collection methods and protocols were kept as consistent as possible. However, the length over which data collection occurred, over five years, and the large number of individual researchers who contributed to observation, means that there will inevitably be some inconsistencies. These may have been overlooked at the time, but in hindsight may affect the patterns we see in the data. The first of these inconsistencies, already addressed, is the assignment of co-feeding behaviour to offspring, who

according to the definition cannot co-feed. The next exists in “unknown” (U) and “blank” (Bl) data points. Inconsistencies in researcher methodology meant that it was unclear whether U and Bl denoted a lack of observation (not-forest-time), or an observation (forest-time) where the specific activity being undertaken was not seen. The consistency with which researchers distinguished the two codes is also unknown. To create some consistency, SK imposed the rule that Bl indicates not-forest-time, and U indicates forest-time, but unseen activity. Therefore, Bl and U points were adjusted so that every point before the first behaviour of the day and every point after the last behaviour of the day was recorded as Bl. Every Bl point between the first and last recorded behaviour of the follow day became a U. Bl data points were then removed, as they denote a lack of observation and therefore are irrelevant to creating budgets and looking at behavioural patterns of the focal individuals.

The U points in the data still posed a problem, as no assumption can be made as to what they might represent. The likelihood of a U representing any other behaviour can be inferred from the frequency of those other behaviours in the rest of the data. The effect of calculating this would be the same as just deleting the U points. Annual and diurnal distributions of U data points for the mother dataset (Fig. 11 & Fig. 12) and the offspring dataset (Fig. 13 & Fig. 14) can be visualized as proportions of a bar representing all of the data collected in any one month and in any one hour. The proportions of U points seem to be fairly consistent, excluding the 04:00 and 18:00 hours. Looking at the distribution of U’s at the level of individual follow days gives maximums (mother: 34.7 %, offspring: 63.6 %), minimums (mother: 0 %, offspring: 0 %), means (mother: 2.4 %, offspring: 24.9 %) and standard deviations (mother: 3.8 %, offspring: 17.3 %). This gives an impression of the consistency of the amount of U’s recorded. These figures are relatively meaningless without contextualizing them within the dataset they represent. For more meaning we can look at the means and standard deviations of the primary activity in this study, feeding, before removing U values and after removing U values, both for the mother dataset (Tab. 5) and for the offspring dataset (Tab. 6). The key values in determining whether removing U’s is appropriate are the behaviour means before removing U points. If the behaviour mean before removing U’s is bigger than the standard deviation of the proportion of U’s, then for the purposes of studying this behaviour, it will be appropriate to remove U’s from the dataset. In the offspring dataset, feeding behaviour can be tested in a data set with unknown data points removed and the results can still be expected to represent the actuality of the individuals’ activity budgets (mean before removing U’s-19.1 %>standard deviation of U’s in dataset-17.3 %). The same exclusion of U's is appropriate for the mother dataset (mean before removing U’s-58.9 %>standard deviation of U’s in dataset-3.8 %). On this basis, for the purposes of studying feeding behaviour, data points recorded as unknown were excluded from the dataset.

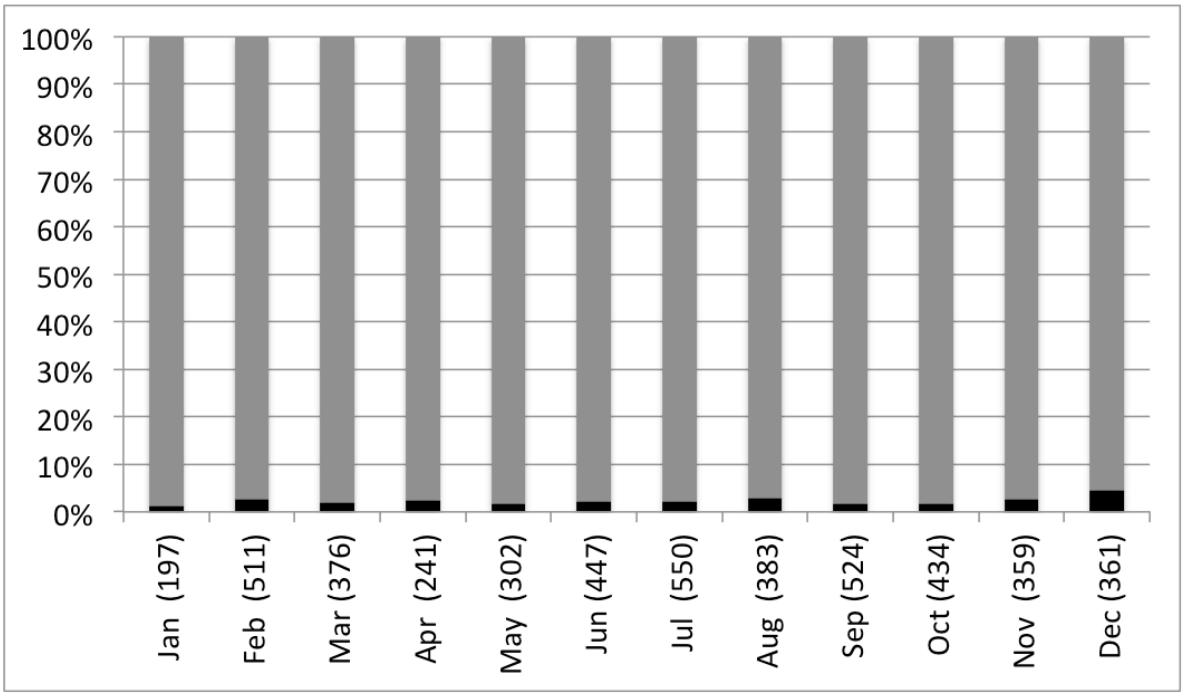


Figure 11: Proportional distributions of known (grey) and unknown (black) data points in the mother dataset per calendar month. Total equivalent hours of observation collected in each calendar month shown in brackets.

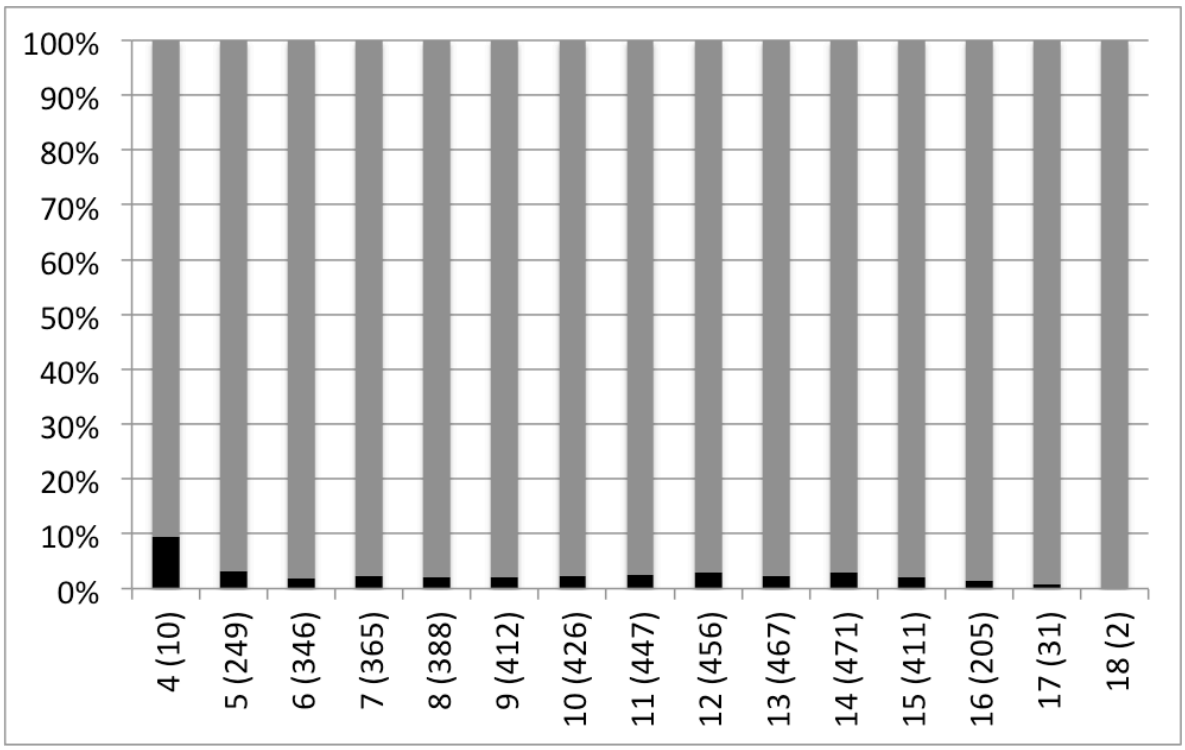


Figure 12: Proportional distributions of known (grey) and unknown (black) data points in the mother dataset per hour. 4=04:00-04:59, 5=05:00-05:59, etc. Total equivalent hours of observation collected in each recurring 60-min period shown in brackets.

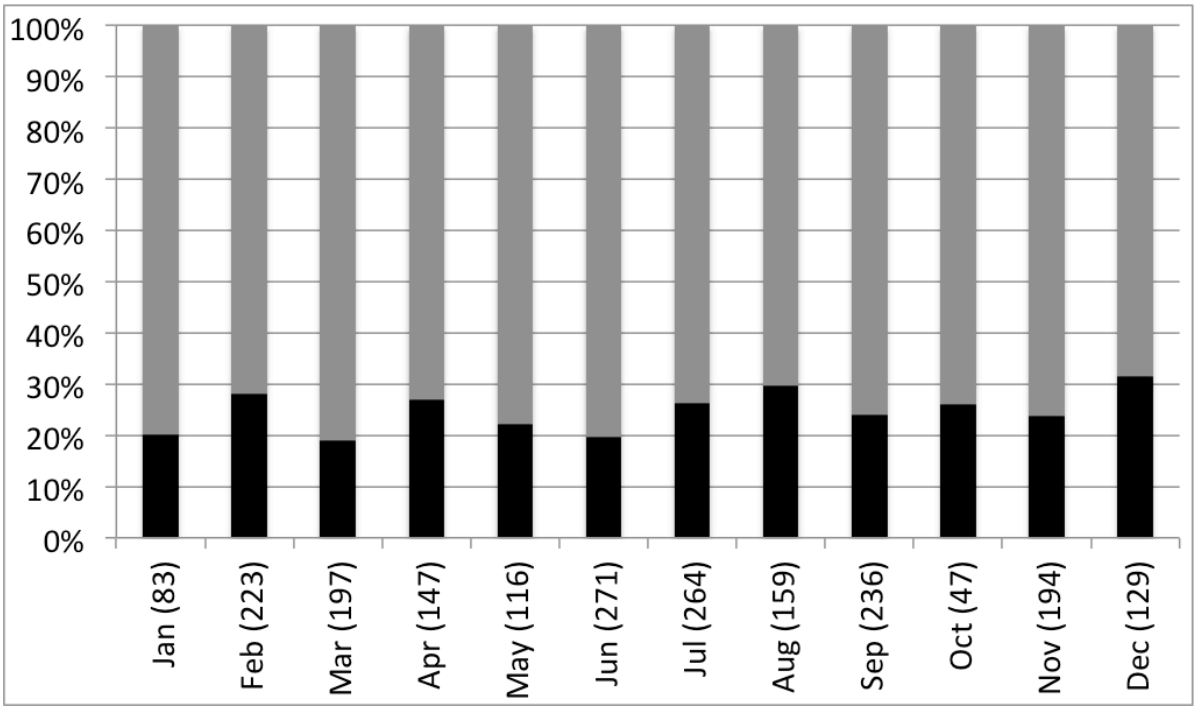


Figure 13: Proportional distributions of known (grey) and unknown (black) data points in the offspring dataset per calendar month. Total equivalent hours of collected in each calendar month shown in brackets.

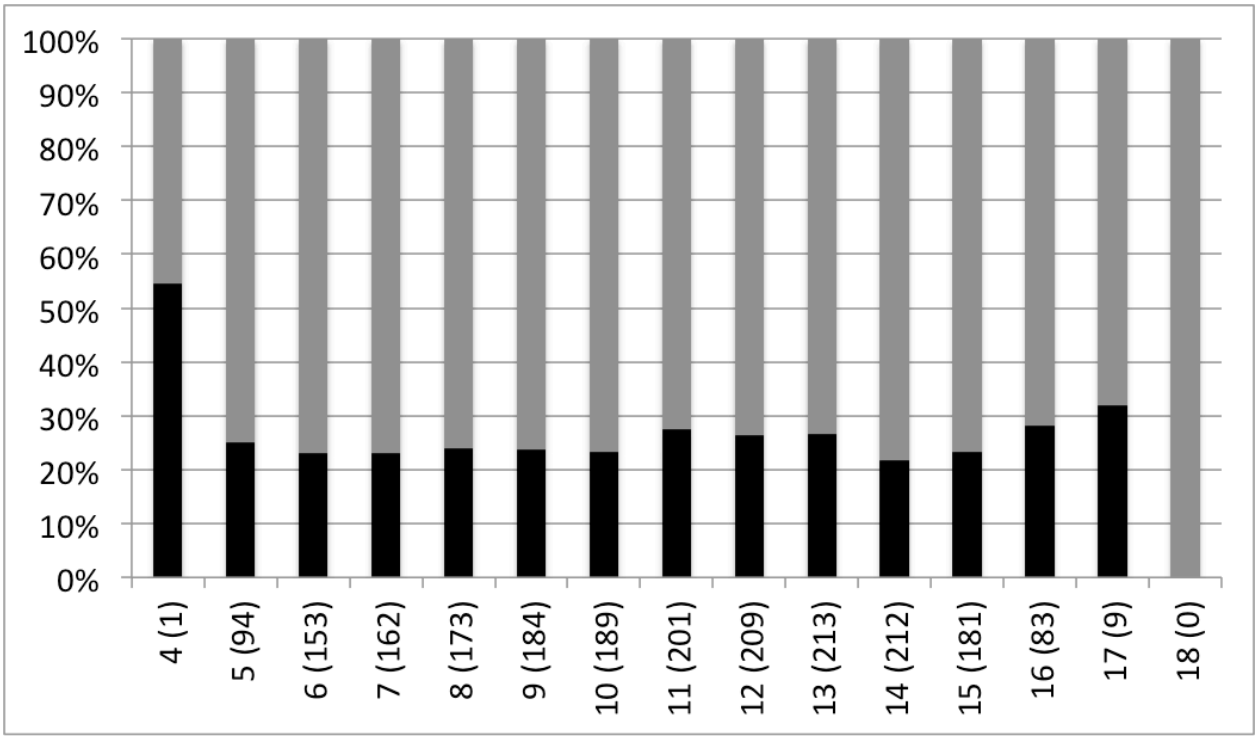


Figure 14: Proportional distributions of known (grey) and unknown (black) data points in the offspring dataset per hour. 4=04:00-04:59, 5=05:00-05:59, etc. Total equivalent hours of observation collected in each recurring 60-min period shown in brackets.

Table 5: Mean and Standard deviation observed in mother dataset before removing U points and after removing U points.

		Feeding
BEFORE removing “U”s	Mean	58.86 %
	STD	17.52 %
AFTER removing “U”s	Mean	60.33 %
	STD	17.55 %

Table 6: Mean and Standard deviation observed in the offspring dataset before removing U points, and after removing U points.

		Feeding
BEFORE removing “U”s	Mean	19.13 %
	STD	17.39 %
AFTER removing “U”s	Mean	19.14 %
	STD	17.40 %

Imposing controls

Two datasets, now clear of unknown or blank values, display variation in the amounts of data available across a year (Fig. 15 & Fig. 17) and a day (Fig. 16 & Fig. 18).

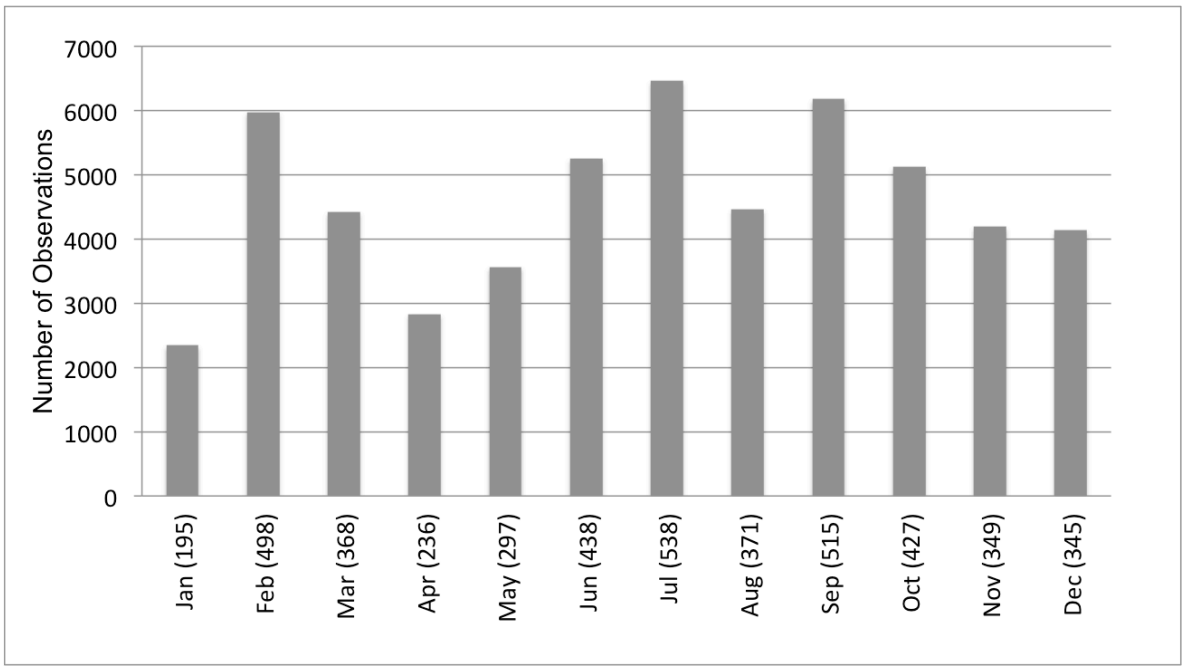


Figure 15: Annual distributions of data collected in the mother dataset. Total equivalent hours of observation collected in each calendar month shown in brackets.

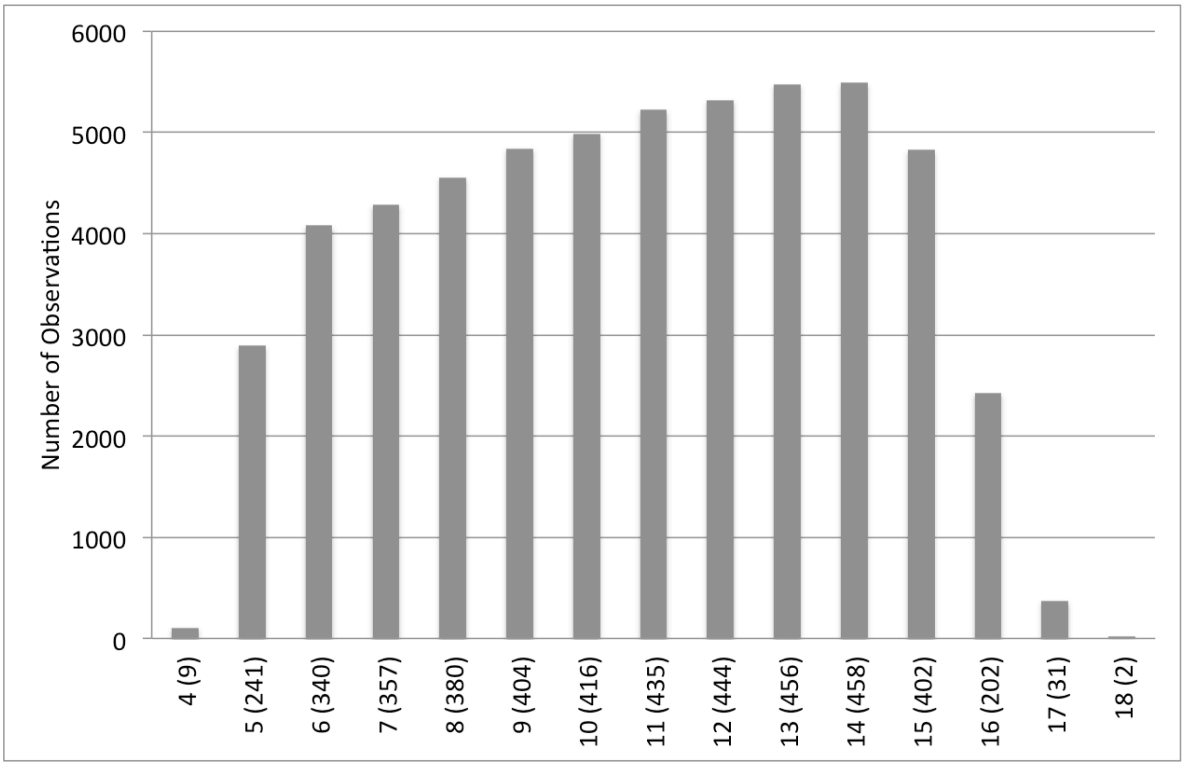


Figure 16: Diurnal distributions of data collected in the mother dataset. X-axis: 4=04:00-04:59, 5=05:00-05:59, etc. Total equivalent hours of observation collected in each recurring 60-min period shown in brackets.

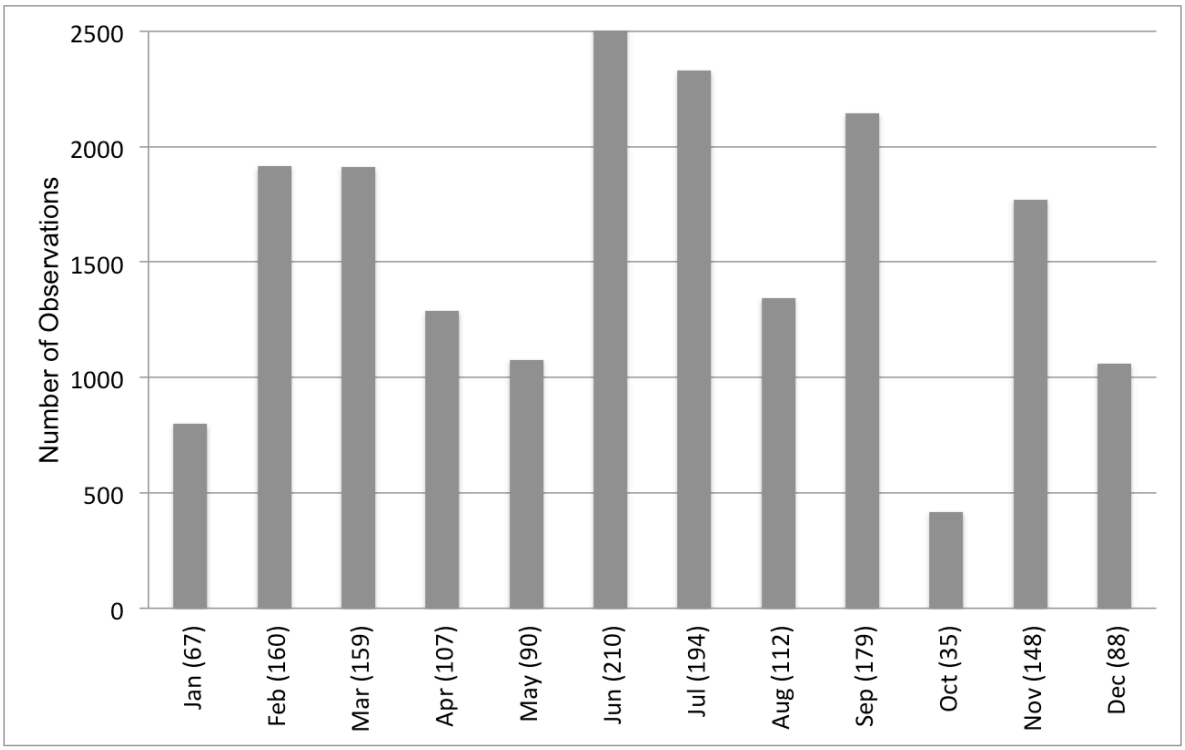


Figure 17: Annual distributions of data collected in the offspring dataset. Total equivalent hours of observation collected in each calendar month shown in brackets.

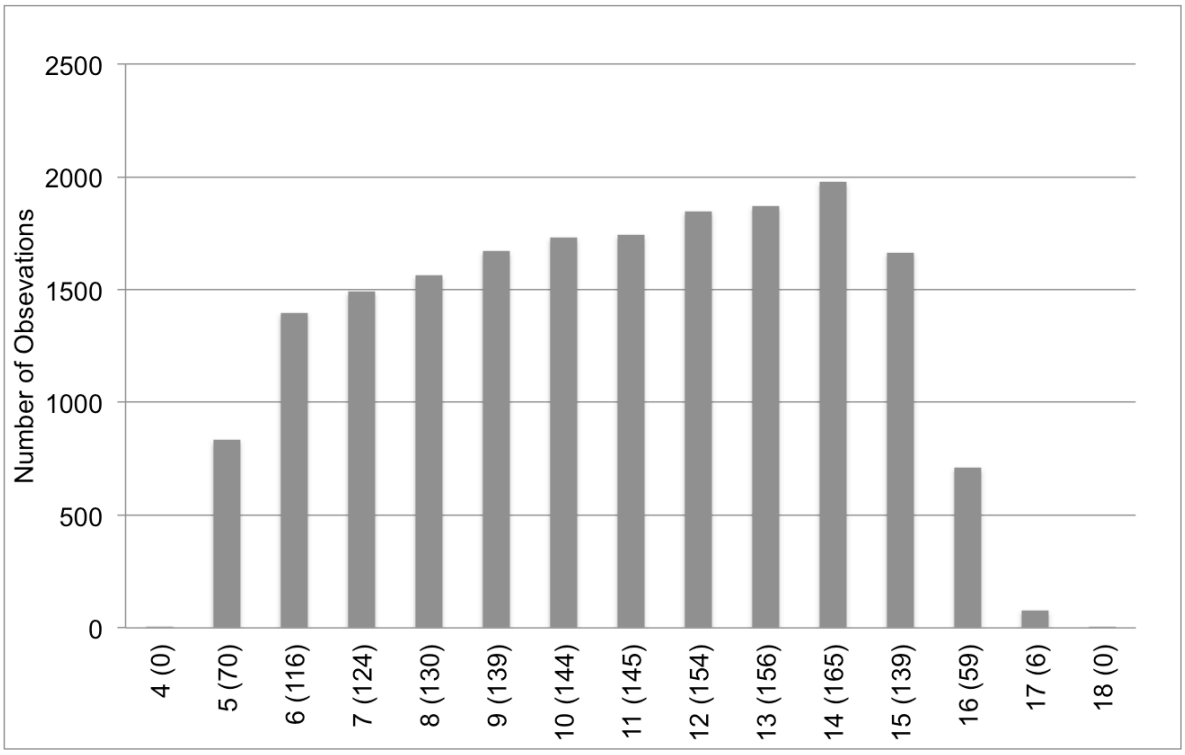


Figure 18: Diurnal distributions of data collected in the offspring dataset. X-axis: 4=04:00-04:59, 5=05:00-05:59, etc. Total equivalent hours of observation collected in each recurring 60-min period shown in brackets.

From these charts, it is clear that the first and last hour of the day, 04:00 and 18:00 yield a very low number of observations, in both the offspring dataset and the mother dataset. This may be because 04:00 and 18:00 hours are the extremities of a day, and it is quite rare that a focal orang-utan is active at this time. Alternatively, this could be a result of researchers being tired/distracted, or unable to see focals during these darker hours, resulting in many void data points. As already discussed, there is the potential to create inconsistencies by removing U points from the dataset at the beginning and end of follows. For these reasons, data collected during 04:00 and 18:00 was excluded from the final datasets. The annual variation for the offspring (cf. Fig. 17), and for the mother datasets (cf. Fig. 15), indicates that there were suitable amounts of data for each month. Annual and diurnal variation could imply that the proportion of activity observed is potentially unreliable. If an orang-utan offspring is observed feeding 20 % of the time, from 17:00 to 17:59 on a day in Oct, this proportion will likely not be very accurate as it is based on a relatively small number of observations. By imposing controls on the data, it is possible to minimize the probability that trends seen within the data are a result of observational bias, and eliminate seasonality as a factor. This will be particularly important for feeding activities, as all elements of *Pongo pymaeus*'s diet vary with seasonal change, reflecting for example, fruit availability.

Diurnal and annual controls were imposed together, as opposed to controlling for one first and then the other. The example of calculating and imposing correction factors for 'Feeding" behaviour in mothers is used below to demonstrate the steps taken to complete corrections for diurnal and annual data collection biases. The first step was to create a matrix, using the pivot table function in Excel, of

the percentage of observations of the behaviour (in this example, “Feeding”) in each hour and in each month (Tab. 7).

Table 7: (Step 1 in the correction process). Percentages of time mothers are observed feeding per hour and per month. 5=05:00-05:59, etc.

	5	6	7	8	9	10	11	12	13	14	15	16	17
Jan	49.3	66.9	66.7	65.7	68.4	69.3	74.9	78.5	66.3	59.8	58.2	38.5	16.7
Feb	36.3	63.5	58.2	51.1	56.1	46.7	59.7	67.0	66.8	69.0	57.7	41.5	23.8
Mar	49.5	63.1	62.6	62.8	58.0	57.1	55.1	66.7	63.7	63.9	56.2	49.8	33.3
Apr	53.3	69.6	73.3	69.8	62.9	62.4	76.2	75.8	69.6	66.4	67.9	65.2	27.3
May	54.1	77.3	74.9	61.8	54.5	64.3	61.6	64.1	65.2	60.8	47.1	16.7	16.7
Jun	43.6	72.0	74.2	70.5	65.3	74.0	66.5	67.1	66.8	65.3	60.7	34.2	7.1
Jul	46.2	68.0	69.8	66.3	62.1	60.1	68.7	70.2	65.5	62.8	54.5	34.2	35.8
Aug	53.4	69.2	54.3	59.5	64.6	64.3	60.5	65.6	68.1	71.0	61.4	52.4	26.8
Sep	56.1	64.7	67.6	59.8	60.4	57.0	56.3	66.4	63.3	64.0	59.1	50.3	30.4
Oct	50.2	60.8	59.3	55.9	50.5	47.9	55.1	55.5	62.1	60.1	50.8	47.0	40.0
Nov	45.4	56.8	55.9	62.2	54.9	53.4	60.5	58.1	57.7	59.9	58.6	44.2	35.3
Dec	57.8	67.4	57.8	62.1	58.3	60.1	59.0	73.5	69.6	60.4	54.5	54.3	25.0

Next, a mean was calculated of these percentages (57.65 %). This value is the percentage of time that, on average, a mother orang-utan of any sex or age dependent offspring spends feeding in an hour, at any time of the year, at any hour between 05:00 and 17:00. This mean was then used to calculate correction factors. By dividing the mean by each of the observed percentages (cf. Tab. 7) a table of correction factors (Tab. 8), all of which multiply by the observed values to give the expected mean of observations of feeding per hour (57.65) was created. Correction factors can be applied by multiplication or addition. Here, the multiplication method of correction was used because a) any value represented as 0 % in the observed data would be represented as >0 % with a positive correction factor added to it, and this seems presumptuous for behavioural observation of autonomous individuals b) activity budget data is based on proportions and rates; using multiplication instead of addition will change these rates proportionally to their value. The combination of the month and the hour in which the piece of data was collected indicated a specific correction factor by which the observed proportion of feeding was multiplied. This was calculated using the offset function in Excel. The result is a set of expected values, some of which now were over 100.00 %. These values are no longer proportions out of 1.00, and are not percentages, but Relative Feeding Times (RFT) and will henceforth be referred to as such. I shall also be employing the similarly defined term, Relative Co-Feeding Time (RCFT).

Table 8: (Step 2 in the correction process). Correction factors for mother feeding behaviour. 5=05:00-05:59, etc.

	5	6	7	8	9	10	11	12	13	14	15	16	17
Jan	1.2	0.9	0.9	0.9	0.8	0.8	0.8	0.7	0.9	1.0	1.0	1.5	3.5
Feb	1.6	0.9	1.0	1.1	1.0	1.2	1.0	0.9	0.9	0.8	1.0	1.4	2.4
Mar	1.2	0.9	0.9	0.9	1.0	1.0	1.0	0.9	0.9	0.9	1.0	1.2	1.7
Apr	1.1	0.8	0.8	0.8	0.9	0.9	0.8	0.8	0.8	0.9	0.8	0.9	2.1
May	1.1	0.7	0.8	0.9	1.1	0.9	0.9	0.9	0.9	0.9	1.2	3.5	3.5
Jun	1.3	0.8	0.8	0.8	0.9	0.8	0.9	0.9	0.9	0.9	1.0	1.7	8.1
Jul	1.2	0.8	0.8	0.9	0.9	1.0	0.8	0.8	0.9	0.9	1.1	1.7	1.6
Aug	1.1	0.8	1.1	1.0	0.9	0.9	1.0	0.9	0.8	0.8	0.9	1.1	2.2
Sep	1.0	0.9	0.9	1.0	1.0	1.0	1.0	0.9	0.9	0.9	1.0	1.1	1.9
Oct	1.1	0.9	1.0	1.0	1.1	1.2	1.0	1.0	0.9	1.0	1.1	1.2	1.4
Nov	1.3	1.0	1.0	0.9	1.1	1.1	1.0	1.0	1.0	1.0	1.0	1.3	1.6
Dec	1.0	0.9	1.0	0.9	1.0	1.0	1.0	0.8	0.8	1.0	1.1	1.1	2.3

These corrected values have been used to obtain all of the test results presented in this dissertation.

RESULTS

Initial analysis focussed on the changing relationship between offspring age and mother and offspring behaviour. A subsequent further analysis looked at the impact of offspring sex on these same behaviours. The results presented below are based on the proportion of an hour spent performing a given behaviour.

Feeding

Mother independent feeding

The change over time of the frequency of independent feeding behaviour was tested for significance. In this study, increased independent feeding behaviour for a mother indicates decreased time that she must provide direct infant care, and decreased time she is directly and visibly assisting her offspring with feeding. It appears that Relative Feeding Time (RFT) levels in all six mothers are fairly consistent, with some outliers for Feb, Gracia and Indy (Fig. 19).

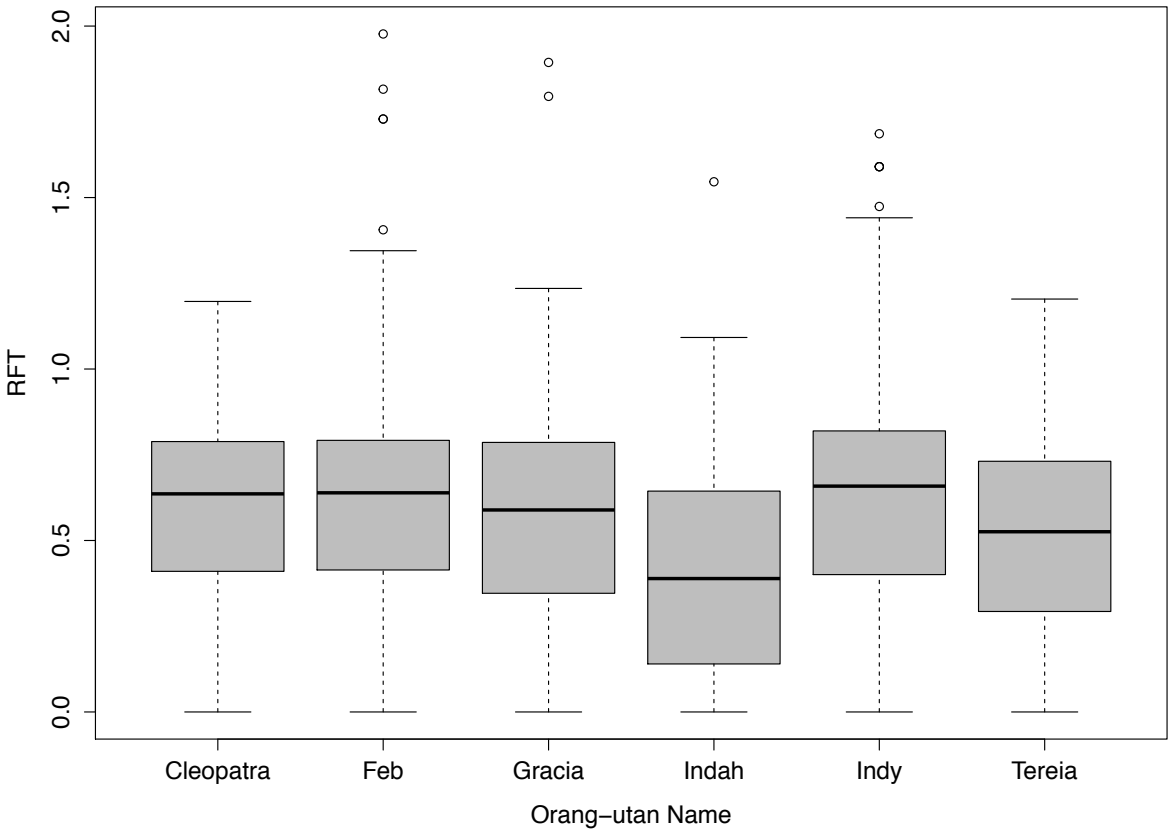


Figure 19: Distribution of maternal Relative Feeding Time (RFT). Values of RFT are corrected, and so some are above 1.

A regression of the development of RFT in mothers shows an increase in time spent feeding by a mother, as her offspring gets older (Fig. 20).

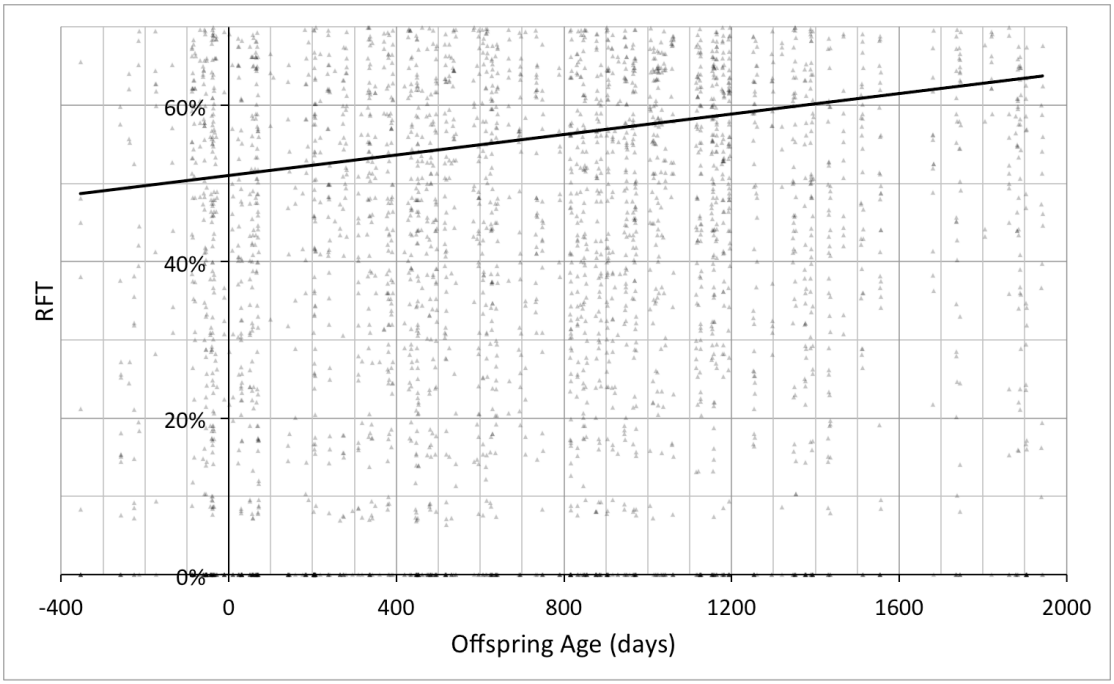


Figure 20: Relative Feeding Time (RFT) in one hour by mothers with aging offspring. 36 % of data points lie above 70 % RFT, and are not displayed on the chart.

A simple linear regression showed this to be highly significant ($p \sim 0^{***}$). Although the sample size is longitudinally very large, caution must be taken as there are only six mothers in the study. To check that no single individual is driving up the means and therefore the patterns seen in an analysis of all the individuals, the random affects of individual identification were controlled for using a mixed effects model. When this was done, significance disappeared, with the mixed effects model showing a non-significant tendency (t-value: 1.45✧).

Simple linear regressions showing feeding time observed in mothers with male offspring and female offspring of progressing ages appear to be different (Fig. 21).

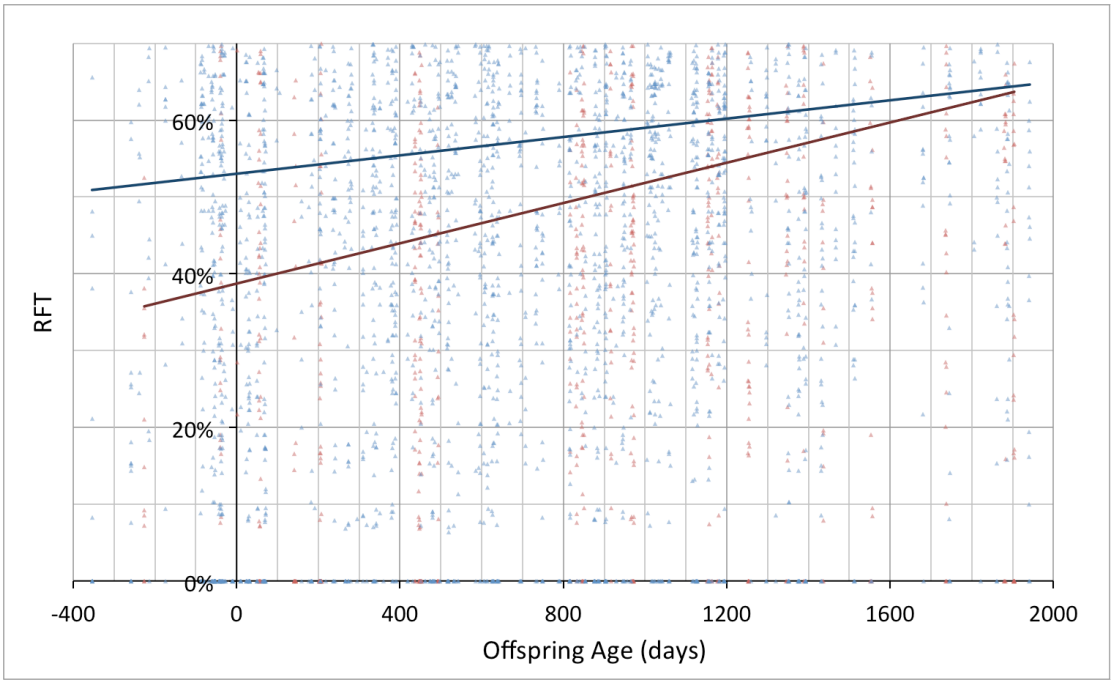


Figure 21: Relative Feeding Time (RFT) in one hour by mothers with male (blue) or female (red) offspring, including trendlines. 36 % of data points lie above 70 % RFT, and are not displayed on the chart.

A multiple regression showed that the interaction between offspring age and sex has a highly significant effect on mother independent feeding. In other words, there is a significant difference between independent feeding changes in mothers of males and mothers of females ($p \sim 0^{***}$). However, when a mixed effects model was used to control for individual variation, this difference was shown to be non-significant (t-value: 0.67 ns).

Mother co-feeding

The data below represents the levels of co-feeding occurring in one hour of feeding behaviour. The sample of Relative Co-Feeding Time (RCFT) is much sparser than that for independent feeding (Fig. 22). Although sociality as a primary behaviour was not suitable for analysis, the distribution of co-feeding behaviour could be as a proxy for sociality, as it indicates where the focal individual was eating in the same tree as another independent individual.

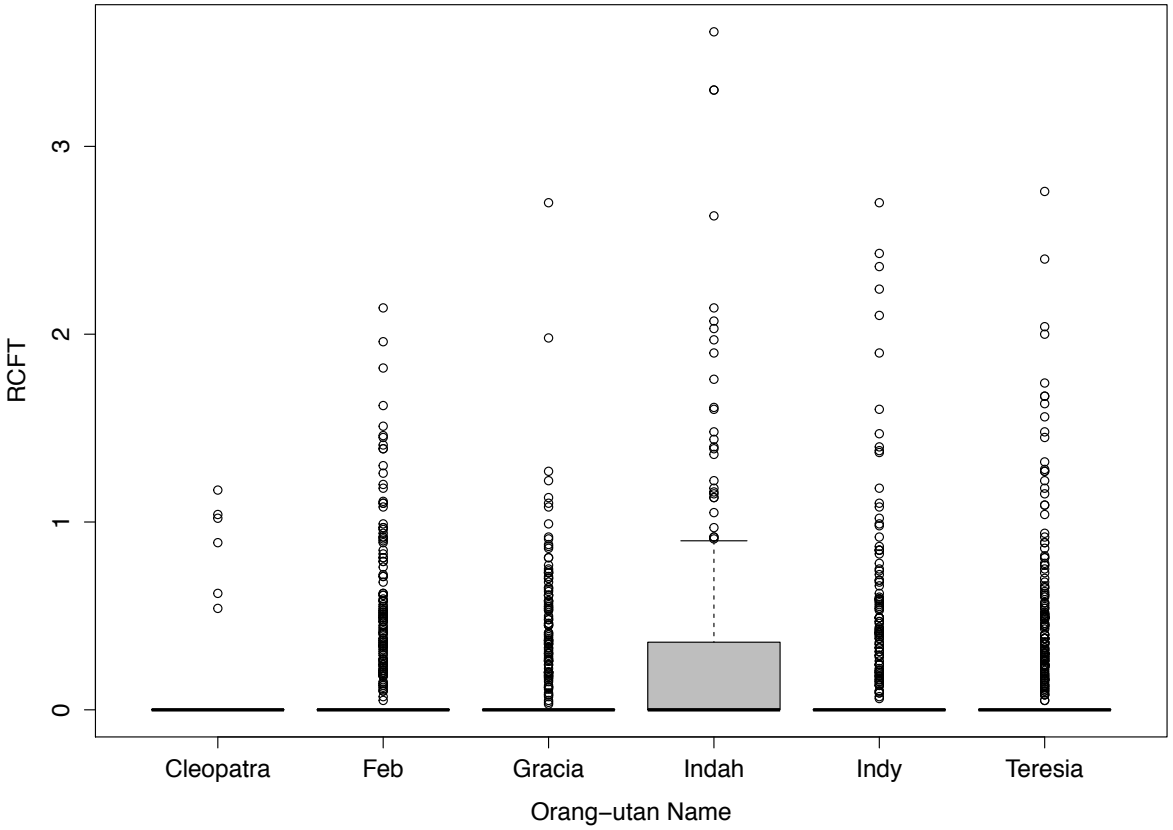


Figure 22: Distribution of maternal Relative Co-Feeding Time (RCFT). Values of RCFT are corrected, and so some are greater than 1.

A regression of the development of RCFT in mothers shows a decrease in time spent co-feeding by a mother, as her offspring gets older (Fig. 23).

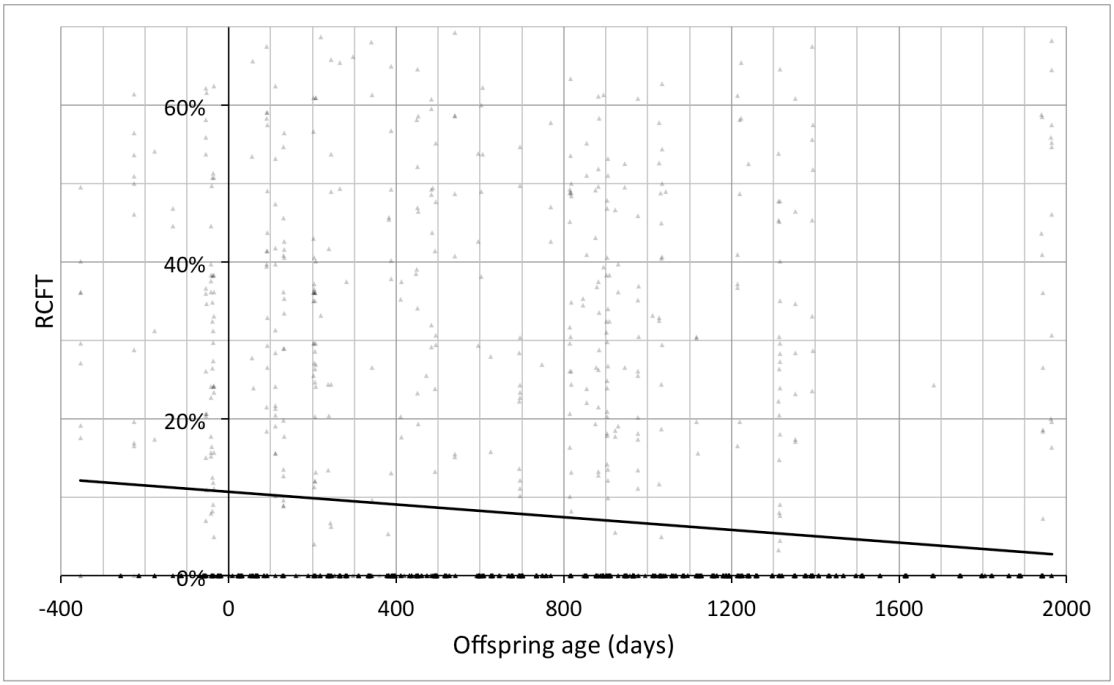


Figure 23: Relative Co-Feeding Time (RCFT) in one hour by mothers with aging offspring. 3.4 % of data points lie above 70 % RCFT, and are not displayed on the chart.

A simple linear regression showed this to be highly significant ($p \sim 0^{***}$). The affect of individual identification was controlled for using a mixed effects model. The model showed a non-significant trend (t-value: 1.68 ☆).

Regressions of RCFT in mothers of male offspring and mothers of female offspring of progressing ages appear different (Fig. 24).

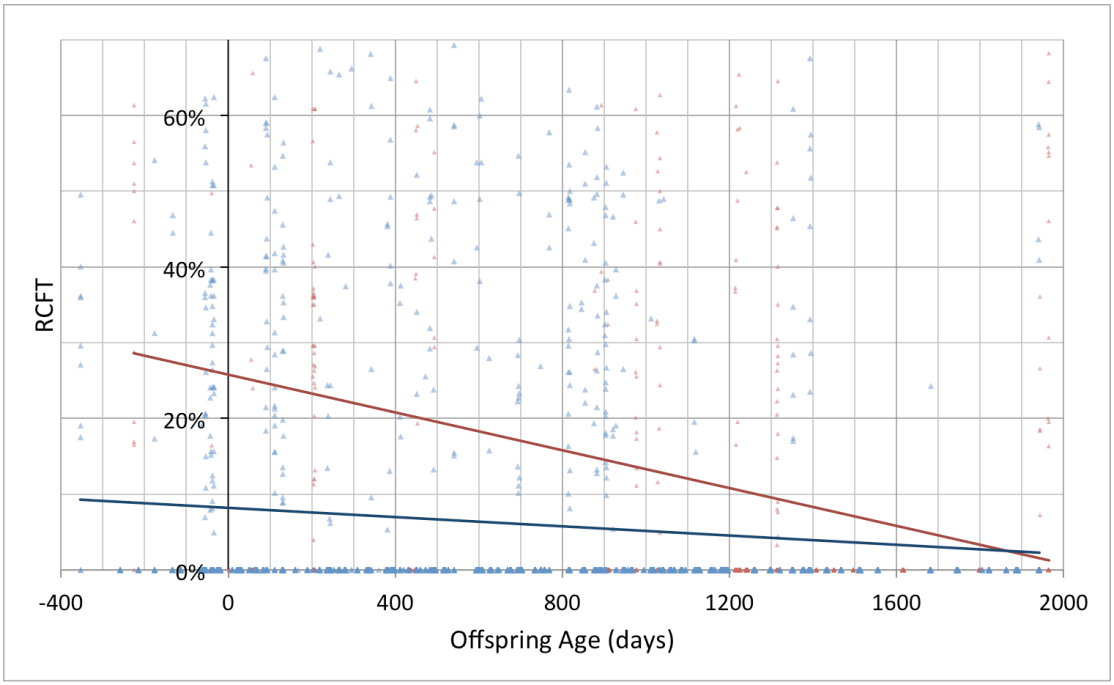


Figure 24: Relative Co-Feeding Time (RCFT) in one hour by mothers with male (blue) or female (red) offspring, including trendlines. 3.4 % of data points lie above 70 % RCFT, and are not displayed on the chart.

A multiple regression showed that the interaction between offspring age and sex has a highly significant effect on mother co-feeding. In other words, there is a significant difference between co-feeding changes in mothers of males and mothers of females ($p \sim 0^{***}$). However, a mixed effects model accounting for individual variation showed the difference to be non-significant (t-value~0 ns).

Offspring feeding

All offspring feeding events, whether undertaken alone or in the presence of other orang-utans, are categorised simply as feeding (see earlier definition provided), but does not include suckling or direct food transfer between mother and offspring. An increased feeding behaviour in an offspring therefore may indicate an increased level of independence, and ability and willingness to find and process food alone, but we cannot be confident in this assumption. It appears that Relative Feeding Time (RFT) in all six offspring is fairly low, with numerous outliers for all individuals (Fig. 25). This suggests that the sample is fairly spread, with little predictable pattern and consistency.

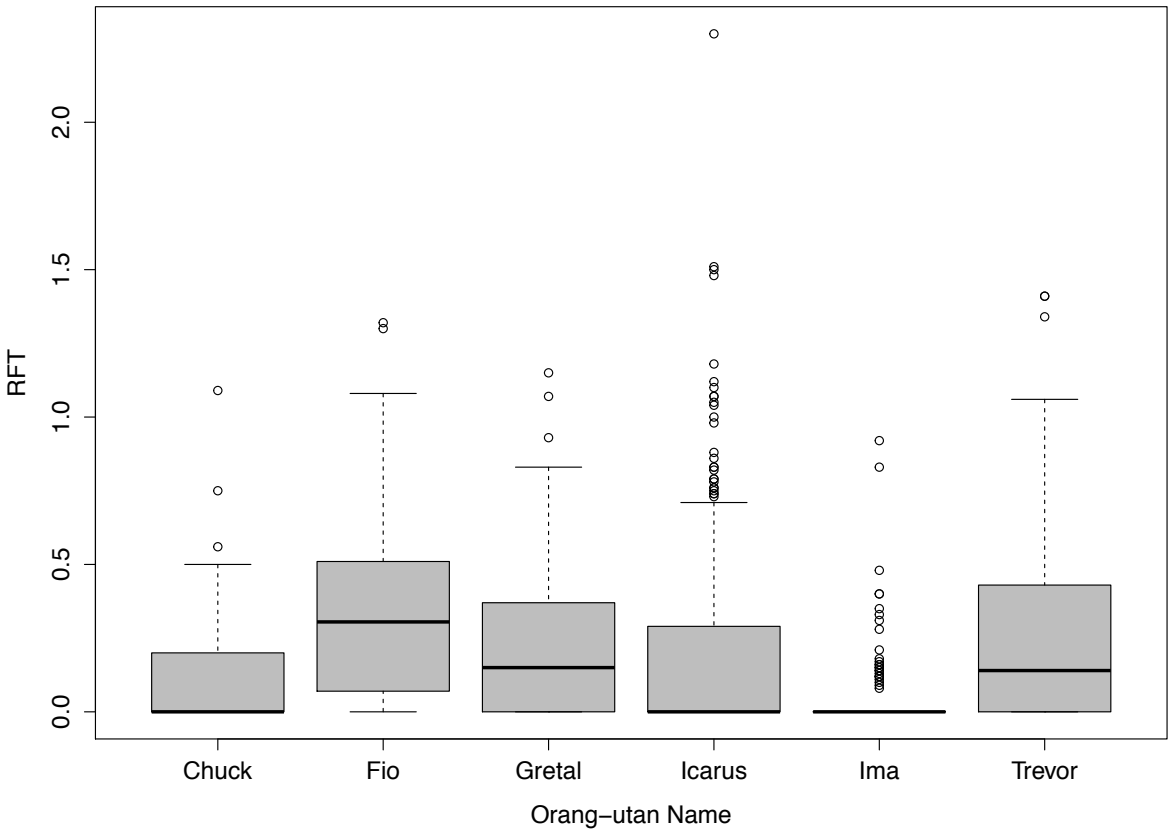


Figure 25: Distribution of offspring Relative Feeding Time (RFT). Values of RFT are corrected, and so some are greater than 1.

A regression of the development of RFT in offspring shows an increase in time spent feeding by offspring, as they get older (Figure 26).

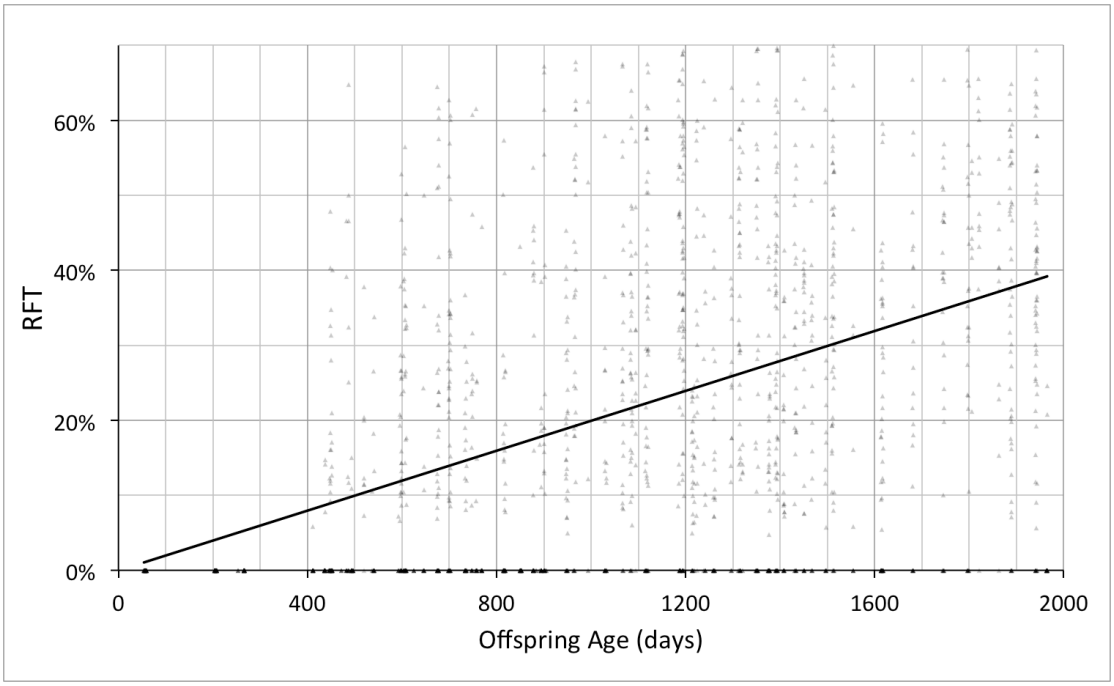


Figure 26: Relative Feeding Time (RFT) in one hour by aging offspring. 6.5 % of data points lie above 70 % RFT, and are not displayed on the chart.

A simple linear regression showed this to be highly significant ($p \sim 0^{***}$). The affect of individual identification was controlled for using a mixed effects model, and the regression remained highly significant (t-value: 8.53^{***}).

Regressions for RFT in male offspring and female offspring of progressing ages appear to be different from each other (Fig, 27).

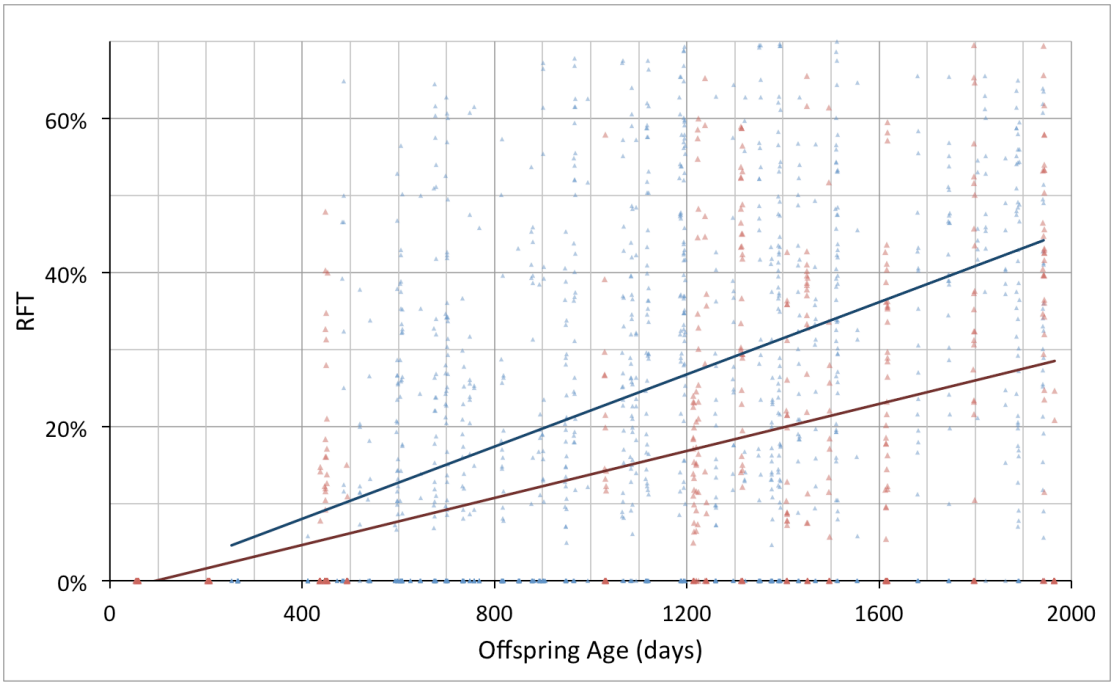


Figure 27: Relative Feeding Time (RFT) in one hour by male (blue) or female (red) offspring, including trendlines. 6.5 % of data points lie above 70 % RFT, and are not displayed on the chart.

A multiple regression showed that the interaction between offspring age and sex has a highly significant effect on offspring feeding. In other words, there is a significant difference between feeding development in males and females ($p \sim 0^{***}$). A mixed effects model, accounting for individual variation, showed a non-significant tendency in the difference (t-value: 1.37✧).

Mother Vs. Offspring

Given the non-significant decreasing trend seen for co-feeding in mothers as their offspring age, and the significance seen in the increase of offspring feeding as they age, it may be worthwhile to look at the two regressions on one graph (Fig. 28). We can see that when the offspring is very young, the mother co-feeds relatively frequently. But as the offspring feeds more independently, the mothers rate of co-feeding drops, as she must find her own patch to sustain her offspring instead of sharing with another individual. As offspring get older and more independent they require less direct care and need more food. This graph appears to support the idea that older offspring can't be sustained on a shared food patch, and since it is easier for mothers to travel between food patches with an older offspring, she does so.

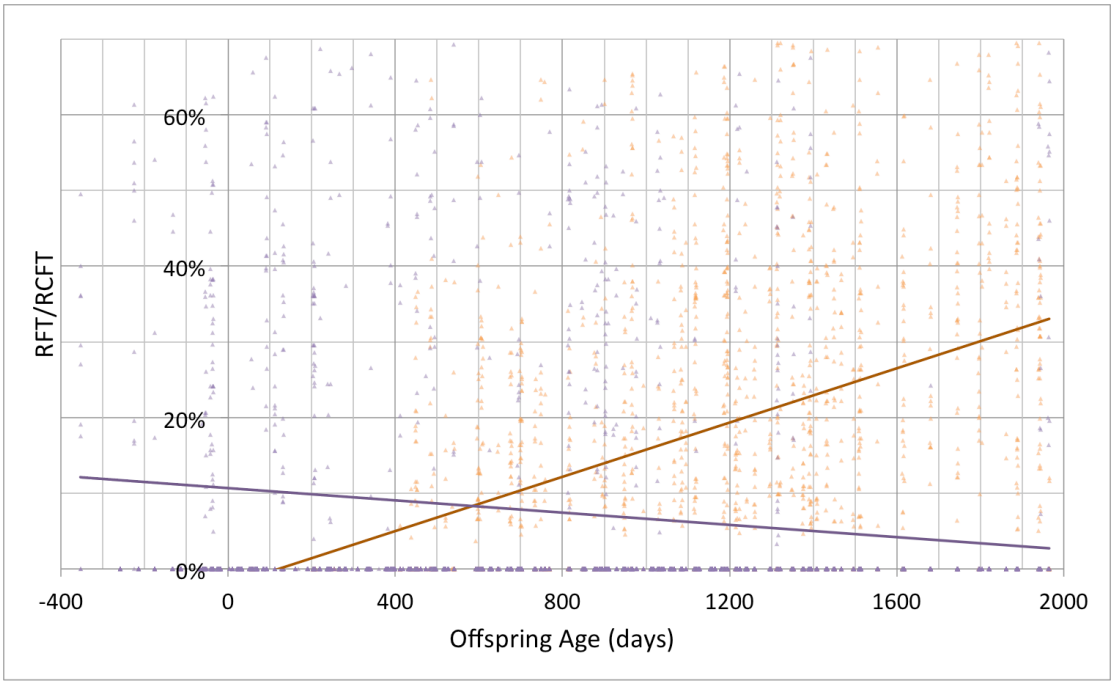


Figure 28: Relative Feeding Time (RFT) in one hour by offspring (orange) and Relative Co-Feeding Time (RCFT) in one hour by mothers (purple). For offspring feeding 6.5 % of data points lie above 70 % RFT and are not displayed on the chart. For mother co-feeding, 3.4 % of data points lie above 70 % RCFT and are not displayed on the chart.

Proximity

Proximity between mother and offspring may be taken as a proxy for independence, and therefore we might expect proximity to decrease (distance between mother and offspring to increase), as the offspring gets older.

Overall proximity

Average proximity was obtained by calculating a mean from the 12 instantaneous data points collected in one hour. Each value of proximity is an absolute distance, in meters, and represents the average distance between mother and offspring over one hour. There is an increase in distance between the mother and offspring, as the offspring gets older (Fig. 29).

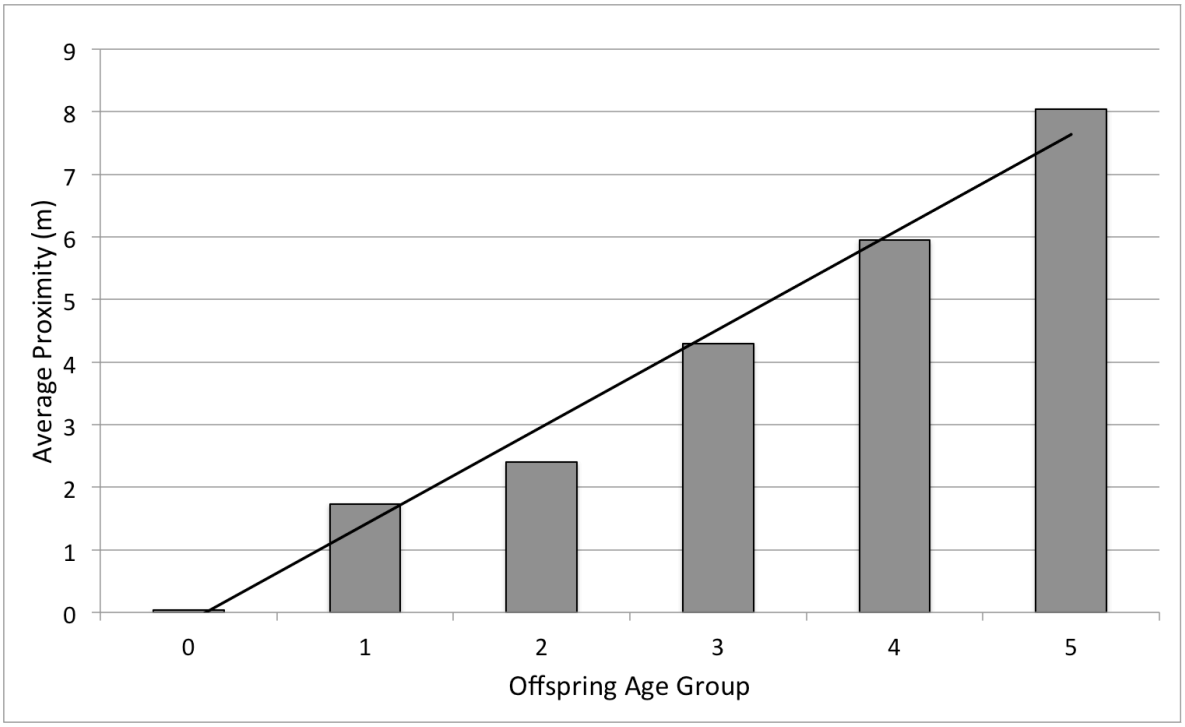


Figure 29: Average proximity between mother and offspring per hour. 1=0-364 days, 2=365-729 days, 3=730-1094 days, 4=1095-1459 days, 5=1460-1824 days.

A Kruskal-Wallis test was performed, the results suggesting that this increase in distance is highly significant (p~0***). However, individuals may vary in their preference, independently from their age. When a mixed effects model was applied to control for individual variation the relationship between offspring age and proximity remained highly significant (t-value: 4.86***).

There is an apparent difference in the change in proximity between male offspring and their mothers, and female offspring and their mothers (Fig. 30).

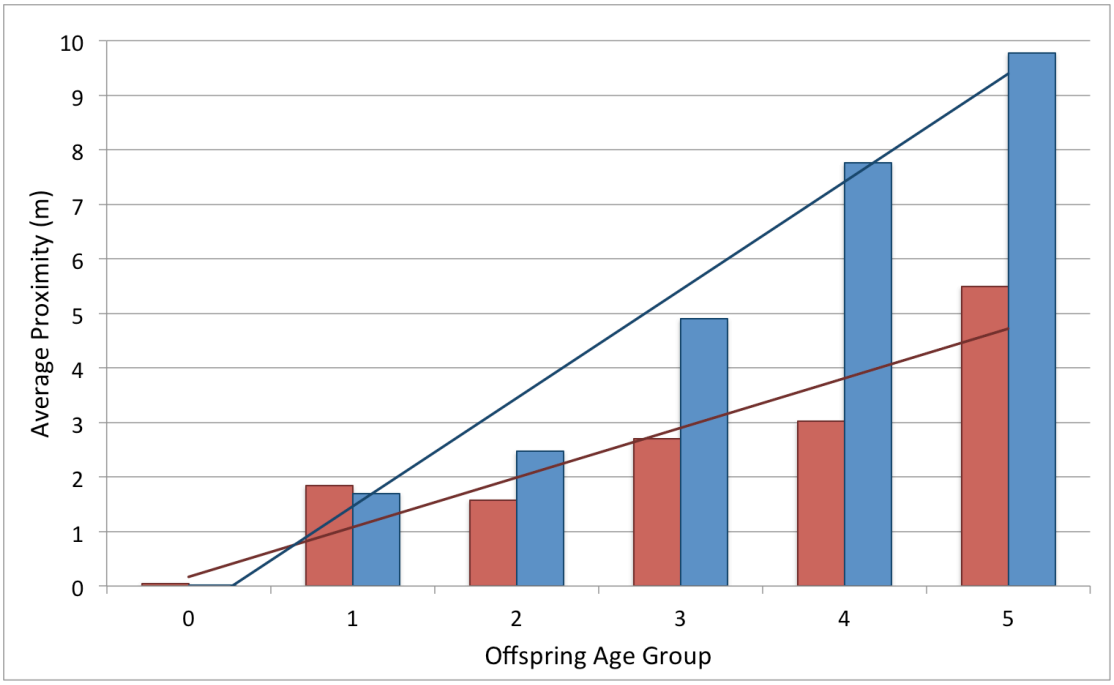


Figure 30: Average proximity between mother and male offspring (blue) and mother and female offspring (red) per hour, including trendlines. For age group definitions see Figure 29.

A multiple regression showed that the interaction between offspring age and sex has a highly significant effect on mother-offspring proximity. In other words, there is a significant difference between the development of proximity to their mothers in males and females ($p \sim 0^{***}$). A mixed effects model was applied to the data to control for individual variations in proximity, showing this difference to be non-significant (t-value: 0.22 ns).

A more accurate proxy than general proximity may be the proximity when performing a given behaviour. It might seem natural that as an offspring gets older he or she will feel more confident and able to play, travel and eat more independently from their mother. Doing these things independently means at a further distance from the mother, because of the physical assistance offspring receive in these activities when they depend on their mothers.

Proximity when mother feeding independently

There is an increase in distance between the mother and offspring when the mother is independently feeding, as the offspring gets older (Fig. 31).

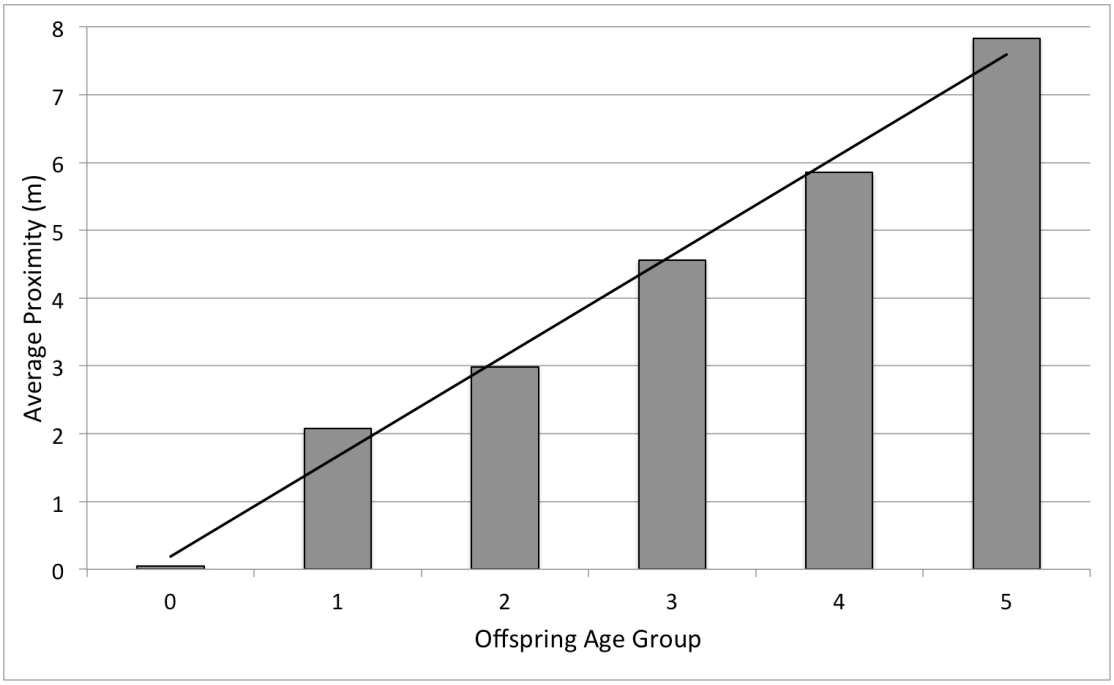


Figure 31: Average proximity between mother and offspring per hour, when the mother is feeding independently. For age group definitions see Figure 29.

A Kruskal-Wallis test was performed, and showed a highly significant relationship between proximity when the mother is feeding independently and offspring age ($p \sim 0^{***}$). A mixed effects model, controlling for individual variation, also showed the relationship between proximity and age to be highly significant (t-value: 9.44^{***}).

There is an apparent difference in the change in proximity between male offspring and their independently feeding mothers, and female offspring and their independently feeding mothers (Fig. 32).

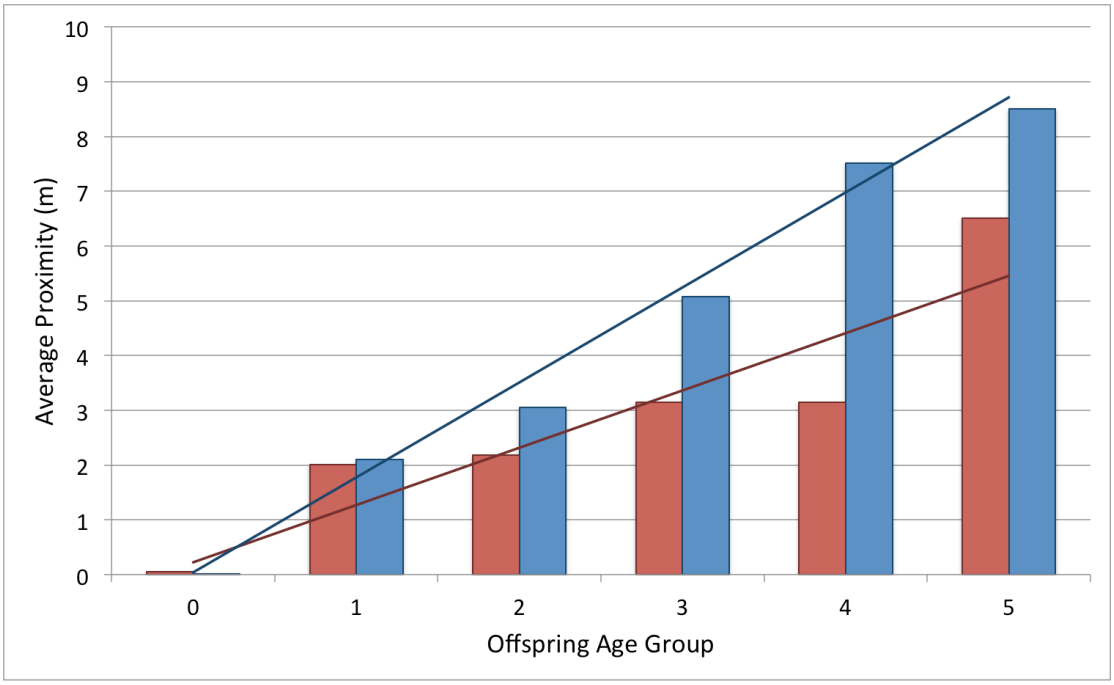


Figure 32: Average proximity when mother is feeding independently, between mothers and male offspring (blue) and mothers and female offspring (red) per hour, including trendlines. For age group definitions see Figure 29.

A multiple regression showed that the interaction between offspring age and sex has a highly significant effect on mother-offspring proximity, when the mother is feeding independently. In other words, there is a highly significant difference between these regressions ($p \sim 0^{***}$). A mixed effects model was applied to the data to control for individual variations in proximity, showing this difference to be non-significant (t-value: 0.19 ns).

Proximity when mother co-feeding

There is an increase in distance between the mother and offspring when the mother is co-feeding, as the offspring gets older (Fig. 33).

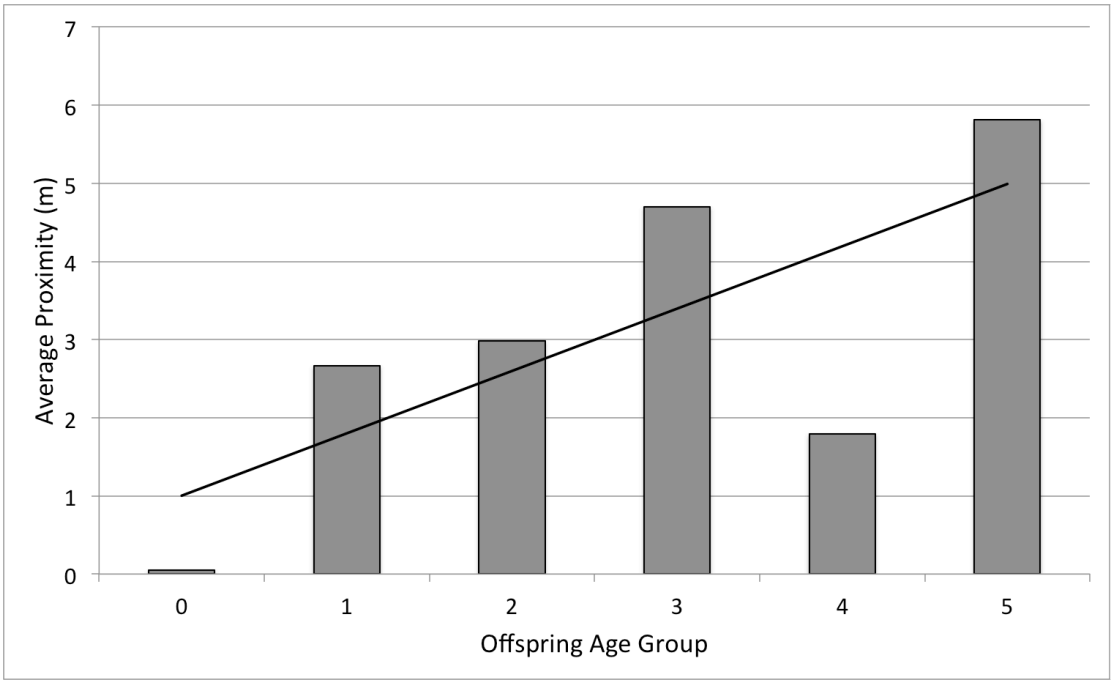


Figure 33: Average proximity between mother and offspring per hour, when the mother is co-feeding. For age group definitions see Figure 29.

A Kruskal-Wallis test determines high significance in the relationship between offspring age and the other-offspring proximity when the mother is co-feeding ($p \sim 0^{***}$). A mixed effects model, controlling for random individual variation, also showed the relationship between proximity and age to be highly significant (t-value: 4.49^{***}).

There is an apparent difference in the change in proximity between male offspring and their co-feeding mothers, and female offspring and their co-feeding mothers (Fig. 34).

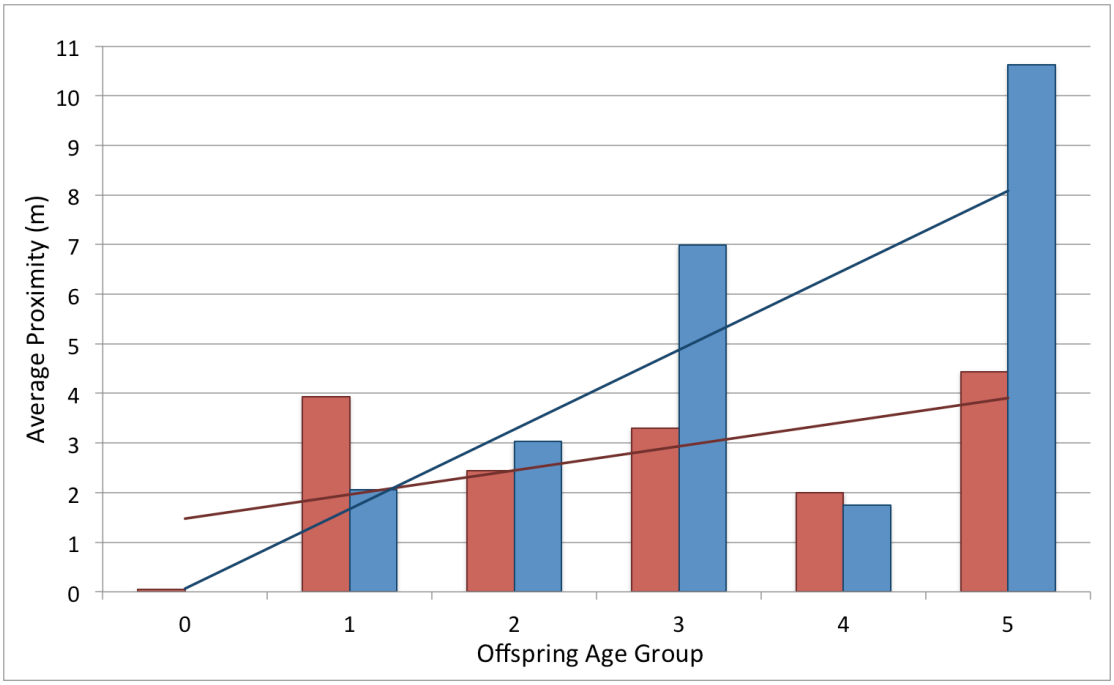


Figure 34: Average proximity when mother is co-feeding, between mothers and male offspring (blue) and mothers and female offspring (red) per hour, including trendlines. For age group definitions see Figure 29.

A multiple regression showed that the interaction between offspring age and sex has a highly significant effect on mother-offspring proximity, when the mother is co-feeding. In other words, there is a significant difference between these regressions ($p=0.05^{*}$). A multiple regression determined a significant difference between the proximity between a mother and her male offspring and a mother and her female offspring, when the mother is co-feeding. But when a mixed effects model was applied to the data to control for individual variations in proximity this difference between mothers of male offspring and mothers of female offspring was shown to be non-significant (t-value: 0.47 ns).

Proximity when offspring feeding

There is an increase in distance between the mother and offspring when the offspring is feeding, as the offspring gets older (Fig. 35).

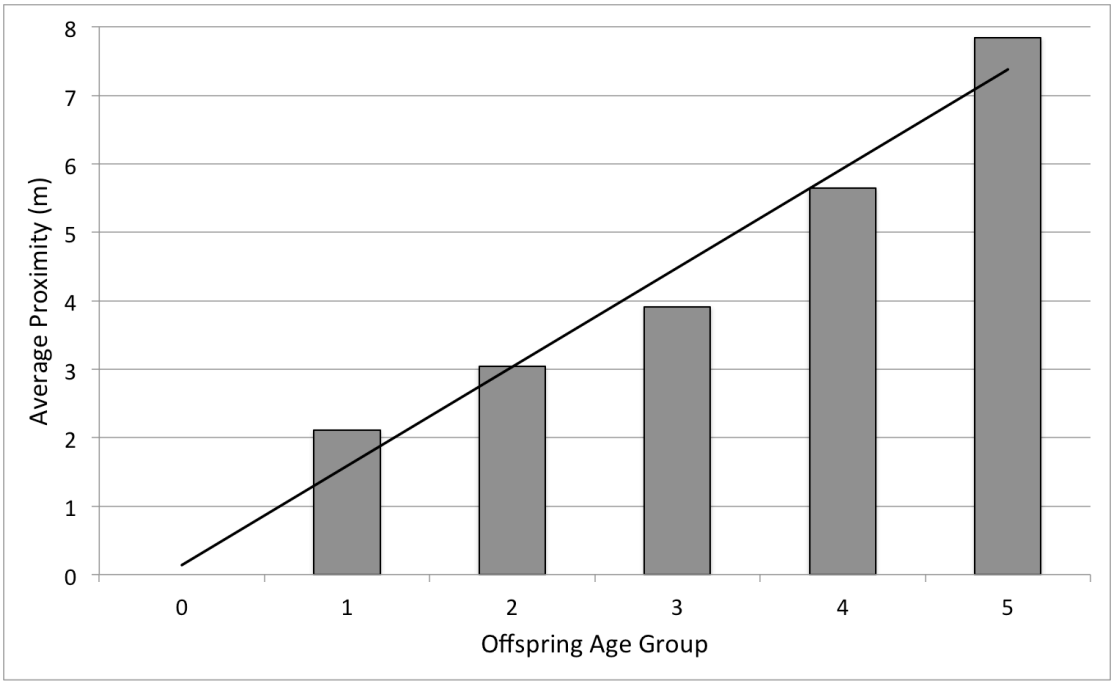


Figure 35: Average proximity between mother and offspring per hour, when the offspring is feeding. For age group definitions see Figure 29.

A Kruskal-Wallis test was performed to determine if there is significance to this increase in the average distance between mother and offspring. The change is highly significant ($p \sim 0^{***}$). However, individuals will vary in preference, independently from their age. A mixed effects model, controlling for individual variation, also showed the relationship between proximity, when the offspring is feeding, and age to be highly significant (t-value: 3.45^{***}).

There is an apparent difference in the change in proximity between feeding male offspring and their mothers, and feeding female offspring and their mothers (Fig. 36).

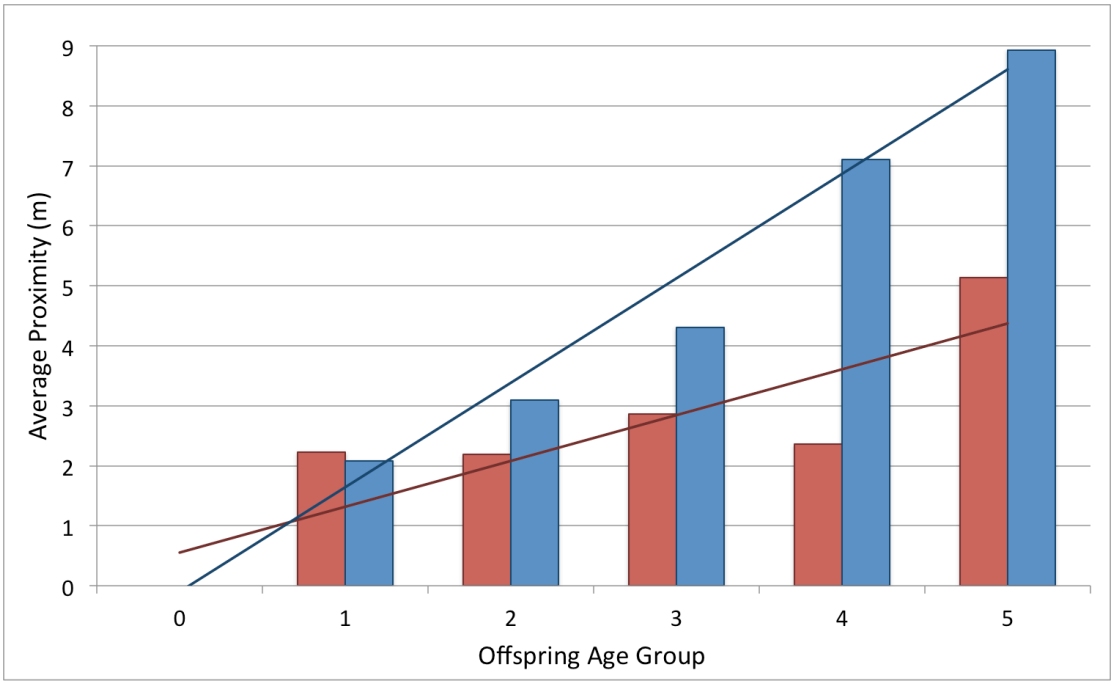


Figure 36: Average proximity when offspring is feeding, between mothers and male offspring (blue) and mothers and female offspring (red) per hour, including trendlines. For age group definitions see Figure 29.

A multiple regression showed that the interaction between offspring age and sex has a highly significant effect on mother-offspring proximity, when the offspring is feeding. In other words, there is a highly significant difference between these regressions ($p \sim 0^{***}$). A mixed effects model was applied to the data to control for individual variations in proximity, showing this difference to be non-significant (t-value: 1.11 ns).

Summary of Results

Table 9: Results of tests using linear regression models.

Test	Intercept	Offspring Age	Offspring Sex	Age: Sex
Mother independent feeding by offspring age	0.51***	+***		
Mother independent feeding by offspring age and offspring sex	0.39***	+***	+***	-***
Mother co-feeding by offspring age	0.11***	-***		
Mother co-feeding by offspring age and offspring sex	0.26***	-***	-***	+***
Offspring feeding by age	0.00(ns)	+***		
Offspring feeding by age and sex	-0.01 (ns)	+***	+ ☆	+***
Proximity by age		+***		
Proximity by age and sex	0.32	+**⋆	-***	+***
Proximity by age, when mother independently feeding		+***		
Proximity by age and sex, when mother independently feeding	0.4	+***	- ☆	+***
Proximity by age, when mother co-feeding		+***		
Proximity by age and sex, when mother co-feeding	0.83*	+***	- ☆	+*
Proximity by age, when offspring feeding		+***		
Proximity by age and sex, when offspring feeding	1.23*	+*	- ☆	+***

ns = non-significant (p≥ 0.20 or -1.28 ≤ t ≤ 1.28)

✧ = a non-significant tendency (p< 0.2 or -1.65 ≤ t ≤ -1.28, 1.28 ≤ t ≤ 1.65)

☆ = a non-significant trend (p< 0.1 or -1.96 ≤ t ≤ -1.65, 1.65 ≤ t ≤ 1.96)

* = significant (p< 0.05 or -2.58 ≤ t ≤ -1.96 1.96 ≤ t ≤ 2.58)

** = clearly significant (p< 0.01 or-3.29 ≤ t ≤ -2.58, 2.58 ≤ t ≤ 3.29)

*** = highly significant (p< 0.001 or-3.29 ≥ t ≥ 3.29)

+ indicates a positive coefficient
- indicates a negative coefficient

Table 10: Results of tests using mixed effects models. Symbols are defined in Table 9.

Test	Intercept	Offspring Age	Offspring Sex	Age: Sex
Mother independent feeding by offspring age	0.48***	+✧		
Mother independent feeding by offspring age and offspring sex	0.42***	ns	+✧	ns
Mother co-feeding by offspring age	0.12***	-☆		
Mother co-feeding by offspring age and offspring sex	0.17*	ns	ns	ns
Offspring feeding by age	-0.05**	+***		
Offspring feeding by age and sex	-0.01(ns)	+***	ns	+✧
Proximity by age	-0.32 (ns)	+***		
Proximity by age and sex	-0.35 (ns)	+***	ns	ns
Proximity by age, when mother independently feeding	0.16 (ns)	+***		
Proximity by age and sex, when mother independently feeding	-0.11 (ns)	+***	ns	ns
Proximity by age, when mother co-feeding	0.35(ns)	+***		
Proximity by age and sex, when mother co-feeding	0.8 (ns)	+✧	ns	ns
Proximity by age, when offspring feeding	0.28 (ns)	+***		
Proximity by age and sex, when offspring Feeding	1.23 (ns)	ns	ns	ns

DISCUSSION

This study draws on data collected on twelve wild Bornean orang-utans, *Pongo pygmaeus wurmbii*, in The Sabangau Forest in Central Kalimantan. Six habituated mother orang-utans, and the single dependent offspring of each, were followed for up to 16 hours each day, and their behaviour recorded over a period spanning five years. Data was captured from offspring of varying ages, and collectively used to create an impression of the first five years of life for a Central Bornean orang-utan. The sample of six offspring included four males and two females. Activity budgets for both mothers and dependent offspring were recorded, including feeding, playing, travelling, resting and socialising, along with measurements of mother-offspring proximity. All of the above were observed instantaneously at 5-min intervals. Although the data collection period spans five years, data sets for any one individual are often fragmented, as it is not uncommon for an individual to be followed and then subsequently not found for a long time. By combining the data from six mother-offspring dyads, with offspring ages ranging from one month to just under five years, a picture of the longitudinal development of a typical young Bornean orang-utan, and its changing relationships with its mother, emerges. Although there are limitations to this approach that will be discussed below, similar methodology has been successfully employed elsewhere. For example in *Tarsius bancanus* (Roberts 1994), *Gorilla gorilla gorilla* (Nowell & Fletcher 2007) and *Pongo spp.* (Jaeggi et al. 2010, Morrogh-Bernard et al. 2009, van Adrichem et al. 2006). Rather than seeking to analyse all of the different behaviours observed during data collection, this study focuses on two of them. The first is feeding by the focals, because being able to feed oneself is a key aspect of being independent. The second is proximity between mother and offspring, because before independent offspring can live outside of the mother's range they must first separate from her. New-born Bornean orang-utans remain in constant physical contact with their mothers for the first four months of life (Miller & Nadler 1981). By the time they are ready to assume their solitary status, Bornean orang-utans need to be confident and competent enough to sustain themselves with no input from the mother. For this reason feeding and proximity have been considered together. Again there are precedents for this approach. For example, in *Cercopithecus aethiops sabaeus* (Alexander & Hines 2002), *Homo sapiens* (Campbell & Eaton 1999), *Pan trogladytes* (Lonsdorf et al. 2004) and *Alouatta spp*. (Bicca-Marques & Calgaro-Marques 1994). For female offspring, their range will abut that of their mother, and they will have limited intermittent contact with her when they are independent (Morrogh-Bernard et al. 2011). For male offspring, their range will be further away, in part to facilitate the seeking of mates, and they will no longer be in contact with their mother. With this difference in mind, as well as physical sex differences, some tentative questions about the impact of offspring sex on the pattern and timing of developmental changes will be considered.

Linear Regressions And Mixed Effect Models

It is important at this point to acknowledge the limitations inherent in a study that relies on such a small number of focals, who may or may not, between them, offer a broadly representative picture of the behavioural changes Bornean orang-utan mother and offspring undergo during the period from birth to offspring independence. The first level of data analysis in this study, using linear regressions,

assumed that the 12 focals were indeed representative, and took no account of the possibility that they might be behaving differently at different ages because of individual idiosyncrasies. The results for the development of feeding in offspring, of independent feeding and co-feeding in mothers of aging offspring, and of mother-offspring proximity, as the offspring grow older, were highly significant. In addition, linear regression was used to look for sex differences, with the results once more highly significant across the same fields. At this stage of the analysis, a minimal claim is that a strong pattern is present in these study individuals, with apparently significant sex differences (Tab. 9). The nature of this pattern and what it might suggest will be discussed below. Further analysis was however considered essential, in order to control for identification, thereby allowing variation between individuals to be removed as a confounding factor. A mixed effects model was employed, after which the results for offspring feeding by age and all tests between proximity and age remained significant. Possible implications of this will be discussed below. Independent and co-feeding in mothers of aging offspring, and sex differences across all the fields did not (Tab. 10). There are two possible explanations for why significance seen in a linear regression disappeared after applying a mixed effect model. The first explanation is that the apparent significance of a linear regression was an artefact, caused by individual characteristics, unrelated to age. The second explanation is that the sample size is simply too small. Nevertheless, given the statistical significance after linear regression, the results are suggestive that the latter may be true. Further research using a larger number of focals would help determine this.

Feeding

Both after linear regression, and mixed effects modelling, the relationship between offspring feeding and offspring age is statistically significant (cf. Fig. 26), with offspring spending an increasing proportion of their activity budgets feeding as they age. This is consistent with the growing offspring's increasing energy needs, as well as demonstrating an increasing ability to supply these needs independently. The levels of independent feeding of the mothers appear significant after linear regression but this significance disappears after mixed effects modelling (cf. Fig. 20). As discussed above, it is possible that this loss of significance is related to the power of the sample size. If so, one implication might be that, as the offspring feeds itself more and more, the mother is able to focus more attention on her own calorie intake, and therefore we see an increase in her independent feeding. Alternatively, there may indeed be no significant change in mother feeding as her offspring ages, suggesting that it may be the offspring, rather than the mother, who is determining changes in their own feeding budget. In human infants it is observed that the infant prefers to be the one to take control of their own development and initiate separation, physically and behaviourally, between themselves and their mother (Sroufe & Waters 1977), an adaption that may have evolved to counter the conflict that will arise when a mother tries to break close ties with the offspring. In addition, by sustaining an activity level that changes little, the mother may be demonstrating how to survive as an adult, as well as providing a stable and reliable attachment figure from which to explore and develop. This is important in human development, and likely to be important in orang-utans development (Ainsworth & Bell 1972, Bowlby 1969; 2005, Stroufe & Waters 1977). The semi-solitary nature of orang-utans may

also be a factor (Poirier 1968), with the responsibility of having a dependent offspring falling predominantly on the mother, whereas in other primates, for example Nilgiri langurs, *Presbytis johnii*, their sociality, and related mechanisms like alloparenting, means that the mother is able to vary her maternal behaviour more. Finally, it is important to remember that the methods of data collection for feeding in this study – feeding in offspring, versus co-feeding and independent feeding in mothers – were not entirely comparable, and may have imposed unforeseen limitations for analysis purposes.

Proximity

Both after linear regression and mixed effects modelling, proximity is significantly correlated with age when the mother is feeding independently or co-feeding, when the offspring is feeding, and generally (regardless of behaviour) (cf. Fig. 31, 33, 35 & 29). In other words, there is evidence to suggest that as offspring age they spend more time away from their mother, they feed further way from her, and they wander further afield when she is feeding alone or feeding with another adult. A relationship between age and proximity has also been found in other primates (Hinde & Atkinson 1970, Poole 1987, van Adrichem et al. 2006) whales (Thomas & Taber 1984) and dolphins (Mann & Smuts 1999). Unfortunately, a directional proximity quotient indicating which member of the mother-offspring dyad was responsible for creating and closing space between the pair, similar to Thomas and Taber's (1984), was not recorded in the collection of this data. This is a potentially interesting area for further research. Attachment theory states that the biological function of attachment is protection from predators, and proximity between mother and offspring the means of achieving this functionality. Although Bornean orang-utans have few predators, additional 'attachment motives' such as gaining access to food may be at play (Bowlby 1969; 2005, Stroufe & Waters 1977).

Sex Differences

As discussed earlier, male and female adult orang-utans are physically different and have different ranges and mating strategies (see Methods). An interesting question is therefore whether developmental changes in early behaviour vary according to sex. Statistically significant sex differences in offspring feeding, in independent feeding and co-feeding in mothers, and of mother-offspring proximity, as the offspring grow older, were seen following linear regression, but disappeared once mixed effects models were applied. There was however a trend in the relationship between offspring age and sex, and their feeding levels (cf. Fig. 27). Male and female orang-utans grow at different rates and it has been suggested that males are more active in infancy than are females, and so we might expect to see different rates of feeding in male and female offspring (Campbell & Eaton 1999, Zihlman 1997). Given the difference in sociality in males and females when mature, namely that females form stronger social bonds with each other than males do (Broad et al. 2006), that males are more solitary than females (Zihlman 1997), and that independent males ultimately range much further from their mother than females do, levels of co-feeding and also development of mother-offspring proximity might be expected to reflect this. There are however just four male offspring and two female offspring in this study. As a consequence, after controlling for the fixed effect of sex, together with the

random effects of individual identification, the sample is so small that significance is highly unlikely to appear. A larger number of study individuals would be the only way around this problem.

While acknowledging all of these provisos, it is still interesting to examine the results after linear regression and to think what these significant differences might mean, if replicated in a larger sample. For instance, mother feeding activity for a mother of a male and a mother of a female appear to be initially different and converge over the first 2000 days of an offspring's life. Might this show mothers preparing to return to the state that they were in before having the current offspring: solitary and with an activity budget that only supports herself in her environment? Furthermore, might it indicate that the effect of offspring sex on the mother is larger when that offspring is younger; if so, why? Then there is the apparent increasing divergence of behaviours between male and female offspring throughout the dependency period (Fig. 37). If replicated in a larger sample, this would be consistent with the theory that sexual differences build up gradually, rather than happening all of a sudden as sexual maturity is reached (Zihlman 1997). This has previously been described in humans, where sexual difference increases with age (Campbell & Eaton 1999).

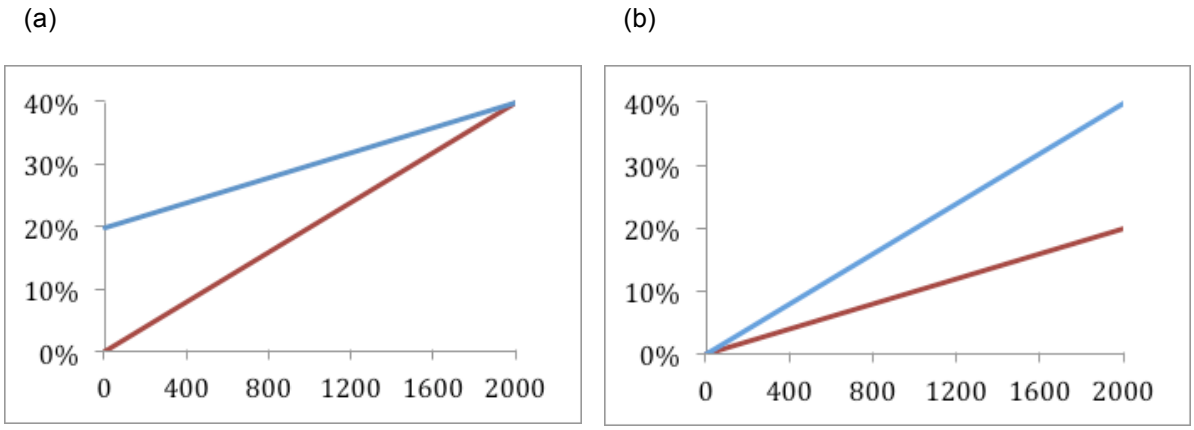


Figure 37: Heuristic models showing general patterns of Relative Feeding Times (RFT) in (a) mother results-regression for mother of female (red) and mother of male (blue) (b) offspring results-regression for female (red) and male (blue). X-axis =Offspring Age (days). Y-axis =RFT. Note that no data was used to generate these models. Design: Sophie Kirklin.

Some Limitations of the Study

Feeding behaviour is particularly vunerable to temporal change, as every aspect of orang-utan diet is highly subject to seasonality (Galdikas 1988, Knott 1998, White 1998). While seasonal change has been controlled for in the data sets used, variation in seasonal patterns over multiple years has not, and this may have a significant effect on the results. For example, during Aug 15 and Sep 15 the El Niño effect, due to a warm ocean current resulting in large climactic warming events and occurring every five to six years, led to extreme drying of the forest (pers. obs., Trenberth 1997). Together with the effect of a human culture of burning land to clear it for various reasons, fires were almost uncontrollable and the tinder-like forest was filled with thick smoke, lowering visibility dramatically. Forest fires are a problem every year in Kalimantan, but the extent of the haze created in 2015 was worse than ever recorded (Taconni 2016, Chisholm et al. 2016, Abood et al. 2016). This only occurs

once every five or six years, and so is not considered when attempting to control for the effects of annual seasonality. Given the effects on energy levels and general health of the human researchers, it is reasonable to assume that the orang-utans were also affected. A young orang-utan observing his or her mother adapting her behaviour to deal with these conditions would have an important but relatively rare opportunity to learn a lesson that may one day save his or her life. Another affect of the drying El Niño was apparent in Jul 15. Female orang-utans were found far from their expected home ranges, very likely due to fruit shortages (pers. obs.). Fruit shortages have been seen to significantly effect range and activity levels of wild primates (Doran 1997, Gadikas 1988, Hemingway & Bynum 2005, Vogel et al. 2009). The deviations observed were, presumably, an attempt to locate alternative food sources. This could in turn lead to an increase in sociality, with orang-utans coming closer together, as they migrate towards scarcer-than-normal food patches. In addition to changes in home range, this is likely to result in alternate food types, such as fungus and epiphytes, being eaten more regularly than normal. Foraging with the correct techniques and for the correct species (especially in the case of fungi which may be poisonous) are skills that may ensure the survival of an independent offspring, but can only be observed and learnt at certain times in the year, or over the course of multiple years. Processing techniques can be complex: in late July 15, SK observed a mother orang-utan on the floor with her infant picking large flat fungi off of a log, and carefully folding them before ingestion (pers. obs.), possibly to avoid a certain taste or texture on part of the mushroom. Gorillas have been observed doing something similar with leaves from a thistle, *Carduus nyassanus* (Byrne & Byrne 2001). In addition, these new ranges may lie in different forest-types in which fruit availability, other animal presence, and tree density may impact on other behaviours. For example, in May 15, OuTrop researchers observed an infant orang-utan playing with an infant gibbon (OuTrop, pers. comm.). For all these reasons and more, the assumption in this study, that each orang-utan exists in a habitat that is comparable to that of the others, may be simplistic.

There are also practical difficulties associated with the observation of wild mothers with offspring, for example the heightened level of protectiveness and territoriality in mothers (Kingsley 1977, Miller & Nadler 1981), meaning it is not always easy to see what is happening during follows. Where most other primates are social, orang-utans are semi-solitary, which can make collecting data on a large number of individuals labour-intensive. The length of data collection, and number of researchers involved in this study, meant that there were some ambiguous recorded data. The protocols did however remain constant, and there was surprisingly little inconsistency in the data.

Future Research

This project would benefit greatly from a larger sample size of focal orang-utans, and although, longitudinally this data set is quite sizeable, data collection spanning an even longer time period would be beneficial. This data covers a five-year period. Given that the dependency period can last up to eight-years, it would be helpful to have data spanning this timescale. An extended period of data collection, perhaps even beyond the dependency period, would enable further examination of individuals' life histories. In females it would be interesting to know if their own experiences during the dependency period have implications for their own mothering styles, or in males on their mating

strategies. Collaboration with and inclusion of additional research sites in the research project could increase the sample size and provide a larger dataset. This may, potentially, increase variation due to geographical or cultural factors, providing the advantage of being able to more effectively identify and control for these random effects, as well as the opportunity to identify exciting implications of great ape culture. A higher level of consistency in data collection could be implemented in order to allow further analysis of the data. In addition, a new definition allowing us to denote offspring co-feeding with another orang-utan, other than his or her mother), would allow for an analysis of offspring sociality associated with feeding.

The dataset collected in Sabangau included a total of 14 primary behaviours, countless secondary behaviours and additional information on sociality, distance above the forest floor, and proximity to other individuals, all collected instantaneously, every 5 minutes. The focus of this dissertation, feeding behaviour and mother-offspring proximity, uses only a small part of the dataset. Other potential factors that would be interesting to analyse include dietary breakdown, modes of travel, types of play, nest building and sociality, and how these correlate with age and sex. Other interesting variables include the number and sex of siblings of the offspring, parity of the mother (although this was shown to have no effect in vervet monkeys by Hauser & Fairbanks [1988]) and the involvement of other female relatives, like older sisters, in offspring rearing. In addition, recording a "quotient" in regards to proximity (Thomas & Taber 1984), would help to identify who initiates and maintains proximity in a mother-offspring dyad, with implications for the processes of weaning, weaning conflict and reaching independence in Bornean orang-utans.

CONCLUSION

This study has focussed on changes in feeding and proximity as a way of trying to understand some of the behavioural changes that take place in both mothers and offspring as Bornean orang-utans move ever closer to a state of independence and solitary existence. While the sample size was small, reducing the power of the study, the results for offspring feeding and proximity being related to age were highly significant, for mother feeding and age, suggestive, and demonstrated a trend for a sex differences in offspring feeding levels. Further research, involving a larger sample size, with data collected over a longer period of time, offers the best opportunity to strengthen the study's power and develop a more nuanced picture of the development of this fascinating species.

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