How do male interactions with infants affect mothers and infants in Barbary macaques (Macaca sylvanus)?

PAGANO, MARIE-CLAIRE

How do male interactions with infants affect mothers and infants in Barbary macaques (*Macaca sylvanus*)?

Marie-Claire Pagano

A thesis submitted for the degree of Master of Science by Research in Biological Anthropology

Depatment of Anthropology
Durham University
September 2017

Abstract

In Barbary macaques, males handle infants to regulate relationships among themselves. Previous studies of male infant handling have focused on its function from the perspective of male handlers, while the effects on the mother and infants have not yet been considered. Since infant care is costly, being unencumbered by their infants may enable mothers to spend more time feeding. However, mothers may also experience elevated anxiety when separated from their infants. Since handlers may be less restrictive than mothers, infants may benefit from a greater number of interactions with others and higher rates of independent locomotion and exploration. I assessed the immediate behavioural effects of male infant handling on the mothers and infants involved. I studied a semi-free ranging population of Barbary macaques at La Montagne des Singes, Kintzheim, France. First, I observed behaviours of mothers when they were with their infants and when male group members handled them. I compared the rates of self-directed, grooming and vigilance behaviours and the proportion of time mothers spent feeding. Second, I observed infants when with their mother and when with male handlers. I investigated the infants' rates of independent locomotion, number of social partners and exploratory behaviours and distress behaviours, such as squealing. I analysed the data with a negative-binomial GLMM. When they were away from their infants, mothers exhibited greater rates of self-directed behaviours, vigilance and groomed others for longer compared to when they were with their infants. Mothers did not differ in the duration of time they spent feeding when away from than when with their infants. Infants exhibited greater rates of distress behaviour when with males than when with

their mothers. Infants did not differ in the rate of independent locomotion or exploration between conditions or interact with more individuals when with the male than their mother. These results show that in a provisioned group of macaques, mothers and infants do not appear to directly benefit from male infant handling but may pay a cost. Infants and mothers were distressed when separated from each other. Mothers and infants may gain long-term benefits such as agonistic support, access to resources and earlier infant weaning from associating with males in the group.

Acknowledgements

I would like to thank Prof. Jo Setchell for always offering her advice and providing me with prompt and helpful feedback on all versions of this thesis. I am also grateful to Ellen Merz, Gilbert de Turckheim and all the staff at La Montagne Des Singes for welcoming and accommodating me, imparting their knowledge and most importantly, for permitting me to conduct my study on their group of macaques. I would like to thank my colleagues and friends from the Anthropology department and Primatology group for their support and discussions. Thank you to my examiners for their helpful comments.

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1 Non-maternal infant handling

In many group-living species, infants are a source of interest and individuals other than the mother often handle them (Hrdy 1976; Maestripieri 1994b; Jin *et al*. 2015). Non-maternal infant handling interactions are common across the primate order, occurring in tarsiers (Gursky 2000), macaques and baboons (McKenna 1979), wild capped langurs (*Presbytis pileata*) (Stanford 1992) , owl monkeys (*Aotus azarai*) and tamarins (*Saguinus oedipus*) (Rotundo *et al.* 2005; Tardiff *et al.* 1990*)*. Infant handlers can be male or female, adult or juvenile. Numerous hypotheses have been proposed to understand the function of non-maternal infant handling from the perspective of the infant handler with few focusing on the other individuals involved (Riedman 1982; Paul & Kuester 1996; Mitani & Watts 1997).

In several Old World monkey species, female group members are more interested in infants than males (Chism 2000). Young and primiparous females may benefit from handling another's infants by practicing their mothering skills (learning to mother hypothesis, Lancaster 1971). Handling another female's infant increased the chances that juvenile female vervet monkeys (*Cercopithecus aethiops*) raised their own infant successfully (Fairbanks 1990). Females may also be strongly attracted to infants as a result of strong selection on mothering behaviour (natal attraction hypothesis: Silk 1999; Paul 1999; Silk *et al.* 2003). Older and multiparous females may also handle infants as a form of competition, to reduce another group member's fitness by injuring or kidnapping their infant (Silk 1980; Maestripieri 1994a). Older bonnet macaque (*Macaca radiata*)

females are more likely to handle infants roughly than young females (Silk 1999).

In mammals, males are not expected to interact extensively with infants since females perform the majority of infant care. This stems from the different investment strategies in males and females. For female mammals, reproduction involves producing a small number of energetically demanding gametes, gestation and post-natal care (Trivers 1972, pp 136–179). Moreover, due to internal fertilisation, females are certain that the infant is theirs and can therefore increase their reproductive fitness by offering care to ensure the infant reaches sexual maturity (Broad *et al* 2006). Males experience reduced certainty that they have sired the infant due to the time difference between fertilisation and birth and the possibility that other males mated with the female. Therefore, for males it would pay off to mate with many females to increase their reproductive fitness through higher chances of siring offspring. As a result, their contribution to infant care is reduced (Trivers 1972, pp 136–179). Despite this, in 40% of primate species males interact in some form with infants (Woodroffe & Vincent 1994; Riedman 1982). During these interactions, males handle, carry and sometimes protect infants from conspecifics.

An obvious reason for why males would interact with infants is as a form of paternal care. This occurs if the male is the infant's sire and his participation in infant care has a positive effect on the infant's survival. Paternal care is observed in several monogamous breeding species such as owl monkeys (Rotundo *et al.* 2005) and siamangs (*Symphalangus syndactylus*) (Lappan 2008). However, it is

difficult for males to determine paternity in species with polyandrous mating. Despite this, in some cercopithecine species such as savannah baboons (*Papio cynocephalus)* (Buchan *et al.* 2003) and Assamese macaques (*Macaca assamensis*) (Langos *et al.* 2013), males handle and protect their genetic offspring from conspecifics more often than non-related infants.

In several species of cercopithecine, such as baboons and macaques, males handle infants regardless of their kin relationship to the infant or mother (Paul & Kuester 1996; Kümmerli & Martin 2008). In these cases, we need alternative explanations for why males would handle infants. These can be divided into three main hypotheses, which involve various degrees of exploiting the infant.

First, males exploit infants by using them as social tools to regulate the formation and maintenance of relationships with other males in the group, termed agonistic buffering (Deag 1980). For example, males of some species carry infants to other males to form a triadic interaction. During these interactions, males greet each other in a ritualised manner, often lip smacking with the infant as the focus of attention (Deag 1980; Small 1990; Paul *et al.* 1996). This behaviour is often seen in yellow baboons, and Barbary, Assamese and bonnet macaques (Smith & Whitten 1988; Small 1990; Minge *et al.* 2016; Kubenova *et al.* 2017).

Second, males use infants as protection against aggression (Hrdy 1976). Male geladas (*Theropithecus gelada*) (Dunbar 1984), olive baboons (*Papio anubis*) (Packer 1980) and bonnet macaques (*Macaca radiata*) (Silk and Samuels 1984)

that carry infants are immune to aggression from other male group members, enabling them to approach higher-ranking individuals.

Third, males carry an infant to increase their mating opportunities (Smuts 1985; Ménard *et al.* 2001). Species of both Old and New World monkeys such as baboons and buffy headed marmosets (*Callithrix flaviceps*) secure more mating opportunities with the mother, by employing this care-then-mate strategy (Woodroffe & Vincent 1994).

These explanations for male infant handling are not mutually exclusive and males may accrue a combination of benefits from handling infants (Figure 1). For example, Barbary macaques who handle infants experience greater mating opportunities with the infants' mother during successive mating seasons and also use infants to maintain and regulate relationships amongst themselves (Ménard *et al.* 2001) (Figure 1).

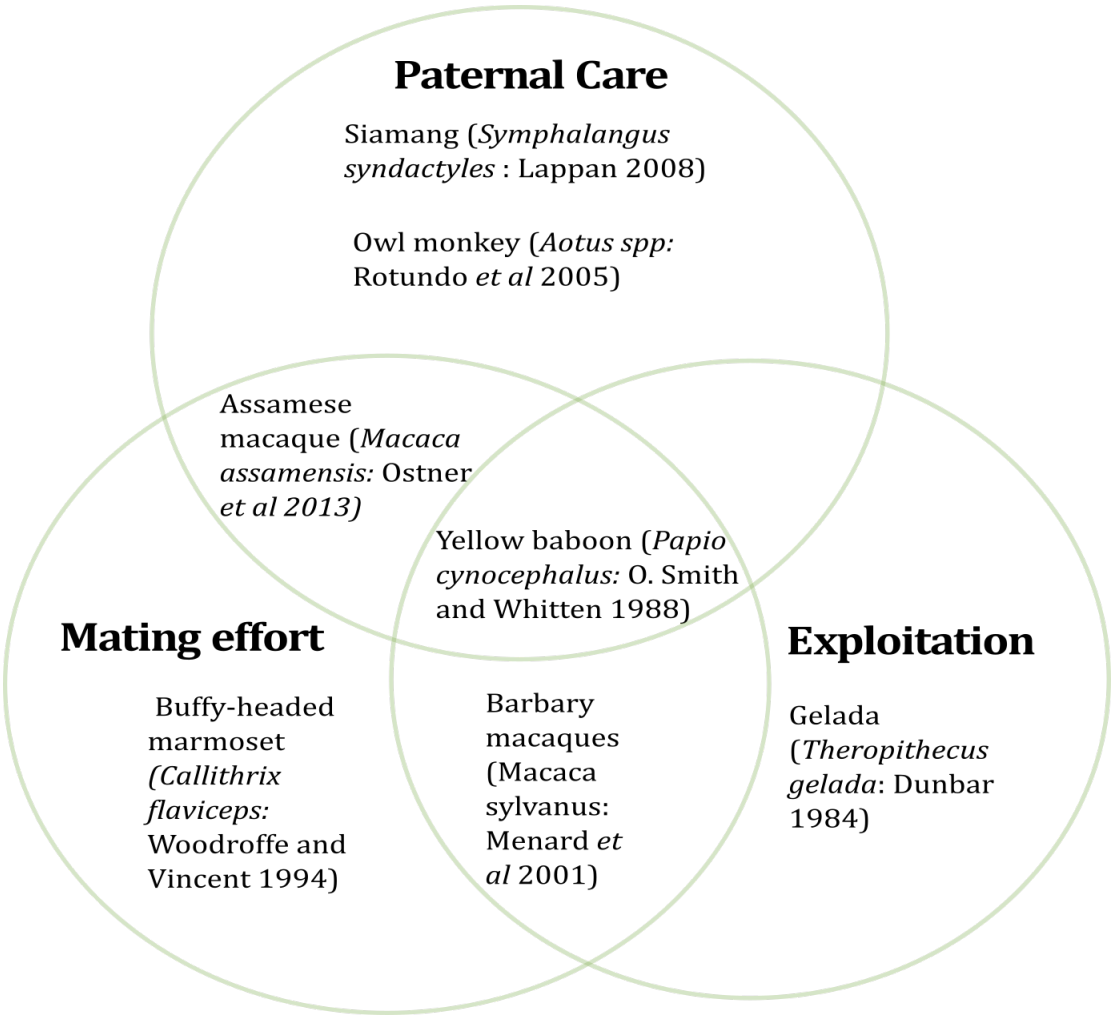

Figure 1: Evolutionary explanations for why male primates care for infants

Since male infant handling involves three individuals: the mother, infant and male, evolutionary explanations should examine its effects from all perspectives (Mitani & Watts 1997). The benefits and costs incurred by the mothers and infants involved in male infant handling have been subject to less investigation than those of the males (Xiang *et al.* 2010; Kerhoas *et al.* 2016). Since the infant's fitness is dependent on the mother and vice versa, the costs incurred and benefits gained from male infant interactions are expected to overlap.

Barbary macaques show the most prevalent and intense male-infant interactions among cercopithecines. Males handle and carry infants from when they are a few days old (Small 1990; Kuester & Paul 1992; Paul *et al*. 1996). Males interact extensively and positively with infants that are not their offspring or matrilineally related in two ways (Paul *et al*. 1996; Kümmerli 2001; Kümmerli & Martin 2008). First, during male-infant dyadic interactions, males carry, groom and protect infants and respond to infants' vocalisations, as their mother would (Kümmerli & Martin 2008; Kubenova *et al.* 2017). These dyadic interactions can last more than 20 minutes. Second, during triadic interactions, two males hold and manipulate an infant between them while exchanging affiliative and social gestures in a ritualised manner (Deag 1980; Paul *et al.* 1996).These triadic interactions last only several seconds (Kümmerli & Martin 2008). Combining these two types of interactions, males can take infants from their mothers for up to 20% of the day, although not all infants are handled by males (Paul *et al.* 1996).

In this study I aim to determine whether and how male infant handling influences the mothers and infants involved, focusing on the proximate effects of this behaviour. I do not focus on the influence that female infant-handling has on the mother and infants involved because the evolutionary function of handling another female's infant differs between males and females (Silk 1999; Chism 2000; Paul *et al* 1996), and female-infant handling is likely to have a different influence on the mother than male infant handling. My thesis is divided into five chapters. After this introduction, Chapter 2 introduces the study site, species and general methods I used. Chapter 3 focuses on how male infant handling affects

the mother's behaviour and Chapter 4 on how male handling affects infants. Chapter 5 presents a general discussion.

2 General methods

2.1 Study species

Barbary macaques are the only species of macaque found outside Asia. In the wild, they inhabit the semi-deciduous forests of the Atlas and Rif mountains of northern Africa (Fooden 2007). They live in multi-male, multi-female groups with a strong matrilineal hierarchy and are considered egalitarian and tolerant (Paul 1999). Females reach sexual maturity at 4 years old and the singleton infants are reliant on their mothers for nutrition up to 1 year but begin to ingest solid food at 45 days (Fooden 2007).

2.1.1 Study site

I carried out my study at Las Montagne des Singes, Kintzheim, France, a 60 acre park with approximately 200 semi-free ranging Barbary macaques. Three groups of 70 individuals were available to view by the public (De Turckheim and Merz 1984, pp. 241-261).

I conducted the study from 1 June to 31 July 2016 and collected data for mothers for 31 days and for infants for 14 days. The park was open to visitors between the hours of 10:00-12:00 and 13:00-18:00 from June to mid-July, then from 09:30-18:00 h. The macaques were fed primate pellets, fruit vegetables and seeds at regular intervals and also foraged for insects and plants that were naturally available. Visitors were provided with popcorn to feed the macaques that venture onto the paths but were not permitted to feed macaques carrying infants. Visitors were restricted to paths in the forest and the macaques could

venture off into the forest out of sight. The park staff gave informative presentations at three feeding areas once every 30-60 mins, alternating between the groups. During these presentations, the visitors gathered around the feeding area and the staff provided the macaques with vegetables and fruit.

2.1.2 Data collection

I carried out focal sampling (Altmann 1974) on 13 mothers and 11 infants on alternating days (Table 1, see sections 3.1.1 and 4.1.1 for more detail). I recognised mothers based on facial and sexual swelling features and any markings specific to the individual such as colouration patterns. Since it was difficult to identify infants based on characteristics, I identified infants indirectly by recognizing the mother and directly from the infant's characteristics such as their sex and age, which I determined from their size and the colour of their fur. When an infant was in the care of a male, I identified the mother as the female who often remained in the vicinity and reunited with the infant after the handling event. I did not observe infants I could not identify. I did not record the mothers' behaviour if a female carried her infant.

I intended to identify the male infant handler but this proved difficult when recording the behaviour of the mother or infant at the same time. Moreover, males often pass infants onto other males during the triadic interactions. Therefore, I investigated the mother's and infant's behaviour when infants were handled by males, regardless of the male's identity. I identified whether infants were in the care of males or their mothers based on their proximity to the adult,

who carried the infant, who restricted the infant's contact with others by physically restraining the infant and chasing away other individuals when they attempted to interact with the infants and who the infant ran to for physical contact.

Table 1: Details of female and infant subjects in the three groups (A, B and C).

Group	**Female**			**Infant**		
	ID	Age (years)	Parity	Sex	Date of birth	Mean age during the study (days)
A	Tate (T81)	21	multiparous	F	15 May	41.45
A	Woopie (P35)	5	primiparous	M	24-May	34.5
A	P27	5	primiparous	F	24-May	42.19
A	P34	5	multiparous	F	04-Jun	18.41
B	C128	17	n/a	n/a	17-Jun	8.46
B	Poppy (B107)	n/a	multiparous	M	29-Apr	54.92
C	Les Clos (D151)	16	multiparous	F	02-May	56.82
C	Tiny (Q48)	4	primiparous	M	18-Jun	15.99
C	Winnie (C127)	17	multiparous	M	24-Apr	60.1
C	Z (M280)	8	multiparous	M	02-Jun	20.43

2.1.3 Ethical statement

I received ethical approval to conduct my study from the Animal Welfare Ethical Review Board (AWERB) at Durham University. My study was non-invasive and I stopped observing if any monkey showed signs of distress, shown by them watching or threatening me with a facial gesture. I remained on the visitor path for the majority of observations, as I did not want to cause the animals distress.

2.1.4 Limitations

The main limitation of my study is the small sample size of 10 individuals and the short study period. I alternated observation days between mothers and infants leading to an inevitable compromise between collecting enough data for each condition across three groups and having a larger sample size to increase statistical power for both studies. Optimal sample sizes are often not reached in behavioural studies due to time, financial constraints and the number of individuals available to study (Taborsky 2010).

3 How does male infant handling affect the mother?

Primates have a relatively small number of infants during their lives. Infants develop slowly, rely on their mother for nutrition, thermoregulation and transport, and receive care for extended periods of time (Lee 1996). The energetic costs of raising an infant and the costs of losing it are high, so mothers restrict access to their infants to avoid harm to them.

Reproducing is costly for female primates. Alongside their own growth, females must distribute limited energetic resources across gestation, post-natal care and recovering body condition for future breeding attempts (Gittleman & Thompson 1988). Fitness increases with the number of infants reared to breeding age, hence mothers must also balance their investment between current and future offspring (Trivers 1972; Clancey *et al* 2013, pp.281–302). Investing heavily in the current offspring can lead to delayed recovery of body condition for breeding and lengthen inter birth intervals, limiting the number of infants a female can have.

Lactation is the most energetically demanding form of maternal investment in primates. Lactating primate mothers increase their food intake by up to 50% to maintain healthy body condition (Dunbar *et al.* 2002). Carrying an infant can also be costly, especially in species such as baboons that travel long distances daily (Altmann & Samuels 1992). Foraging can also be disrupted when carrying and attending to an infant. For example, gelada are less likely to forage when in contact with their infants than not in contact with them (Barrett *et al.* 1995).

Mothers may gain benefits from male infant handling in a similar way as when females handle their infants. When other animals are caring for their infant, mothers are free to engage in activities such as foraging, grooming or resting (Stanford 1992; Xiang et al. 2010; Chism 2000) while not leaving their infants alone and vulnerable (Fairbanks 1990). For example, in capped langurs (*Trachypithecus pileatus*), mothers spent more time feeding when another female handled their infants than when they handled them (Stanford 1992). In the long-term, increased energetic intake could translate into faster infant growth rates, earlier infant weaning and shorter inter-birth intervals so that the mother can resume cycling (Mitani *et al* 1997; Ross & Maclarnon 2000). For example, vervet mothers (*Cercopithecus aethiops*) experienced shorter inter-birth intervals when their infants were in the care of another female more often than in their own care (Fairbanks 1990).

Mothers may also incur costs when males handle their infants. Males that handle infants for exploitative reasons may not be competent or attentive to the infant's needs and risk injuring them (Silk 1999). As a consequence, mothers may experience elevated anxiety, a state of anticipated danger at the outcome of an uncertain event (Maestripieri 1994). Prolonged high stress levels can reduce immune function and body condition and diminish a mothers' ability to nourish their infants (Cameron 1997). For example, female vervets with low body condition withdrew maternal investment from their infants and risked infant mortality, presumably to recover for future breeding attempts (Fairbanks 1990).

Male infant handling may also disrupt the mother's activity budget. Mothers might be more vigilant when their infants are in the care of males to keep track of the infants' location (Maestripieri 1993b). For example, female howler monkeys (*Alouatta pigra*) were more vigilant when their infants were away from them and moving independently than when with them (Treves *et al.* 2003). Increased vigilance could indicate anxiety and interferes with other activities such as foraging.

I aimed to determine whether and how mother Barbary macaques are affected by male infant handling. I tested two hypotheses:

1: If mothers benefit by being free to feed for longer and engage in other activates such as grooming when infants are in the care of males, then

a. mothers will spend more time feeding when the infant is with a male than when it is with the mother
b. mothers will spend more time grooming other group members when the infant is with a male than when it is with the mother.

2: If mothers experience anxiety when male group members are handling their infants then:

a. mothers will exhibit higher rates of self-directed behaviours (self-scratching and auto-grooming) when the infant is with a male than when the infant is with the mother. Self-directed behaviours have been used as a reliable, non-intrusive behavioural indicators of anxiety in primates (Manson and Perry 2000; Palagi and Norscia 2011) and particularly in

Barbary macaques (Kaburu *et al* 2012; Molesti and Majolo 2013). The use of pharmaceuticals has also confirmed the correlation between self-directed behaviours and stress where the rate of self-directed behaviours in primates increased and decreased with the addition of anxiety inducing and anti-anxiety drugs (Troisi et al. 1991; Castles et al. 1999).

b. mothers will watch and look-around more often when the infant is with a male than when the infant is with the mother.

3.1 Methods

3.1.1 Data collection

I used 10 of the 13 mothers I observed for analyses as I did not observe the other three mothers away from their infants during the study (Table 2). I observed mothers for 20 minutes, recording when they changed behaviour to measure the duration of behavioural states, and tallied behavioural events (Table 3; Appendix 1). For each observation I recorded the date, weather, time of day, subject identity, and whether she was in contact with her infant or not. Every time she changed behaviour, I also noted the identity of the nearest neighbour, distance to nearest neighbour, whether the interaction between the male and infant (dyad) or multiple two males with an infant (triad) was visible to her, how far the dyadic and triadic interaction was from her, her gaze direction and an ad lib column (Appendix 1 data collection sheet).

Table 2: The number of focal samples and the total time (hours, minutes and seconds) I observed mothers when they were with their infants (handling) and not with their infant (not handling), in which time the male was handling it**.**

Female	**Number of observations**		**Time observed (h:m:s)**	
	Handling	Not Handling	Handling	Not Handling
C128	5	1	01:40:00	00:20:00
LC	11	11	03:19:47	03:05:40
P27	10	2	02:34:18	00:40:00
P34	13	5	03:48:36	01:11:50
Poppy	4	6	00:59:45	01:39:04
Tate	7	8	02:12:53	02:23:23
Tiny	8	3	02:31:23	00:37:37
Winnie	6	3	01:45:08	00:32:16
Woopie	9	10	02:34:36	02:31:06
Z	11	5	02:56:44	01:23:12
Mean +/- SD	**8.4**	**5.4**	**02:26:19** +/-00: 49:42	**01:26:25** +/-00:57:18

Table 3: Ethogram for female behaviour

Behaviour	**Definition**
States	
Feeding	Subject places food item into mouth and ingests
Grooming other	Subject sweeps hands through the fur of another animal, inspecting and picking at debris
Being Groomed	Subject is groomed by another individual
Auto-groom	Subject makes sweeping action of hand through own fur inspecting and picking for debris often concentrating on one place of their body
Rest	Subject is lying or sitting with eyes closed, little or no head movement
Scanning	Subject looks around facing the ground in search of food with clear movement of the head from side to side either when sitting, walking or standing
Events	
Look-around	Subject scans with clear obvious head movement with their head constantly moving and not fixed for longer then 2 seconds
Watch	Subject stares at an object, individual or direction with their head fixed for more than 2 seconds
Self-scratch	Subject moves the fore or hind limb dragging their fingers or toes through their fur quickly in a repetitive up and down motion

I abandoned observations when the focal subject was out of sight for 5 consecutive minutes because I would not obtain an accurate record of behaviour durations and did not know whether or not she was in contact with her infant. When observing mothers in contact with their infants, I ceased observations when the infant was not with the mother or the male.

When observing mothers away from their infants, I stopped observations when she regained contact with her infant and waited 30 mins before observing her again because her behaviour may have been affected by their reunion. I selected mothers to observe based on who I sighted first when walking a pre-selected route in the park. I then ensured that I observed all females in contact and away from their infants at least once every observation day. I rotated between starting with one of the three groups on different days. If I did not locate a female on one day, I prioritised her on the next observation day. I matched observations of mothers when with and when away from their infants by prioritising those that had an imbalance in observation time with or without their infants.

3.2 Data Analysis

3.2.1 Data selection

To decide whether I needed to remove observations that lasted less than 20 minutes long, I compared the mean and standard deviation duration for each behaviour exhibited by the mothers. Most behaviour categories had a greater standard deviation than their means, suggesting high variation in their duration. I decided to remove samples under 5 minutes in length because they were most

likely biased against behaviours that were longer lived such as grooming and feeding.

To visualise the data, I calculated the proportion of time spent in each behavioural state by dividing the total duration of time the mothers exhibited them by the total time I observed each mother during the study. I calculated rates of events by dividing the number of times I observed each behaviour by the total time in hours I observed each mother with and without their infant during the study. I created the graphs using the ggplot2 package (Wickham 2009) and ggthemes (Jeffery 2017).

3.2.2 Analysis

I used a generalized linear mixed model (GLMM) with individual as a random effect to account for the repeated observations of individuals. I accounted for the different duration of time I observed each mother by offsetting for the total duration of time (seconds) that I observed her each week. I summarised data weekly to account for the influence of infant age on the mother's behaviour. I fitted a negative binomial GLMM with a log link function using the glmmADMB package (Fournier *et al.* 2012) in R 3.3.2 because data were over-dispersed with a Poisson distribution. The response variables were the duration spent in each behavioural state and counts for events (looking around, watching and self-scratching) per week. The predictor variables (fixed effects) were: infant age (in weeks), whether the mother was primiparous or multiparous (parity), and whether she was with her infant or not (infant with mother).

To determine whether being with her infant or not influenced the mothers' behaviour I compared the full model with a control model including the random effects and control variables (infant age and maternal experience). I did this by using a likelihood ratio test (LRT) with r function "anova" (procedure based on; Kerhoas *et al.* 2016; Ruiz-lambides *et al.* 2017). I set significance at $p<0.05$.

I first fitted a glmm with Poisson distribution, which was over-dispersed as the ratio of residual deviance to degrees of freedom were greater than 1 (Crawley 2015, pp. 236-237). I therefore fitted a negative binomial model. I plotted the model residuals against predicted residuals to check that model assumptions were met and there was no unexplained variance (Zuur *et al.* 2010). I used "car" package (Fox and Weisberg 2011) in R to check for correlations among the predictor variables (infant age, mothering experience and contact with infant) and found no collinearity (highest variance inflation factor = 1.19). I fitted a qq plot of the residuals for each model, which showed a normal distribution, and that the models fit the data.

3.3 **Results**

Whether they were with their infants or not predicted how long mothers spent auto-grooming and grooming other individuals significantly better than the control model (Table 4). Mothers spent more time auto-grooming and grooming other individuals when their infants were away from them than when they were together (Figure 1). The presence of an infant did not predict how long mothers spent feeding and resting or how long she was groomed by others better than the control model (Table 4). Figure 1 suggests that mothers spend more time feeding when away from their infants than with them. However, the figure does

not take into account the other factors that may have influenced the mothers' behaviour such as parity and infant age. Furthermore, the figure summarises data for each individual whereas the data in the model are summarised by Individual per week.

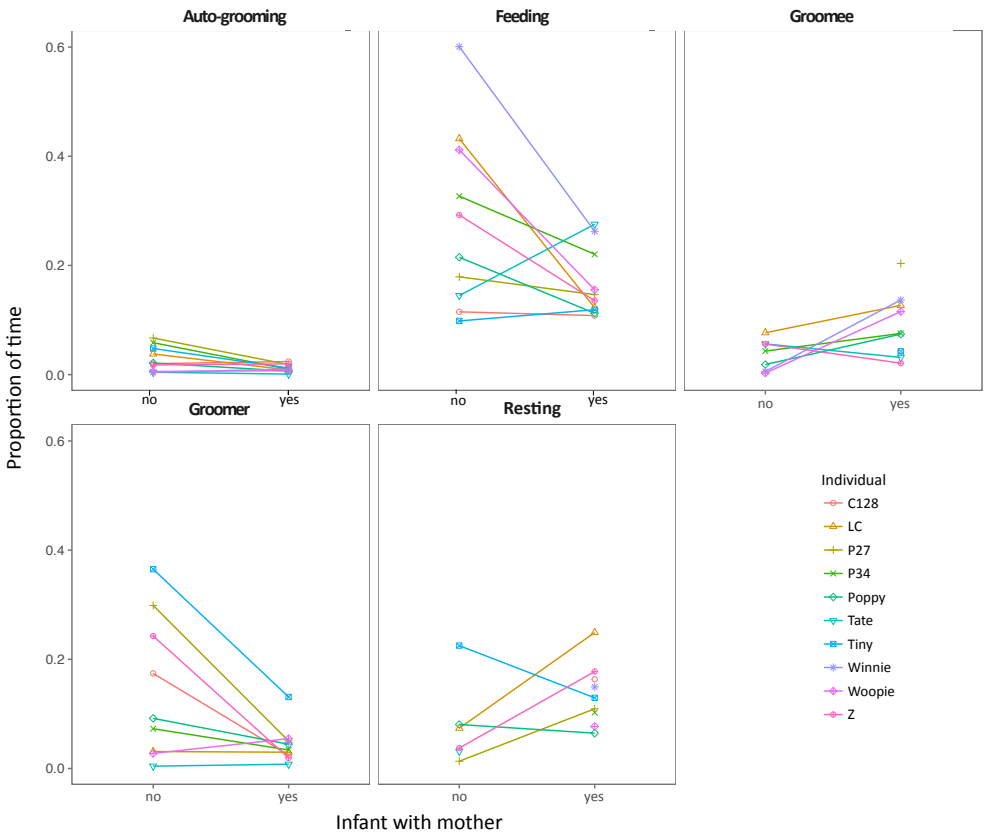

Figure 2: Proportion of time mothers exhibited behaviours when away from their infants (no) and with them (yes).

Table 4: Results of likelihood ratio tests comparing the full model (all terms and contact with infant) with the null model (control variables, offset and random effect) for each behaviour state. Bold indicates significant results

Response variable	No.Obs	Log likelihood	Deviance	P value
Feeding	67	-467.72, -466.38	2.68	0.100
Groomer	44	-273.48, -270.55	5.86	**0.015**
Groomee	44	-276.85, -276.84	0.02	0.890
Auto-groom	48	-236.87, -233.53	6.69	**0.009**
Resting	44	-260.54, -259.92	1.25	0.260
Scanning	69	-378.72, -384.07	10.68	**<0.001**

Infant contact predicted how often mothers watched and self-scratched significantly better than the control model but did not better predict how often they looked around (Table 5). Mothers watched and self-scratched more often when away from their infants than when with them (Figure 2)

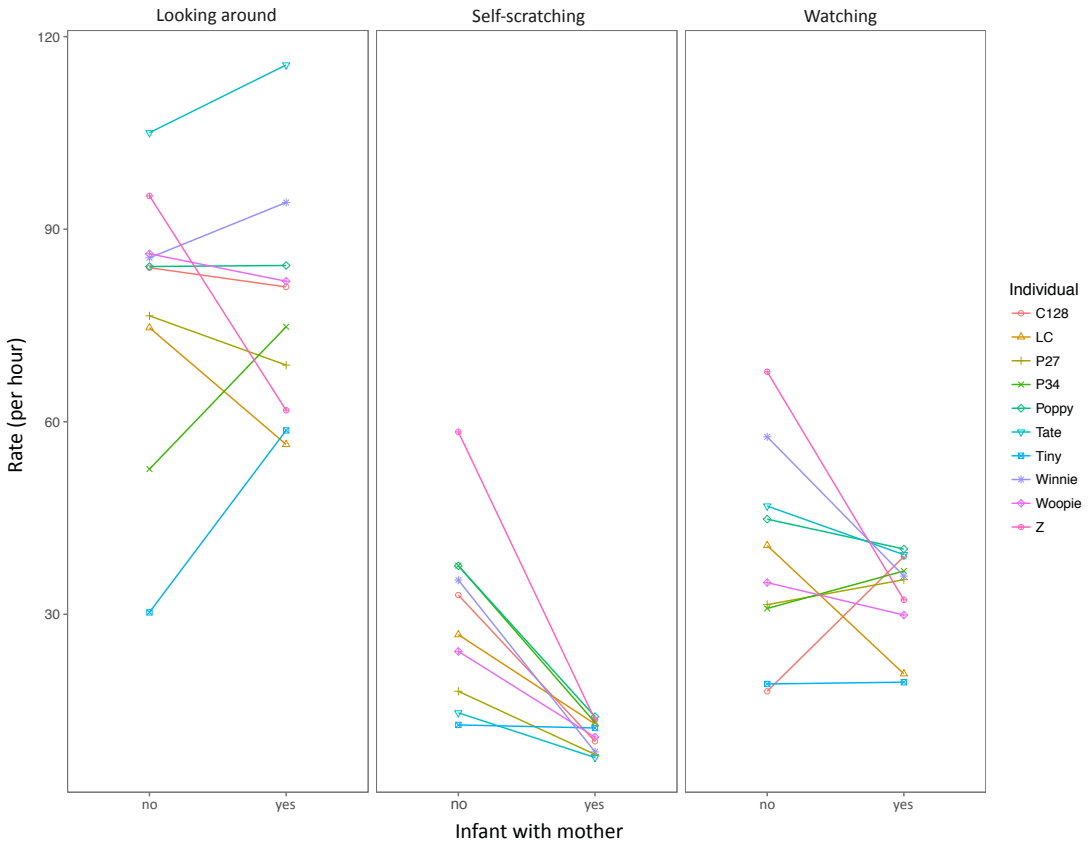

Figure 3: Rate (events per hour) that mothers looked-around, self-scratched and watched when away from their infants (no) and with (yes) their infants.

Table 5: Results of likelihood ratio tests comparing the full model (all terms and mother with or without infant) with the control model (controls, offset and random effects) for each behaviour state. N=10 females. Bold indicates significant results

Response variable	Number of observations	Log likelihood	Deviance	P
Looking-around	73	-297.94, -297.77	0.34	0.560
Watching	73	-256.59, -253.36	6.46	**0.011**
Self-scratching	68	-216.23, -197.63	37.21	**<0.001**

3.4 **Post hoc analysis of locomotion whilst foraging**

Feeding is just one aspect of foraging and caring for an infant may also affect the mother's ability to search for and find food. I therefore conducted a post hoc analysis to explore the foraging behaviour of mothers when infants were with them and away from them. I used a negative binomial generalized linear mixed model with log link function. The response variables were the mother's locomotion type when she was feeding and scanning for food (walking, sitting, standing and lying). The predictor variables were the same as in the main analyses (Section 1.6.2).

When their infants were away, mothers stood for greater proportions of time when feeding than when infants were with them (Table 6a, Figure 3). They did not differ in the proportion of time they sat while eating. When scanning for food, mothers walked and stood for greater proportions of time when away from

their infants than when with them (table 6b, Figure 4). Sitting while scanning did not differ with changes to infant-mother contact (Figure 5).

Response	Number of observations	Log likelihood	Deviance	P
Walking	7	-15.555, -18.017	4.924	0.026
Sitting	66	-443.93, -444.34	0.822	0.364
Standing	63	-347.39, -354.56	14.34	**<0.001**

Table 6: Results of likelihood ratio tests comparing the full model (the mother's locomotion whilst feeding, all terms and whether with or without her infant) with the control model (controls, offset and random effects) for each behaviour state. N=10 females. Bold indicates significant result

Table 7: Results of likelihood ratio tests comparing the full model (the mother's locomotion whilst scanning, all terms and whether with or without her infant) with the control model (controls, offset and random effect) for each behaviour state. N=10 females. Bold indicates significant results

Response	Number of observations	Log likelihood	Deviance	P
Walking	65	-329.10, -334.57	10.958	**<0.001**
Sitting	59	-243.59, -243.59	0.09	0.761
Standing	42	-172.43, - 178.44	12.032	**<0.001**

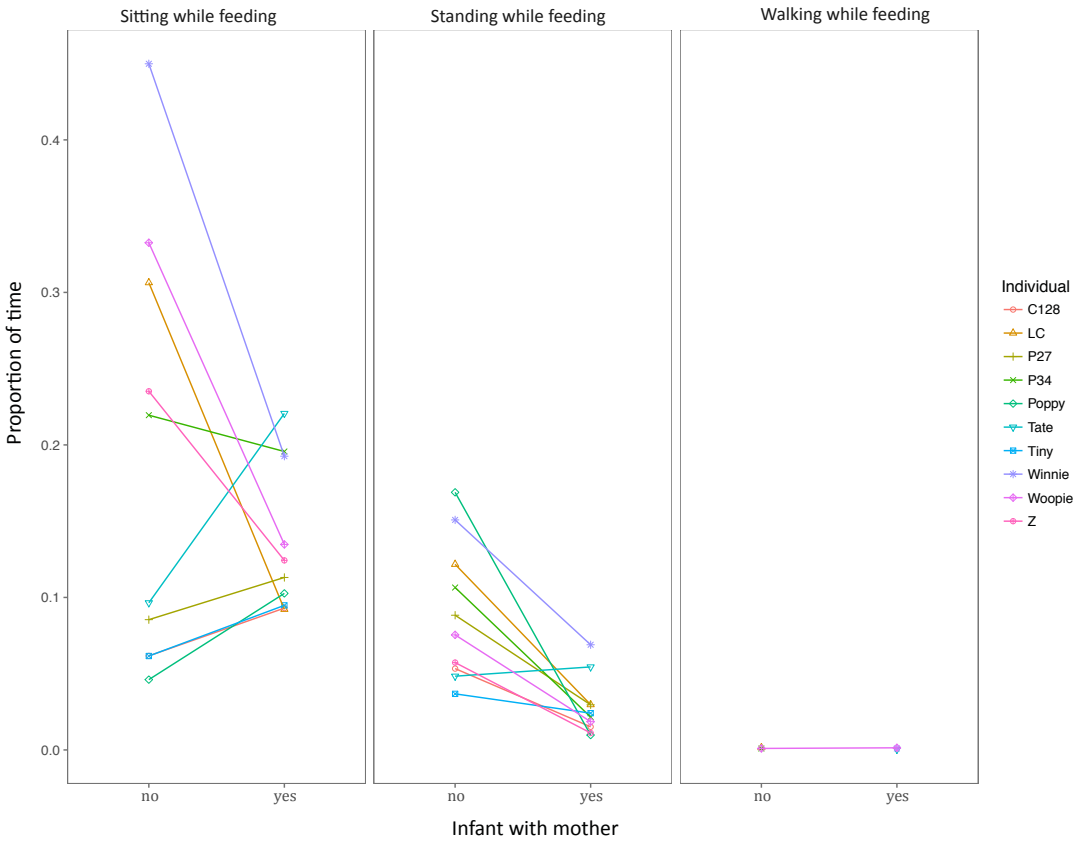

Figure 4: Proportion of time mothers spent sitting, standing and walking while feeding when they were with and without their infants.

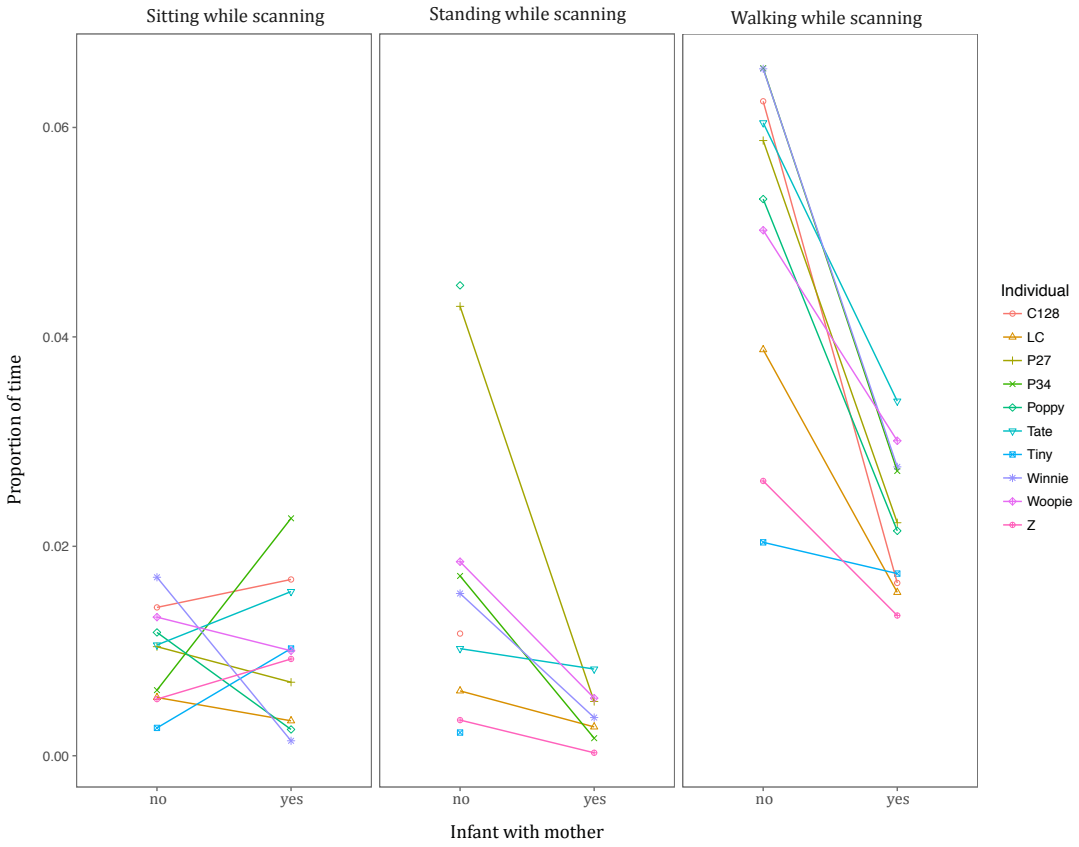

Figure 5: Proportion of time mothers spent sitting, standing and walking while scanning for food when they were with and without their infants.

3.5 **Discussion**

I found mother Barbary macaques behaved differently when their infants were with males than when their infants were with them. Contrary to my first prediction, and unlike previous studies of female infant handling (Fairbanks 1990; Stanford 1992), mothers did not feed for longer when their infants were away than when with them. However, partially in line with my second prediction, when not with their infants, mothers increased their rates of self-scratching, auto-grooming, watching, scanning and groomed other group members for greater proportion of time than when with their infants. Mothers did not look around or receive grooming for different proportions of time when their infants were away from them than when with them.

3.5.1 Feeding

It appears that mothers did not use the time away from their infants to increase the duration of time they spent feeding. These findings can be interpreted in several ways. First, in a provisioned semi-free ranging group, mothers may not be constrained energetically by maternal investment as they have constant access to food. Second, the infant might not have affected their ability to consume food. The mothers may have fed while infants were nearby but not in physical contact with them. For example, gelada females encouraged their infants to reduce direct contact with them when they fed (Barrett *et al.* 1995). Third, when infants were in the care of males, mothers were free to spend time grooming or were distressed, both of which would disrupt feeding activity.

Infant care did not affect how long mothers fed for but it did affect how long they scanned for food. When mothers were away from their infants, they spent greater proportions of time scanning for food. Mothers also walked and stood more often whilst searching for food when infants were not in their care than when with them. These findings reflect those for long-tailed macaque mothers who were less likely in contact with their infants when foraging than feeding (Karssemeijer *et al* 1990). Carrying an infant may make searching for food inefficient. Carrying costs should be low in the semi-free ranging group where individuals do not have to travel long distances to find food. Semi-provisioned groups of Barbary macaque spend less of their daily activity budget foraging and walking compared to non-provisioned groups (El Alami *et al. 2*012). Therefore, in wild settings mothers might benefit even more from being apart from their infants whilst foraging (Fairbanks 1990; Altmann & Samuels 1992).

Other factors might account for the differences in the mothers foraging behaviour. Mothers may have fed on different types of food items when away from their infants. Small, dispersed items require more search time compared to one food item, such as an apple. A large item of food may also require longer processing time than smaller items but can be done whilst sitting down (Karssemeijer *et al* 1990). Mothers may also have been more mobile when away than with their infants because they attempted to follow the infant and male and whilst doing so, searched for food.

3.5.2 Stress and vigilance

When away from their infants, mothers self-scratched and auto-groomed at greater rates than when with them. In laboratory studies, females had raised anxiety levels when separated from their infants (Vogt & Levine 1980). In a social context, anxiety may be attributed to several interacting factors. These include maternal motivation, the proximity of other group members to themselves and their infants and their emotional reactivity (Troisi *et al. 1*991; Maestripieri 1994b).

Anxiety is an emotional state, which results from expecting a negative outcome (Maestripieri 1994; Castles *et al.* 1999). Mothers might experience social anxiety, if they are threatened by the social context or maternal anxiety where the threat is posed to their infant (Maestripieri 1993a). Mothers may be more anxious when infants were in the care of males because they perceived males as a threat to their infants and risk injuring them (Maestripieri 1994; Packer 1980). Rhesus macaque (*Macaca mulatta*) mothers exhibited high rates of self-scratching when infants were away from them and when their infants were close to high-ranking females and to males than to other group members (Maestripieri 1994). It is also challenging for mothers to retrieve an infant from a male as they often restrict the infant from returning to its mother (Packer 1980). Therefore, they may have also experienced frustration over not being able to respond to their infant's distress calls or retrieve them from the care of males (Castles *et al.* 1999).

In addition to maternal anxiety, social relations such as grooming and being in close proximity to others can cause anxiety, especially for low ranking individuals (Troisi *et al.*1991; Castles *et al.* 1999; Kaburu *et al.* 2012; Molesti & Majolo 2013). Thus mothers may have experienced social anxiety when they approached or were approached by a male handling their infant or with the intention of initiating an interaction with it (Kaburu *et al.* 2012).

Since male Barbary macaques are selective about which infants they handle, mothers have the opportunity to interact repeatedly with the main infant handler. Repeated interactions could promote the formation of a stable association or 'friendship' between the mother and male infant handler, as seen in baboons and Assamese macaques (Ostner *et al.* 2013; Kubenova *et al.* 2017). With repeated interactions, mothers might experience reduced anxiety as they can better predict the outcome of interactions between males and their infants (Castles *et al.* 1999). However, since males use infants to interact with other male group members, possibly less well known to the mother, these interactions may still be a source of uncertainty and thus, anxiety. It would be interesting to assess how mothers respond to particular males interacting with their infants and if their anxiety reduced with repeated exposure to the main infant handler.

Increased visual monitoring can also indicate anxiety (Maestripieri 1993b). Mothers watched more often when they were away from than when with their infants but they did not differ in the proportion of time looking-around. These contrasting findings may be attributed to the different purposes of the vigilance behaviours. Looking-around may involve a combination of social and

environmental vigilance for the purpose of keeping track of others within the group and surrounding environment. In this study, mothers were also exposed to large crowds of visitors, regardless of whether they were caring for their infants or not. It is difficult to disentangle looking around for their infants from the other environmental and social factors that influence this behaviour.

Watching requires a fixed gaze in a specific direction or object (Maestripieri 1994a). Mothers may have been watching the infant during male-infant interactions since female Barbary macaques can recognise their infants' distress calls (Hammerschmidt & Fischer 1998). Although I recorded gaze direction, it was difficult to identify the mother's gaze as the male-infant interactions were often out of sight and mothers may have instead gazed in their direction when responding to the infant's vocalisations.

3.6 **Allo-grooming**

Mothers spent more time grooming other individuals when their infants were with males than when infants were with them. Grooming has several important functions in primate societies, including maintaining social bonds (Dunbar 2010). Primates exchange grooming for reciprocation and trust, spending 20% of their daily activity budget grooming (Dunbar 2010). It also functions to reduce stress and tension and to maintain hygiene.

When the mother was not preoccupied with infant care, she was free to interact with other group members. Furthermore, as females reciprocate grooming bouts, being away from their infants is a good opportunity for mothers to allo-

groom (Frank & Silk 2009). Grooming may also counteract the mother's anxiety when away from their infants as grooming another individual correlates with reduced stress levels in Barbary macaque (Shutt *et al.* 2007). Therefore, when males handled infants, it appears that mothers used the time to maintain their relationships whilst possibly at the same time seeking comfort.

Group members often groom mothers to make contact with another's infant (Henzi & Barrett 2002; Gumert 2007; Tiddi *et al.* 2010). Interactions that involve an exchange of services for access to a commodity, in these cases grooming for infant access, are an example of a biological market place (Noë *et al.* 1991). However, in this study, mothers did not receive more grooming from others when they had their infants than when separated from them. Instead, Barbary macaque mothers might allow others close contact with their infants through other services. For example, spider monkeys (*Ateles geoffroyi*) exchange embraces with the mother for infant contact (Slater *et al.* 2007). Since Barbary macaque females also carry out triadic interactions with other group members (Small 1990; Paul & Kuester 1996) they might use triadic interactions to gain access to infants. This behaviour requires risky close contact and it may enable mothers to assess the others' intentions and thus to control how and when others interact with their infants (Whitham & Maestripieri 2003; Slater *et al.* 2007).

3.6.1 Conclusion

In this study mothers appeared to be anxious when males handled their infants as they showed more self-directed behaviour when their infants were away than

when with them. Their anxiety may stem from social interactions with other group members or concern over their infants well being. Since I compared the mother's behaviour when their infants were with them and with a male, it is likely that the females were distressed in response to being separated from their infant. Mothers did not use the time away from their infants to increase the time they spent feeding. They may not have been energetically constrained because they were provisioned with food. It is also likely that they were unable to feed for longer because they groomed others more often when away than with their infants. Grooming is important in primate societies for maintaining social relations and reducing anxiety and in the case when food is available, may have taken precedence over feeding. Mothers also watched more often when their infants were away than with them which also disrupts feeding behaviour. The elevated anxiety that mothers experienced when males handle their infants could be detrimental to their fitness by reducing immune function and body condition. This may be further emphasised in non-provisioned populations where food resources are scarce or competition for resources is high.

4 How does being handled by males affect infants?

The development of motor and social skills is an important part of primate infancy. As infants age, they increasingly explore their physical and social environment. In cercopithecines, infants stay in close contact with their mothers during the first 7 weeks of their lives after which, there is a marked increase in them interacting with other group members (Lee 1984; Deng 1993). With increasing age, the responsibility for maintaining contact switches from the mother to the infant (Lee 1984).

The infant's first and most influential relationship is with its mother (Deng 1993; Cords & Förster 2005). Mothers are important for nutrition, warmth, protection and a safe base from which the infant can venture (Deng 1993; Suomi 2005). Mothering style can affect infant development and behaviour (Bardi & Huffman 2002). Mothers can be permissive or restrictive depending on socio-demographic factors such as rank, age, mothering experience and individual temperaments, including how they react to stress-inducing events (Fairbanks 1996; Maestripieri 2011).

Mothering style affects who mothers permit their infants to interact with (Berman & Kapsalis 1999) and how far their infants venture from them (Deng 1993; Cords & Förster 2005; Suomi 2005). An infant's social network resembles that of its mother (Berman 1982; Berman & Kapsalis 1999). Protective mothers raise infants that explore their environment less than infants that are rejected by their mothers at high rates (Bardi & Huffman 2002). Thus, the infants of protective mothers reach independence later than those of mothers that are not

(Lee 1984). Mothers also encourage independent locomotion. For example, female pigtail macaques (*Macaca nemestrina*) often walk away from their infants, presumably to encourage them to keep up, and encourage them to follow through facial signals (Maestripieri 1996).

Mothers have an important role in infant development and survival, but interactions with males in the form of male infant handling may also benefit infants. For example, male baboons, crested macaques and Assamese macaques protect their offspring from infanticide, provide them with access to high quality resources and support them during agonistic interactions (Buchan *et al.* 2003 ; Huchard *et al.* 2013; Kerhoas *et al.* 2014). Recent studies have found that infants are responsible for initiating and maintaining interactions with males, which implies that they benefit from such interactions (Moscovice *et al.* 2009; Huchard *et al.* 2013; Kerhoas *et al.* 2016; Minge *et al.* 2016).

Little is known about how infants benefit from interactions with males that are not their sires (Kerhoas *et al.* 2016). One way infants could benefit from associating with males is through the opportunity to enhance motor skill development. Interacting with a male for extended periods of time, as seen in Barbary macaques, may influence how infants explore their environment and develop. Males may be more permissive than mothers in allowing infants to venture further and explore their environment more, which may ultimately enhance their independent locomotion.

Since male-infant interactions are social in nature, they may offer infants further exposure to social experiences and aid their development of social skills (McKenna 1979; Small 1990). Primate infants are tasked with understanding the complexities of social relations in the group and how others relate to themselves (Small 1990; Deputte 2000; Tomonaga *et al.* 2004). Males may also be less restrictive than mothers regarding whom infants can interact with and enable them to expand their social network beyond that of their mother's (Deng 1993; Förster & Cords 2005). Furthermore, in species where males use infants as social tools, infants are exposed to male social partners and to social and greeting behaviours (Deag 1980; Small 1990). Handling by other group members may promote infants in establishing relationships that last into adulthood. These relations with other males could ultimately translate into fitness benefits such as protection against predators or infanticide and agonistic support (Moscovice *et al.* 2009; Minge *et al.* 2016)

Male infant handling may not be without risks to the infants. Handlers may mistreat infants either intentionally or as a result of inexperience. Being caught up in a group dispute may also place infants in situations where they might risk injury (Packer 1980). Infants may also experience elevated stress levels as a result of being separated from their mother and reduced opportunities to feed, all of which could reduce their growth rates (Chism 2000). However, the influence of separation from their mothers on the time they spend feeding depends on how long and often infants are separated from their mothers for. They may compensate for the time away by suckling after being re-united.

I aimed to determine whether and how being handled by male group members affected infant Barbary macaques in the short-term. I compared how often infants explored their environments, exhibited distress calls and independent locomotion when they were with their mothers or males. I also compared the infant's social partners when they were with their mother or male handlers.

I tested two hypotheses:

1: If being in the care of males provides the infant opportunities to explore their surroundings and interact with different group members, then

a) Infants will explore their environment more often when with males than when with their mothers
b) Infants will locomote independently more often when with males than when with their mothers
c) Infants will interact with more group members when with males than when with their mothers

2: If interacting with males causes infants distress, then

d) Infants will exhibit more distress vocalisations when with males than when with their mothers.

4.1 Methods

4.1.1 Data collection

I observed infants using 20 minute focal samples, recording the infant's locomotion every 30 seconds and tallied their squealing, exploratory and social behaviours (Table 8; Appendix 1). It was difficult to record the infant's behaviour

continuously as the handler often obscured the infant. I observed infants in the order I came across them during a pre-assigned walk around the visitor path and identified infants based on their mother's ID. I did not observe infants I could not identify. I also recorded the date, time, identity of the mother, whether the infant was in contact with the mother or a male, nearest neighbours and whether they were in contact with the infant or not. It was difficult to identify the male infant handlers while simultaneously observing the infant so I could not gather data on how many different males handled the infants and whether a specific male did so more than others. This might ultimately influence the infant and mothers' behaviour since they would repeatedly interact with a male and build up a relationship.

Table 8: Ethogram for infant behaviour

Behaviour	Definition
Exploration	Manipulate object that is not attached to anything with hand, or with mouth, explore object that is attached to something with hand or with mouth, rummage
Independent locomotion	Walking, running, crawling, climbing, leaping
Squealing	Infant vocalises in short lived high pitched bursts or for a prolonged time

4.2 Data Analysis

4.2.1 Data selection

I used 10 infants in analyses, as I did not observe the 11th infant away from its mother (Table 9). To visualise the data, I calculated rates by dividing the frequency of occurrences for each behaviour by the total time (mins) I observed the infants in the care of their mother and then again for when in the care of

males. I calculated the rates infants interacted with other group members in the same way.

Table 9: The number of times and duration of time (mins) that I observed infants in the care of their mothers and males

Infant ID	Number of observations		Time observed (mins)	
	Mother	Male	Mother	Male
Woopie	8	7	284	196
Z	4	2	111	95
Winnie	5	3	149	106
Tate	4	8	129	283
Poppy	3	1	120	17
P30	3	1	92	40
P34	8	1	239	23
P27	7	2	255	75
LC	5	3	182	94
C128	2	1	80	32
Mean	**4.9**	**2.9**	**164.1**	**96.1**
SD	2.13	2.55	68.60	80.19

4.2.2 Data analysis

I fitted a negative binomial generalized linear mixed model using the glmmADMB package (Fournier *et al.* 2012) in R. 3.3.2 to assess whether infants behaved differently when in the care of a male compared to that of their mother. I fitted a separate model for each behaviour (exploration, independent locomotion and squealing) as the response variables. To assess the number of times infants interacted with other group members, I used the frequency of contact

interactions between the infant and females, males, juveniles or infants. I used the mother's ID as a random effect and offset for the time I observed infants with males and with their mothers. I included the mean infant age during the study to account for changes in behaviour due to age.

To determine whether infant behaviour differed when in the care of a male or their mother, I compared the full model with a control model (removing only contact with the infant) using a log likelihood ratio test using anova in R.

I first fitted a glmm with Poisson distribution, which was slightly overdispersed so I used a negative binomial model. I assessed the distribution of the residuals versus predictor variables, which excluded any variation not explained by the model. The residuals also showed a normal distribution indicating a good model fit.

4.2.3 Limitations

The sample size was small due to the limited number of infants born to females in the year and my short study duration. Therefore, I did not analyse rarely observed behaviours such as teeth chattering and self-scratching because I did not collect enough data to avoid a floor effect (Martin and Bateson 2007).

4.3 **Results**

The identity of the infant carer predicted how often the infants squealed significantly better than the control model (Table 10). Infants squealed more often when they were with males compared to when they were with their

mothers (Figure 6). Whether the infant was in the care of its mother or a male did not predict their exploratory behaviour or independent locomotion (walking, running, leaping, crawling and climbing) significantly better than the control model (Table 10), but did predict the number of interactions between infants and other group members significantly better than the control model (Table 11). When in the care of their mother, infants were in physical contact more often with adult females and infants than when in the care of a male. Infants were in direct contact with juveniles more often when in the care of males than with their mothers but contact with males did not differ (Figure 7).

Table 10: Results of a log likelihood ratio test comparing the full model (including who the infant was in contact with) with the control model (control, offset and random effects) for infant behaviour. Df= 1.

Behaviour	**Number of observations**	**LogLik** (full; null)	**Deviance**	**P value**
Exploration	20	-74.746 ; -76.729	3.9662	0.046
Squealing	20	-54.244 ; -57.221	5.9546	**0.015**
Locomotion	16	-52.079 ; -53.166	2.1748	0.140

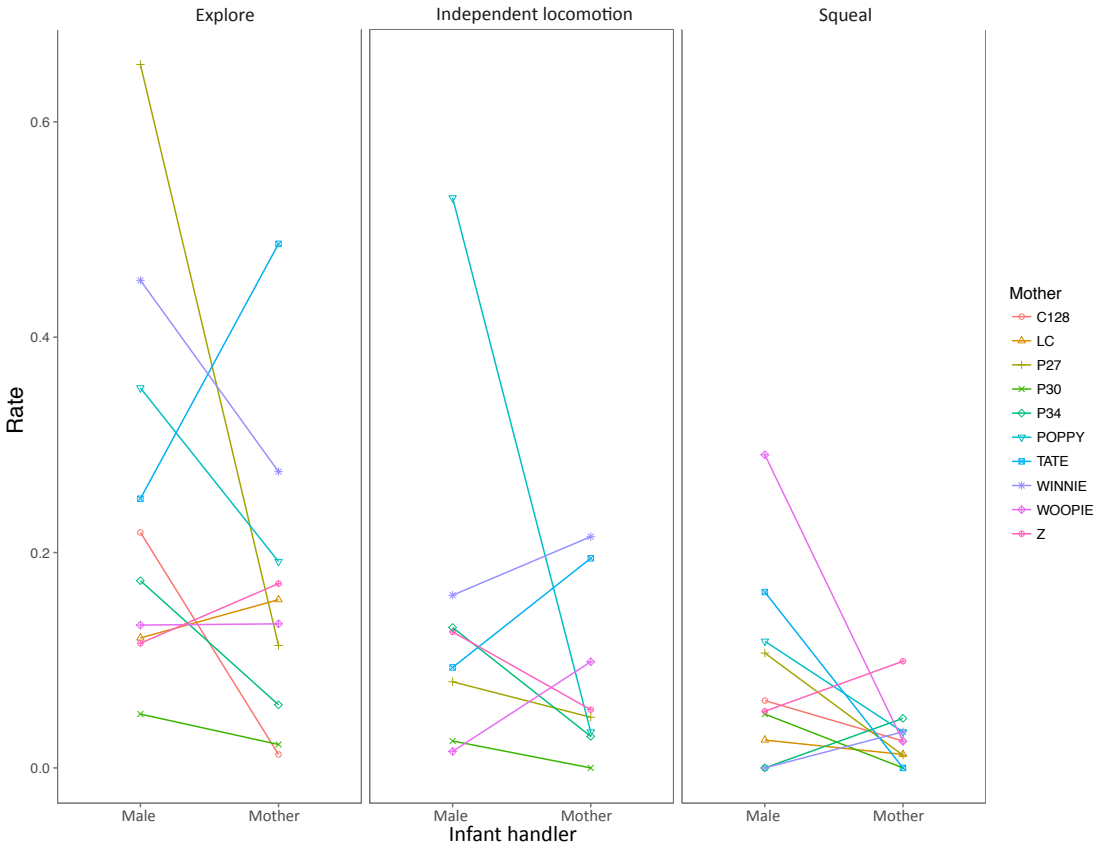

Figure 6: The rate infants explored, squealed and exhibited independent locomotion when in contact with their mother and with males (infant handler).

Table 11: Results of a log likelihood ratio test comparing the full model (including who the infant was in contact with) with the conrol model (control, offset and random effects) for the total number of times infants (n=10) were in physical contact with other group members when in the care of their mothers or males. Df=1.

No. interactions	**Number of observations**	**LogLik** (full; null)	**Deviance**	**P value**
Females	20	--41.717 ; -50.176	16.918	**<0.001**
Males	20	-54.282 ; -54.322	0.0802	0.777

Infants	20	-30.558 ; -35.077	9.0376	**0.002**
Juveniles	20	-14.482 ; -17.046	5.1282	**0.023**

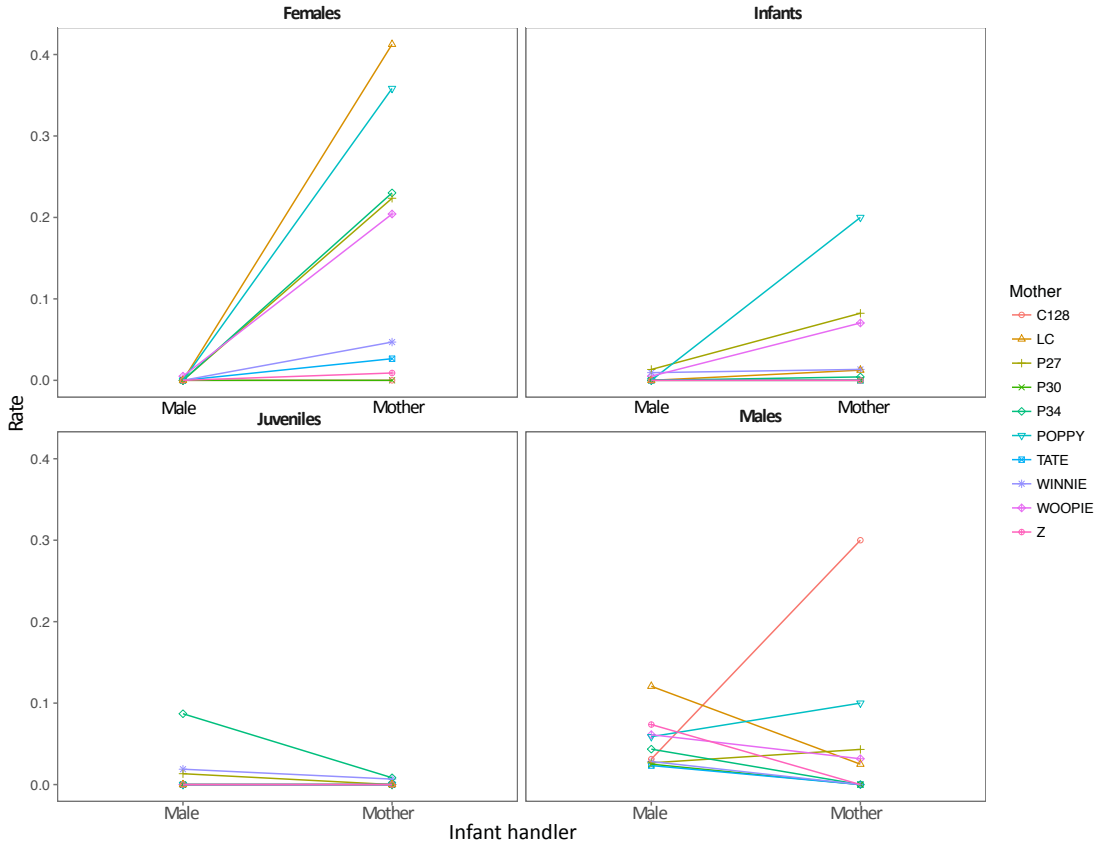

Figure 7: The rate of contact interactions between infants and other group members (males, females, juveniles and infants) when infants were with their mothers or males.

4.4 **Discussion**

Contrary to my first prediction, infants did not explore their environments more often or exhibit greater rates of independent locomotion when they were in the care of males than their mothers In line with my second prediction, when infants were with male group members they squealed more often than when they were with their mothers.. The number of interactions and the identity of the interacting partners differed with the identity of their caretaker. Infants interacted with females and infants at greater rates when with their mothers but juveniles at greater rates when in the care of males. However, they did not interact more often with males when being handled by males than when with their mother.

Squealing may indicate that infants were distressed (Maestripieri & Call 1996). Infants often communicate with their mothers through vocalisations and they may have squealed when with males to regain contact with their mother (Coe *et al.* 1983). However, it is not clear that vocalisations are a simple indicator of distress. Vocalisation rates decreased in infants that were repeatedly separated from their mothers and increased again when they observed or heard their mothers (Coe *et al.* 1983). Thus, other factors also influence vocalisations. Vocalisations may only be used to express distress when the target is present. In this study, infants may have squealed in response to seeing their mothers or as a result of being handled roughly by males. Barbary macaque males often drag infants across the ground by their limbs and sometimes restrain them to prevent the infants from returning to their mothers (Packer 1980; Small 1990). However,

infants also initiate interactions with adult males and this may be dependent on the history of interactions between the infant and specific males (Deag 1980).

As infants age, they become more responsible for initiating interactions with others (citations missing). Thus, as they age, infants should be less distressed in the care of males that they choose to interact with (Huchard *et al.* 2013; Kerhoas *et al.* 2016). A longer study period might capture the transition in responsibility for initiating and maintaining contact and infants that initiate interactions with males might be less stressed than those that do not.

Exploration is an important aspect of development. Infants develop skills required for adult life through exploring their environments (Baldwin & Baldwin 1978). Manipulating objects can aid with muscle development, motor skills for locomotion and climbing and with foraging skills (Sackett 1972). In this study, infants did not explore their physical environment or locomote independently more often when in the care of males than their mothers. Since infants vocalised more often when in the care of males than their mothers, they may have been more motivated to regain contact with their mothers than to explore their surroundings. In addition, infants may not have needed to explore their environment more often when with a male than their mother because mothers may not restrict this behaviour. Barbary macaque mothers are permissive in allowing their infants to venture away from them at early ages (Maestripieri 1995).

Infant socialisation is enhanced by interacting with other conspecifics (Cords & Förster 2005). In this study, being in the care of their mothers exposed infants to more interactions with their peers and other females in the group than when they were in the care of males. These findings support previous studies that show the role of the mother in integrating infants into their social environment and controlling their social interactions (Deng 1993; Förster & Cords 2005). Infants interact with their mother's social partners, who are often female kin and their infants (Berman 1982; Berman & Kapsalis 1999). Infants may not interact more often with juveniles when in the care of their mothers than males because their mothers restricted juvenile contact more than males. Juveniles may pose a greater risk to the infants as they are immature and inexperienced with infant care. Furthermore, the juveniles may have been the offspring from the previous year and the mothers may have rejected them to promote their weaning and independence from her.

When in the care of males, infants were exposed to more interactions with juveniles than when they were with their mothers. Males do not appear to restrict juveniles' access to infants. This may be because they either do not see them as threats or are less attentive to the infant's needs than the mother. It is also possible that juveniles may have formed a long-term relationship with the male handler in previous years and be tolerated by the male (Moscovice *et al*. 2009; Huchard *et al.* 2013). Infants were never in contact with another female when in the care of males. This is not surprising as males tend to interact with other males when handling infants or to handle them alone, forming a dyad with the infant (Deag 1980).

Since the function of male infant handling is to regulate social relationships with other males, I predicted that infants would interact more with males than any other group members when with males than when with their mother. However, this did not occur. One reason for this could be that triadic interactions are rare and occur at lower frequencies than dyadic interactions. A longer study may capture more male-infant-male interactions.

Dyadic interactions between males and infants may be more important in promoting infants' abilities to develop social partners beyond the mother and her kin. I often observed males sitting with infants for long periods of time with no social interactions with group members. Furthermore, Barbary macaque male handlers often handle particular infants, which could further promote the formation of relationships. These relationships may last into adolescence or adulthood and warrant further study (Minge *et al.* 2016). For example, male chacma baboons (*Papio ursinus*) continue to support juveniles during group disputes, so male-infant associations may benefit infants beyond infancy (Moscovice *et al.* 2009).

4.4.1 Conclusion

In this study, infants were more distressed when in the care of males than their mothers. This may stem from being separated from their mothers and it is unclear how much this reduces their fitness. With a longer study it might emerge that infants are less stressed after experiencing repeated interactions with the

same male handlers and with increasing age. Male infant handling does not seem to expose infants to more social partners than they would encounter when in the care of their mothers. However, it may enable them to form long-term relationships with the specific males that handle them. Supporting previous studies, mothers are important in exposing infants to a number of social partners, infants and females, and the male infant handlers. Male infant handling in Barbary macaques does not appear to benefit the infant in terms of their development of social skills and exploration but may benefit them in the long term through access to resources, earlier weaning or agonistic support.

5 General conclusion

In Barbary macaques, male infant handling has been studied from the perspective of males but little was known about how the interaction affected the two other individuals involved; the mother and her infant. In this study, I compared the mothers' and infants' behaviour when together and separated due to males handling infants.

Mothers and infants were distressed when males handled infants. Mothers increased their rates of self-directed behaviours and infants increased their rates of distress vocalisations. This is not surprising since male Barbary macaques do not handle infants for the primary purpose of offering care. Furthermore, mothers may not have much control over who takes an infant and when. The mother and infant may have fuelled each other's distress through visual and auditory signals. Further study could identify whether the infant's and mother's distress reduce with time, and repeated interactions with specific male handlers.

In this provisioned group of macaques, mothers prioritised grooming other group members over spending more time feeding when their infants were away than with them. Their increased stress and vigilance when their infants were in the care of males may have also reduced their motivation and time to forage.

Several limitations to my study stem from the short study period and study design of observing mothers and infants on alternative days, resulting in a small data set. The number of individuals available is a common constraint in

behavioural research (Taborsky 2010) and the number of females that gave birth in the park during that year restricted my sample size to 10 individuals. I used GLMM to account for repeated observations of individuals. An ANOVA of averaged data would have ignored variation within individuals. My findings highlight areas for further investigation in a larger scale study or in the wild.

My findings suggest that male infant handling in Barbary macaque does not benefit all individuals. Mothers and infants appear to pay an immediate cost. However, they may benefit from male infant handling in ways that I did not examine. Male primates form relationships or "friendships" with mothers and infants (Nguyen *et al* 2009; Ostner *et al* 2013) and these might offer some long-term benefits. Moreover, there is evidence to suggest that the interactions between male and infant cercopithecines lasts into the juvenile period and maybe into adulthood (Moscovice *et al* 2009). Long-term studies and social network analyses may further unravel this complex behaviour.

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Appendix 1. Ethogram for mothers and infants

Mothers

Positional Behaviour	**Definition**	**Code**
Sit	Seated position	**S**
Stand	Standing position stationary	**St**
Lie	Lying down	**L**
Walk	Walking	**W**
Climb/Descend	Climbing in any orientation and direction	**CD**
Run	Running	**R**
Leap	Leaping off the ground between objects	**Lp**
Hang	Hanging from an object using any limb	**H**

Vocalisations and Facial expressions	**Definition**	**Code**
Contact call	Call from the mother as she searches for infant (accompanied by vigilance)/ or in response to infant vocalisation	**CC**
Chatter growl	Short repeated growls	**CG**
Threat growl	Growl used in an aggressive context	**TG**
Scream	Screaming used in any context	**SC**
Grunt	Grunting used in any context such as agonistic support	**Gr**
Teeth chatter/lip smacking	Subject opens and closes mouth at a fast pace often baring teeth. Often towards a group member	**TC**
Threat face	Mouth open and often accompanied by a lunge or lowering of head towards another group member/object	**TF**

Behaviour	**Definition**	**Code**
Feeding	Subject places food item into mouth and ingests	**F**
Foraging Scanning Chewing	Searches for food items with hand and scanning the ground	**FO**
Drinking	Head down bent over position at a water source	**D**
Auto-grooming	Subject makes sweeping action of hand through own fur inspecting and picking for debris	**AUT**
Solicitation of grooming	Subject sits or lies in front of conspecific often lip smacking	**SOL**

Groomer	Subject sweeps hands through the fur of another animal, inspecting and picking at debris	**GER**
Groomee	Subject is groomed by another individual	**GEE**
Groomee and feeding	Subject feeds whilst being groomed by another	**GEF**
Reciprocal grooming	Individuals grooming each other at the same time	**REC**
Self-scratching	Subject moves the fore or hind limb dragging their fingers or toes through their fur in a repetitive motion	**SS**
Shake fur	Repeated motion of shaking the body	**SF**
Head bobbing	Subject moves head up and down in a threatening manner	**HB**
Lunge	Subjects jumps towards another/ other individuals in a threatening manner often accompanied by a threat face	**LNG**
Slap	Subject hits the ground or a conspecific in threatening manner	**SLP**
Physically displace	Physically move a conspecific with direct contact	**DSP**
Physically displaced	Focal individual is physically moved by a conspecific with direct contact	**DSD**
Avoidance	Subject purposefully moving away from a conspecific often accompanied by glances	**AV**
Passive displacement	The presence of the focal subject causes conspecific to avoid them/move away	**PDS**
Chase	Subject runs after an individual/s in an aggressive manner often accompanied by threat face and screaming.	**CH**
Grab	Subject extends arm to touch and pull at a conspecific aggressively	**GB**
Bite/wrestle/shake	Aggressive context	**BWS**
Flee	Subject runs away from chaser (aggressive)	**FL**
Submission	Subject lowers head to the ground whilst moving backwards from conspecific, often chattering teeth	**SUB**
Rest	Subject is lying or sitting with eyes closed, little or no head movement	**R**
Follow another individual	Focal individual follows another individual. Specify female, male, juvenile, infant, newborn,	**F…**

(distance)	dyad (eg. FIN, FFE, FMA)	
Waiting for conspecific	Subject stops moving and looks at conspecific, waiting for them to follow.	**W**
Hug	Subject embraces conspecific with one or both arms from any direction	
Glance	Subject quickly looks up or directly a conspecific for 2 seconds or less.	**HUG**
Watch	Subject stares at an object, individual or direction for more than 2 seconds	**Gl**
Scan (looking around)	Subject scans with clear obvious head movement with no fixed gaze longer then 2 seconds	**WA** **LA**
Present anogenital region	Subject stands in front of conspecific presenting anogenital region sometimes accompanied by teeth chattering	
Inspect anogenital region	Subject inspects anogenital region of a conspecific. Can be accompanied by sniffing	**PRS** **INA**

Infant contact	**Definition**	**Code**
Cradle	Subject sits with baby/infant in lap, holding it with one or both hands over back/chest	**C**
Supported Infant	Infant clings to an individual whilst being supported by individual carrying it often with one hand	**SI** **LI**
Look at infant	S holds baby/infant in air with two arms	**HA**
Hold in air	Teeth chatter at ano-genital region of infant/baby, used in triads as a social mediator (occasionally whilst holding baby in air)	**IAG**
Anogenital inspection chattering	Focal individual grabs and holds onto the infant's limb to prevent it venturing further away	**RES**
Restrain infant	Focal individual takes an infant from another group member or from the ground	**RET** **GI**
Retrieve	Focal individual sweeps hand through the fur of the infant inspecting it and picking at debris	**AB**
Groom infant	Focal individual leaves the infant or physically pushes it away	**DRG**
Abandon baby	Focal individual pulls the infant along	
Drag baby	Subject looks at infant whilst lowering the back and teeth chattering to invite it to cling	**INV**
Invite baby		**GBI**
Grab Infant		

Infant Behaviour	Definition	**Code**
Exploration	Subject manipulates object with hand, with mouth, grabs object or rummages parting soil and leaves.	**EX**
Grab fur	Subject extends arm and clasps the fur of another individual	**GF**
Climb on fur	Subject clasps fur of another individual either clinging or crawling on the individual	**CFR**
Mouth fur	Subject grabs the fur of another individual in its mouth	**MFR**
Climb/descend	Subject clambers up and down a tree, twig or rock	**C/D**
Leap	Subject pushes off with back legs and extends front legs to land	**LEP**
Pull away	Subject wriggles and struggles to break the hold of another individual	**PA**
Social play	Subject bounds around with another individual	**SCPL**
Solitary play	Subject bounds around when alone	**SLPL**
Squeal	Subject emits short lived high pitched vocalization or maintains it for longer durations	**SQL**
Walk/Crawl	Subject moves independently on the ground using all four limbs	**W/CR**
Hang	Subject suspends and supports itself from a tree or branch using any limb	**HNG**