MOTHER-INFANT INTERACTIONS IN A WILD POPULATION OF *Macaca nemestrina* (Linnaeus)

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ABSTRACT

Until now, mother-infant relationships have not been studied in a wild population of the Southern Pig-tailed Macaques *Macaca nemestrina.* We observed six mother-infant dyads from April 2016 to September 2016 in the Segari Melintang Forest Reserve, Peninsular Malaysia using focal sampling methods from the perspectives of both individuals. We hypothesized that as infant age increased, the same important mother-infant behaviours, previously observed to change in captive pig-tailed macaque mother-infant studies, would also change over time in field conditions. We expected that as the infant ages, mothers would decrease their rates of restraint and retrieval, and increase their rates of punishment. Two separate generalized linear mixed models (GLMM) of mother permissive behaviour and mother-infant contact duration as the outcome variables each showed infant age as the sole significant predictor variable indicating that as infant age increased, maternal behaviours changed as expected above, and mother-infant contact duration decreased. Mothers' interactions with other group members appeared influenced by mothers' associations with their offspring: adult females and juveniles were significantly more likely to be within 1-5 m proximity of mothers as infant age increased. Our data show that mother permissive behaviour, mother-infant contact duration, and proximity are crucial elements to consider when examining wild Southern Pig-tailed Macaque mother-infant relationships and infant independence, similar to what has been observed in captive settings.

Keywords: dyadic relationships, maternal behaviour, permissive, proximity

INTRODUCTION

In primates, infant dependence on the mother is prolonged compared with most other animals, and the later stages of the mother-infant relationship can vary greatly in terms of maternal permissive behaviours and physical contact, both between and within species living in different settings (Kaufman & Rosenblum, 1969). Physical contact and maternal permissive behaviour have been viewed as critical components of the dyadic mother-infant relationship and significant factors in the attenuation of the bond (Kaufman & Rosenblum, 1969), which gradually leads to increased infant independence.

This study focuses on a wild group of Southern Pig-tailed Macaques *Macaca nemestrina* (Linnaeus). Like other members of this genus, Southern Pig-tailed Macaques live in multi-male multi-female groups that are female-philopatric, where females remain in their natal groups while males leave at sexual maturity (Thierry, 2004). Thierry (2004) places Southern Pig-tailed Macaques into the Grade Two category on his four-grade scale of macaque species based on species-typical patterns of aggression and reconciliation. Grade Two species are characterized by high rates of aggression, high levels of despotism, and relatively low rates of reconciliation (Thierry, 2004). Group size varies between 20 and 80 individuals (Caldecott, 1986), and the dominance hierarchy is stable (Oi, 1990). To date, little is known about this species' mother-infant interactions in the wild, but maternal behaviour has occasionally been studied in captivity.

Captive pig-tailed macaques' mothering styles vary between individuals in measures of maternal protectiveness, rejection and warmth (Maestripieri, 1998). Aggression by other adults and previous maternal experience are both important in shaping

the captive Southern Pig-tailed Macaque mothering style (Maestripieri, 1998). Captive Southern Pig-tailed Macaque mothers affiliated more with their infants if the mothers experienced hostility from other group members (Maestripieri, 1998). Upon caregivers' attempts to force separation of infants from their mothers, infants were extremely vocal and clung to the mothers; once reunited, all signs of stress and vocalizations ceased (Jensen & Tolman, 1962). Separation increased infant-directed behaviour of the mother, and the infant became less likely to separate from the mother during the early stages of the reunion (Jensen & Tolman, 1962). Mother-infant separation led to more differences in infants' physiology and sleep patterns than did peer separation (Boccia et al., 1989). Lower-ranked mothers categorized in the first two grades in Thierry's (2004) four-grade scale were found to be protective, frequently retrieving infants and restricting infant interactions. In captivity, primiparous pig-tailed macaque mothers often neglected their firstborn (Maestripieri et al.,1997).

In the captive environment, pig-tailed macaque mothers initiated the LEN (Lips forward, Ears back and Neck extended) face, a frequent facial expression in this species (Oettinger et al., 2007; also known as "Pucker" face), when distance between them and their infants increased (Maestripieri, 1996). Infants who received more LEN faces from their mothers did not spend as much time in contact with them compared to infants who received fewer LEN faces (Maestripieri, 1996). Because of this apparent correlation the LEN face was suggested as a means of maternal encouragement of infant independence (Maestripieri, 1996).

Rosenblum and Kaufman (1968) designed two studies to compare captive Southern Pig-tailed Macaque mother-infant behaviours with those of other macaque species. They focused on maternal permissive behaviours in Bonnet Macaques *Macaca radiata* (É. Geoffroy Saint-Hilaire) and Southern Pig-tailed Macaques. A female's permissiveness as a mother was measured by scoring three maternal behaviours that tend to change during infant development: restraint of the infant by the mother, retrievals of the infant by the mother, and finally punitive behaviours directed from the mother to the infant (Rosenblum & Kaufman, 1968). Rosenblum and Kaufman (1968) set out to characterize the extent to which a female could be viewed as more or less permissive (both as an individual, and across time) by scoring restraint, retrievals, and punitive behaviours she engages in and how these change as her infant ages. Generally, mothers are expected to restrain and retrieve more and punish less when an infant is younger. As the infant ages, mothers are expected to decrease rates of restraint and retrieval and increase rates of punishment. Their results highlighted physical contact as a critical component in the mother-infant social relationship. In their study, Bonnet Macaques spent a significant amount of time in contact with other members in their group, while Southern Pig-tailed Macaques were not in physical contact with others except when engaged in grooming and mating. Varying contact patterns in adult Southern Pig-tailed and Bonnet Macaques may greatly influence the mother-infant dyadic relationship, and by extension, the social development of the infant (Rosenblum & Kaufman, 1968). Infants of both species initiated breaks in contact early in their lives (Kaufman & Rosenblum, 1969). Mother and infant behaviours were collected separately and scored to reveal the progression of mother-infant interactions over 15 months, which showed a distinct drop in time of maximum separation bouts in Southern Pig-tailed Macaques, while the Bonnet Macaques seemed to remain at a constant maximum time (Kaufman & Rosenblum, 1969).

In another mother-infant study comparing captive Southern Pig-tailed, Stump-tailed *M. arctoides* (É. Geoffroy Saint-Hilaire) and Rhesus *M. mulatta* (Zimmermann) Macaques, Southern Pig-tailed mother-infant pairs spent more time in contact than did Rhesus and Stump-tailed pairs (Maestripieri, 1994). Additionally, Southern Pig-tailed mother-infant pairs showed a gradual decrease over the weeks in the percentage of time spent in contact. Southern Pig-tailed Macaque mothers were more protective than were Rhesus mothers and did not encourage infant independence as much as Rhesus mothers did. Maestripieri (1994) observed mothers self-scratching in all three species, which he attributed to maternal anxiety. In all three species, the rate of mother scratching while the infant was away decreased as the infant aged. The greater protectiveness observed in Southern Pig-tailed Macaque mothers compared with Rhesus Macaque mothers may be related to the rate of infant development and the infant's vulnerability in its environment (Maestripieri, 1994).

The setting in which a mother raises her young can influence mother-infant interactions. In a study that compared Southern Pig-tailed Macaque mother-infant pairs in two different captive environments, group-raised mothers and infants spent more time in ventral contact and less time completely separated than did caged infants (Wolfheim et al., 1970). Nakamichi et al. (1990) compared individually-housed Long-tailed

Macaques *M. fascicularis* (Raffles) and socially-housed macaque mother-infant pairs from other species. As individually-housed Long-tailed Macaque infants aged, body contact between mother and infant, maternal holding, and infant suckling decreased, while mothers showed increased aggression towards their infants. In a comparison of wild and captive Rhesus Macaque mother-infant pairs, Berman (1980) attributed slight differences in protective behaviours to environment type rather than differences between infants. She found captive mothers were more protective and less encouraging of infant independence than their wild counterparts. In both environments, Rhesus Macaque mothers maintained contact and proximity to infants in the early stages of infant development. Gradually, the mother and infant spent more time out of contact, until a point when the infant was primarily responsible for maintaining contact and proximity to the mother, with an increase in maternal rejections. After several years, captive rhesus mother-infant interactions shifted toward patterns seen in wild mother-infant interactions, characterized by less maternal responsibility in maintaining proximity to her infant.

With described variations in physical contact and permissive behaviours existing among captive groups (Kaufman & Rosenblum, 1969; Maestripieri, 1994), and studies on Southern Pig-tailed Macaque and other macaque species showing an impact of setting on mother-infant interactions (Wolfheim et al., 1970; Berman, 1980; Nakamichi et al., 1990), it is important to observe wild Southern Pig-tailed Macaque mothers and infants to develop a more complete understanding of mother-infant interactions in Southern Pig-tailed Macaques. Additionally, no data yet exist regarding the patterns of maternal-infant interactions for the wild Southern Pig-tailed Macaque. We hypothesized that wild Southern Pig-tailed Macaque mother and infant behaviours would change as infant age increased. To test the hypothesis, we made the following predictions:

Mother Perspective:

1. As infant age increased, the mother's amount of permissive behaviour would increase.
2. As infant age increased, the mother's amount of time spent in contact with the infant would decrease.
3. Maternal rank would be negatively associated with maternal permissive behaviours.
4. Parity would be positively associated with maternal permissive behaviours.

Infant Perspective:

5. As infant age increased, time spent in contact with the mother would decrease.
6. As infant age increased, the frequency of mother-directed vocalizations would decrease.
7. Maternal rank would be negatively associated with infant contact time.
8. Parity would be negatively associated with infant contact time.

Proximity:

9. Responsibility for maintaining proximity and contact within the mother-infant dyad would shift from mother to infant as infants aged.
10. As infant age increased, group-member proximity to mothers would increase.

METHODS

Study site

This study took place from 3 April to 10 September 2016 in the Segari Melintang Forest Reserve, Perak, Peninsular Malaysia. The forest reserve is approximately 2,720 ha consisting of coastal lowland, mixed dipterocarp forest and freshwater swamp forest zones. In 2016, the field site received an annual rainfall of 1,586.13 mm (average monthly rainfall of 102.4 mm during the study period) and average annual temperature of 28.3ºC (monthly average temperature of 28.9ºC during the study period; weather station Sitiawan; retrieved from https://www.weatheronline.co.uk). The forest is surrounded by oil palm *Elaeis guineensis* Jacq. plantations, rural settlements and secondary forest (Ruppert et al., 2018).

Study subjects

This study group of Southern Pig-tailed Macaques named group "Amy" has been followed since November 2012 (Ruppert et al., 2018). All the individuals can be identified and classified into their respective age-sex classes. During the study period, the study group comprised 17 adult females, ten adult males, nine juveniles and five to six infants. ED collected focal data on six mothers (Anna, Brienne, Emma, Goldie, Renate and Sandra) and their six infants (Anaconda, Brandy, Emanuel, Gollum, Reggie and Sausage). The home range for the study group is between 84 and 198 ha, depending on calculation method and year (Ruppert et al., 2018). We assigned a David's score (Gammell et al., 2003), a method used to calculate dominance rank within a group by tallying agonistic interactions

and their outcomes, to each adult female within the study group. We assigned mothers to parity groups by counting the number of surviving offspring each had since November 2014. Each mother was classified to a parity category of 1 or 2 (1 or 2 successful offspring).

A total of 19 adult females were present throughout the entire study period and were observed for a total of 2,850 min. Due to staggered births within the sampling period, the numbers of infants and mothers changed. Mothers were observed for a total of 3,270 min (N=6 mothers). Infants (less than a year old at the beginning of the focal observation period) were observed for a total of 2,880 min (N=6 infants).

We used a chi-square goodness-of-fit test to test for total observation time (minutes) between adult females, which showed an even distribution in observation time across all adult females (χ^2=3.84, df=18, N=19, p>0.05). We used a second chi-square goodness-of-fit test to test for total observation time (minutes) between group infants, which showed an uneven distribution in total observation time across infants (X^2=210.08, df=5, N=6, p<0.0001), likely due to a late birth during the study period causing one infant to be observed for less time.

Study ethograms

Through the combination and modification of several published behavioural ethograms used on Southern Pig-tailed Macaques and other related macaque species (Bobbitt et al., 1964; Kaufman & Rosenblum, 1969; Maestripieri, 1994; Schino et al., 1995), we developed two ethograms: one mother-specific (Table 1) and one infant-specific (Table 2). These ethograms described all mother-infant interactions we saw in wild Southern Pig-tailed Macaque mother-infant dyads. The list of mother behaviours included permissive behaviours initiated by the mother and affiliative contact/non-contact behaviours. The infant ethogram had affiliative contact/non-contact behaviours and a vocalization that commonly occurs when infants are separated from their mothers. Each ethogram included the LEN face (Oettinger et al., 2007) and vocalizations that have been observed from both infants and mothers. We also recorded the proximities of other group members to the mother-infant dyad to test how mothers interact with other group members as the infant ages. We scored proximity into three categories: in contact, <1 m, and 1-5 m.

Sampling methods

We used focal animal sampling (Altmann, 1974) to record the mother-infant behaviours. ED collected focal samples daily, between 07:00 h and 19:00 h, for a duration of 30 min per focal individual sample with a five-minute interval between samples to find the next focal individual. We randomized mothers and infants into a combined sequence, which we edited as the study progressed to account for new births. Subsequent sequences were generated upon completion of the previous sequence with a random sequence generator. ED observed all focal subjects before randomizing the sequence again. If a focal subject could not be found after five minutes, she moved to the next subject in the random sequence list. She then tried to find the missed focal animal for at least five minutes before continuing the sequence.

ED recorded the frequencies and durations of both mother and infant behaviours on an iPad mini in the field using Animal Behaviour Pro (University of Kent). The ethogram behaviours were programmed in the application to categorize behaviour frequencies and durations in focal samples.

Inter-observer reliability was assessed at the field site with a reliability value of at least 0.85 for animal identity (Martin & Bateson, 2007). ED's intra-observer reliability for ethogram behaviours was assessed using a pre-recorded video focal of a mother Southern Pig-tailed Macaque scored at the beginning of the observation period and then each subsequent month (N=4). Intra-observer reliability with ethogram behaviours was at a mean of 87% (range 78-94%).

Analyses

We used R 3.3.2 (R Core Team, 2016) in R-Studio 1.0.136 (R Studio, 2016) to test relationships between the variables we measured: contact duration, permissive behaviour, mother-directed vocalizations, maternal rank, parity, self-directed behaviour, proximity and infant age. We used backwards selection in generalized linear mixed model (GLMM) analysis to eliminate non-significant variables and iteratively evaluated model improvement (Zuur et al., 2009). We set alpha at 0.05. All Spearman's rank correlation tests used individual data (multiple observations per individual) and not pooled individual data.

Mother perspective:

The null hypotheses for the correlation tests were 'no change in permissive behaviour as infants aged' and 'no change in contact duration as infants aged'. We used Spearman's rank correlation coefficient to test the predictions that mother permissive behaviour or mother-infant contact time were associated with infant age. A GLMM tested the prediction that mother

Table 1. Mother ethogram.

Behaviour	Definition
Ventral contact	Mother is seated with infant in ventral-ventral contact[4]
Grooming	Inspecting or brushing aside hair using one or two hands[3]
Foraging	Mother is searching for food while infant is physically separated[4]
Ventral contact with cradle	Mother is seated with infant in ventral-ventral contact while also holding infant with hands and/or arms[4]
Ventral contact with grooming	Mother is seated with infant in ventral-ventral contact with grooming[3,4]
Ventral contact with foraging	Mother is seated with infant in ventral-ventral contact while foraging
Mother approach	Mother initiates a decrease in the distance between mother and infant[3,4]
Mother leaves vertically	Mother initiates an increase in the distance between mother and infant in the vertical plane[2,4]
Mother leaves horizontally	Mother initiates an increase in the distance between mother and infant in the horizontal plane[2,4]
Within proximity	Mother is within proximity to infant (within arm's reach) but physically separated[2]
Out of proximity	Mother is not within arm's reach of infant, mother and infant are separated[2]
LEN	Mother makes LEN face, directed at infant[1]
Play	Playful actions with other group members[4]
Restrain*	Mother prevents infant from moving away by holding its limb or tail[3,4]
Bite*	Mother bites infant in punitive fashion, not grooming[2]
Rejection*	Mother denies physical contact with infant[3,4]
Nipple removal*	Mother removes nipple from infant's mouth while feeding[2]
Weaning contact deterrence*	Mother does not allow infant to reach a nipple with its mouth i.e. blocking nipple[2]
Scratching	Repeat movement of the hand/foot where the finger/toe-tips rub the hair[3]
Retrieval due to group movement*	Mother retrieves infant in order to move with the group[2]
Retrieval due to danger*	Mother retrieves infant and places ventrally in reaction to a perceived social or physical danger to the infant by the mother[2]
Cling carriage	Mother actively grasps and supports infant in the ventral-ventral position while in locomotion[2]
Passive carriage	Mother is in locomotion with the infant in ventral-ventral position, but is not actively holding the infant[2]
Groan vocalization	Mother is physically separated from infant and vocalizes a "Moo" sound directed at the infant[1]
Harsh bark	Mother vocalizes a short bark directed at the infant[1]
Out of Sight	Mother is not within observer's view
Other	Any behaviour that the mother presents but is not listed in the ethogram

*Indicates behaviours used for statistical analysis; [1]Bobbitt et al., 1964; [2]Kaufman and Rosenblum 1969; [3]Maestripieri 1994; [4]Schino et al., 1995.

Table 2. Infant Ethogram.

Behaviour	Definition
Ventral contact with cling	Infant is in contact with the mother ventrally using all four limbs with the head close to her chest[2]
Ventral contact with hold	Infant is in contact with the mother ventrally using two to four limbs, with head not in contact with the mother's chest[2]
Grooming	Inspecting or brushing aside mother's hair using one or two hands[3]
LEN	Infant makes LEN face, directed at mother[1]
Play	Affiliative (playful) actions with other group members, e.g. wrestle, chase, mock-bite[2,4]
Infant approach	Infant initiates a decrease in the distance between mother and infant[4]
Infant leaves vertically	Infant initiates an increase in the distance between mother and infant in the vertical plane[2]
Infant leaves horizontally	Infant initiates an increase in the distance between mother and infant in the horizontal plane[2]
Scratching	Repeated movement of the hand or foot where the finger/toe-tips rub the hair and skin[3]
Within proximity	Infant is within proximity to mother (within arm's reach), but physically separated[2]
Out of proximity	Infant is not within arm's reach of mother, mother and infant are physically separated[2]
Coo vocalization	Infant is physically separated from the mother and vocalizes a "Coo" sound directed at the mother[1]
Out of sight	Infant is not within observer's view
Other	Any behaviour that the infant presents but is not listed in the ethogram

[1]Bobbitt et al., 1964; [2]Kaufman and Rosenblum 1969; [3]Maestripieri, 1994; [4]Schino et al., 1995.

permissive behaviour would increase as mother dominance rank decreased and mother permissive behaviour would increase as mother parity increased. We used the packages lme4 (Bates et al., 2015), Elo Rating (Neumann & Kulik, 2014), and ggplot2 (Wickham, 2009) to assess the variables of rank, parity, self-directed behaviour and infant age as predictors of the dependent variable, mother permissive behaviour.

Infant perspective:

The null hypotheses were 'no change in contact duration as infants aged' and 'no change in mother-directed vocalizations as infants aged'. We used Spearman's rank correlation coefficient to test the predictions that mother-infant contact time or mother-directed vocalizations were associated with infant age. A GLMM tested the prediction that mother-infant contact duration would increase with maternal dominance rank and decrease with parity. We used the packages lme4 (Bates et al., 2015), Elo Rating (Neumann & Kulik, 2014), and ggplot2 (Wickham, 2009) to assess the variables of rank, parity, mother self-directed behaviour and infant age as predictors of the dependent variable, mother-infant contact duration.

Proximity:

The Hinde index is used to quantify the mother-infant relationship through the use of mother and infant approaches and leaves to assess responsibility for maintaining proximity within the dyad (Hinde & Simpson, 1975). We used Hinde's index (Hinde & Simpson, 1975) to measure the responsibility infants and mothers took for changes in proximity as the infant developed, with a null hypothesis of 'no change in the indices as infants aged'. The null hypothesis for group-member proximity was 'no significant change in group-member numbers within proximity as infant age increased'. We assessed group-member proximity relative to the mothers within one meter and more than one but less than five meters using Spearman's rank correlation coefficient to test the prediction that as infant age increases, group-member proximity to mothers would increase. Group-members

were separated into three classes: male, female and juvenile. We weighted each class to create an accurate proportion relative to group size.

RESULTS

Analyses conducted from each mother's perspective

Spearman's rank correlation coefficient tested the relationship between infant age and number of permissive behaviours from the infant's mother. We found a significant negative correlation for these two variables (r[5]=-0.735, p=≤0.05). We compiled a table of mothers, their infants and the categorical variables of maternal rank and parity for use in the GLMMs (Table 3).

We used GLMM to further explore what factors predicted a mother's permissive behaviour, focusing on mother dominance rank, parity (Table 4), self-directed scratching and infant age. Because our original data had many potential behaviours with a large number of zeros, we collapsed detailed behaviours into a binomial distribution of presence/absence of permissive behaviour regardless of specific behaviour type. Finally, we designated mothers (N=6) as a random effect to account for inter-individual differences in mothering style. The mother permissive behaviours decreased significantly with increasing age of their offspring (GLMM, -0.006±SE0.003, z=-1.978, p≤0.05; Table 4).

Analyses conducted from each infant's perspective

We found a significant negative correlation between infant age and the duration of mother-infant contact time from the infant's perspective (r[5]=-0.733, p=≤0.05). We did not find a relationship between infant age and frequency of infant vocalizations directed toward their mother (r[5]=-0.054, p=0.604). We used GLMM to test if mother dominance rank, mother parity, infant self-directed scratching and infant age predicted mother-infant relative contact time from each infant's perspective. We transformed the response variable 'mother-infant relative contact time' using a log+1

Table 3. Adult females and associated infants, adult females' dominance rank in descending order, and parity categories.

Mother	Infant	Sex	Birth date	David Score Value	Parity Category
Anna	Anaconda	Male	August 2015	31	1
Goldie	Gollum	Female	July 2015	19	2
Emma	Emanuel	Male	February 2016	0	2
Sandra	Sausage	Female	April 2016	-4	2
Renate	Reggie	Female	July 2016	-4	1
Brienne	Brandy	Unknown	September 2015	-9	2

Table 4. GLMM: infant-directed behaviours (as indicated in Table 1).

Predictor variable	Estimate	SE	z-value	p(>|z|)
Best Fit Model				
Intercept	0.241	0.781	0.309	0.757
Infant Age	-0.006	0.003	-1.978	0.048*

Table 5. GLMM: relative contact time.

Predictor variable	Estimate	SE	z-value	p(>|z|)
Best Fit Model				
Intercept	2.071	0.089	23.300	<2E-16***
SDB*	-0.081	0.056	-1.431	0.152
Infant Age	-0.005	0.001	-9.066	<2E-16***

*Self-directed behaviour; ***Highly significant.

transformation, and then we distributed the contact times into categories of 0.1 percent of time intervals (e.g. 0.01-0.1=1 etc.). We designated the infants (N=6) as a random effect to account for differences among individuals. The relative mother-infant contact duration per focal sample decreased significantly with increasing age of the offspring (GLMM, -0.005±SE0.001, z=- 9.066, p≤0.05; Table 5).

Proximity

The Hinde index in four of the six observed mothers showed the infant as responsible for a greater proportion of contacts broken (Fig. 1).

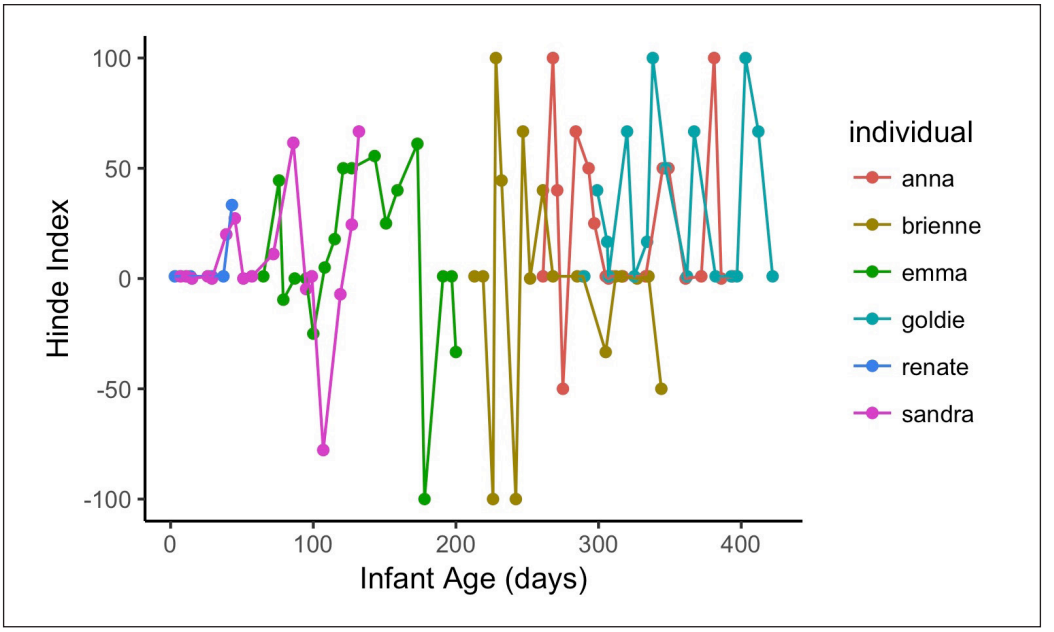

Fig. 1. Proximity graph of combined mothers' Hinde graphs (N=6).

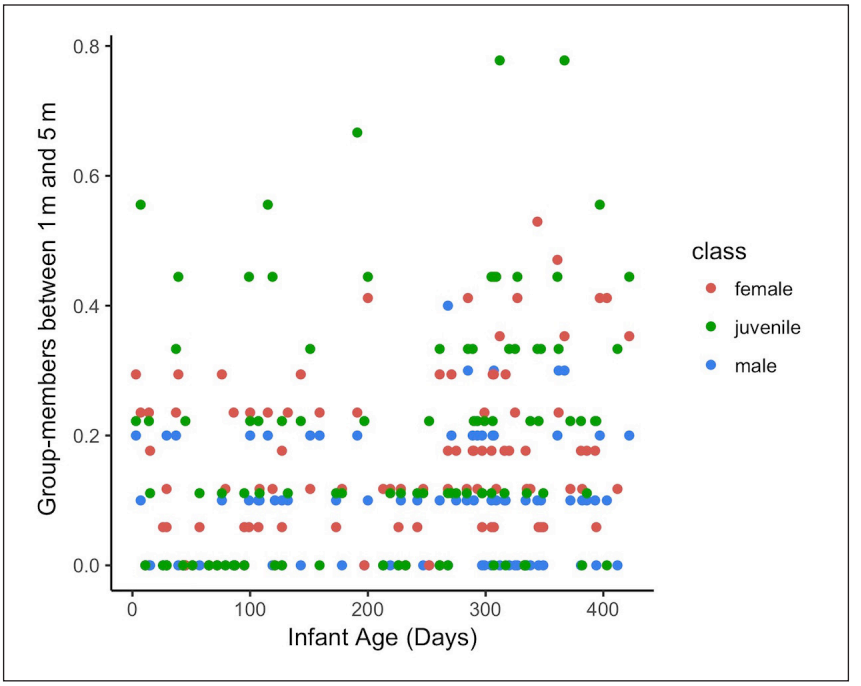

Fig. 2. Scatterplot of adult male, adult female, juvenile proximity frequency at 1-5 m plotted against infant's age.

We used Spearman's rank correlation coefficient to test the relationship between infant age and number of group-members within 1 m proximity and 1-5 m proximity. We found no correlations within 1 m (male $r[5]=0.101$, $p=0.331$, female $r[5]=-0.155$, $p=0.133$ and juvenile $r[5]=-0.156$, $p=0.132$). The results showed significant correlations in the 1-5 m proximity category for adult females and juveniles (adult females: $r[5]=0.278$, $p=\leq 0.05$; juveniles $r[5]=0.274$, $p=\leq 0.05$; Fig. 2). The correlation for adult males was not significant: ($r[5]=0.197$, $p=0.055$; Fig. 2).

DISCUSSION

Mother perspective

The mother's perspective is by far the more common of the two perspectives reported in mother-infant studies, therefore we explored the mother-infant relationship from the perspective of each social partner to gain deeper insight into how the mother-infant relationship changes through time. Our prediction (#1) that 'as an infant ages, the frequency of her or his mother's permissive behaviours would increase was not supported by our results. In captive Pig-tailed Macaque mothers, permissive behaviours increased after the infant reached three weeks of age, regardless of whether the mother was responsible for maintaining or preventing proximity (Rosenblum & Kaufman, 1968). In this study, we instead found a negative relationship between mother permissive behaviour and infant age. It is noteworthy that just before our data collection began (March 2016; we did not observe the exact timeline of takeover events as no observers were in the field), the alpha and beta males left the study group and new alpha and beta males moved in, causing a male hierarchy shift. This sharp turnover in the male hierarchy may have influenced maternal behaviours. At the time of the male dominance shift, a mother-infant dyad within the study group went missing, which may be an extreme response to the dominance shift. Adult females trying to develop relationships with the new dominant males may explain the decline in mother permissive behaviour as infants aged.

We found support for the prediction (#2) that as infant age increases, the duration of mother-infant contact time decreases. Maestripieri (1994) found that captive pig-tailed macaque mother-infant pairs gradually decreased their time spent in contact, a finding that corresponds to the results in this study. Here, the relationship between contact duration and infant age is stronger than the relationship between mother permissive behaviour and infant age. As the infants in the study group aged, they spent less time in contact with their mothers. Captive Southern Pig-tailed Macaque mothers were found to initiate the LEN face when there was an increase in distance from the infant (Maestripieri, 1996). This species-specific behaviour was rarely seen throughout our observation period and was thus not analysed. The small decrease in mother permissive frequency might be explained by the small sample size and difficulties in collecting data on the same developmental periods of all the infants, which were born at different times across the duration of the study.

We predicted (#3) that lower ranked mothers would be more protective of their infants due to greater threats (see also Thierry, 2004). This prediction was not supported by our data. Infant age was the only significant variable that predicted mother permissive behaviour. In captivity, primiparous pig-tailed macaque mothers often neglect their firstborn (Maestripieri et al., 1997), so we expected parity to predict (#4) mother permissive behaviour. Since most of the previous mother-infant Southern Pig-tailed Macaque studies are captive subjects, parity could have been more noticeable in captive populations instead of wild populations. In our GLMM model, there was not a strong correlation between a mother's dominance rank and her degree of permissive behaviour. We used self-directed behaviour (scratching) as a predictor variable to assess maternal anxiety when the infant was separated from the mother. This common behaviour in past captive studies (Maestripieri, 1994) was also commonly observed in our wild study group.

Infant perspective

We collected behavioural observations from the infant's perspective to obtain a complete record of mother-infant contacts. When the same correlations were run from both mother and infant perspectives, we found significant negative relationships between mother-infant contact time and age (#5). Even though infants can show variability, infants in our data set all followed a similar pattern with respect to their ages and contact time with mothers. Maestripieri (1994) also found a gradual decrease in contact time between mother and infant in the captive dyads he studied.

We found no linear relationship between mother-directed vocalizations, infant vocalizations, and infant age (#6). If the infants had moved from the mothers by choice, we expected a general decrease in this behaviour as the infants grew more independent. Gouzoules & Gouzoules (1989) also found that Southern Pig-tailed Macaque agonistic screams/

vocalizations became more fine-tuned with age, indicating that infants would learn which calls were most effective and only use those calls if they needed their mother's help. However, our study group was generally quiet and followed the Southern Pig-tailed Macaque stereotype of rarely vocalizing (Oi, 1990).

We predicted (#7 and #8) that mother-infant contact time would be lower with lower maternal rank and lower parity. Neither of our predictions were supported by our data, and infant age was the only significant variable that predicted contact time duration. Maestripieri (1994) found that captive pig-tailed macaque mother-infant pairs showed a gradual decrease over weeks in percentage of time infants spent in contact with mothers. Contact patterns can greatly influence the mother-infant dyad and ultimately, infant development (Rosenblum & Kaufman, 1968). In Rhesus and captive Long-tailed Macaques, mother-infant pairs gradually spent less time in contact with their mothers as they aged (Berman, 1980; Nakamichi et al., 1990). In Vervet Monkeys *Chlorocebus pygerythrus* (F. Cuvier), Fairbanks (1989) found mothering styles to vary significantly between mothers, with each showing different contact patterns with their infants. An infant leaving the mother could also mean the infant is taking opportunities to play and explore social independence from the mother (de Jonge et al., 1981). In this study, we found a gradual decrease in contact duration between mother and infant, but we also found similar contact patterns across the six mothers and their infants relative to infant age.

Proximity

Proximity is a distinct affiliative behaviour that indicates mutual preference between animals (Troisi et al., 1989). Infants spend most of their early development after birth either in direct contact or proximity to their mothers. In wild and captive macaques, mothers are responsible for maintaining proximity and infant contact in these early life stages (Berman, 1980; Nakamichi et al., 1990). Berman (1980) showed that infants play a more dominant role in proximity maintenance within the dyad at a certain point. Two mothers in the present study never had a negative Hinde index value, which indicated that their infants were responsible for a greater proportion of contacts made with their mothers than contacts broken (*sensu* Brown, 2001). These were the mothers of the oldest infant (born July 2015) and the youngest infant (born July 2016) in our dataset. It was not possible to distinguish a trend between mother dominance rank and the proximity indices calculated because the dyads were not observed at the same stages of infant development. Infants had a greater proportion of broken contacts between 100 and 350 days of age, but infants resumed a greater proportion of contacts made after 350 days of infant age (#9). This period showed the most variation in mother-infant contact and proximity behaviours and points to the start of infant independence within this study group. Pig-tailed Macaque weaning age is 12 months (Sponsel et al., 2002), so the shift in maintaining proximity from mother to infant and again to mother may correspond to infant weaning.

Rosenblum & Kaufman (1968) found that captive Southern Pig-tailed Macaque mothers were reluctant to socially engage with others after giving birth. All age classes in our study showed an increased frequency of proximity to the mothers at the 1-5 m range, but only adult females and juveniles showed significant correlations with infant age. Aggression in the group can play a significant role in shaping mothering styles (Maestripieri, 1998). At our field site, there was some male-male and male-female aggression at the beginning of the observation period, which could have had an effect on mothers' protectiveness and guarding behaviours. Maestripieri (1998) found that pig-tailed mothers affiliated more with their infants if they experienced hostility from other group members. During times of aggression, mothers kept their infants close and away from other group members. While it is surprising that the study group mothers did not appear as careful given the change in male dominance rank at the 1 m to 5 m distance, they did not let many males enter within the 1 m range of proximity, which indicated a few selected males were allowed in close proximity.

We found that Southern Pig-tailed Macaque mothers and infants living in a wild population showed changes in mother-infant interactions over time. Mother permissive and contact behaviours both decreased with increasing infant age. Mothers' ranks and parities did not predict their permissive behaviour. As infant age increased, the duration of mother-infant contact time decreased (from the infant's perspective). We found no correlation between infant age and mother-directed vocalizations, and infant contact time with the Southern Pig-tailed Macaque mothers could not be predicted by maternal dominance rank or parity trends. Responsibility for maintaining proximity and contact changed between mothers and infants as infants aged. Group-member proximity to mothers increased significantly in female and juvenile classes at distances of 1-5 m.

One of the biggest differences between this study

group of wild Southern Pig-tailed Macaque and other macaque species was the lack of influence that maternal dominance rank and parity seemed to have on mother-infant interactions. As a Grade Two (Thierry, 2004) species, this study group did not seem to behave in accordance with what we expected for their position on that scale. The study group members did show the gradual mother-infant contact decrease that has been characterized in mother-infant relationships of many macaque species. As the first study to investigate the wild perspective of Southern Pig-tailed Macaque mother-infant interactions, there are both similarities with what has been reported in the literature for captive individuals of this species, and differences, suggesting that ecological and sociological environments may play a vital role in mother-infant interactions.

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