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Mother-Infant Interactions in a Free-Ranging Population of Pigtail Macaques (Macaca nemestrina)

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MOTHER-INFANT INTERACTIONS IN A FREE-RANGING POPULATION OF

PIGTAIL MACAQUES (*MACACA NEMESTRINA*)

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A Thesis

Presented to

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Central Washington University

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In Partial Fulfillment

of the Requirements for the Degree

Master of Science

Primate Behavior

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by

Emily Munroe Dura

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CENTRAL WASHINGTON UNIVERSITY

Graduate Studies

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ABSTRACT

MOTHER-INFANT INTERACTIONS IN A FREE-RANGING POPULATION OF

PIGTAIL MACAQUES (*MACACA NEMESTRINA*)

by

Emily Munroe Dura

May 2017

The Southern pigtail macaque (*Macaca nemestrina*) is an understudied species in the Cercopithecidae family distributed in Southeast Asia. In this field study, I focused on interactions of Southern pigtail macaques to better understand mother-infant relationships. I observed five to six mother-infant dyads from April 2016 to September 2016 in the Segari Melintang Forest Reserve, Perak, Peninsular Malaysia. I used focal sampling methods to score mother and infant behaviors from two ethograms. I hypothesized that as infant age increased, mother and infant behaviors seen to be important in pigtail macaque mother-infant captive studies, would change over time. As infant age increased, mother permissive behaviors and mother-infant contact duration showed significant negative correlations. A GLMM of mother permissive behavior as the outcome variable only showed infant age as a significant predictor variable. From the infant's perspective, as infants increased in age, mother-infant contact duration showed a significant negative correlation, while mother-directed vocalizations showed no association. A GLMM of mother-infant contact duration as the outcome variable showed only infant age as a significant predictor variable. Infants made more breaks in the

mother-infant dyad between 100-350 days of age. Adult females and juveniles were significantly more likely to be within 1-5 m proximity of mothers as infants aged. These data show that mother permissive behavior, mother-infant contact duration and proximity are crucial elements to consider when examining wild pigtail macaque mother-infant relationships and infant independence.

ACKNOWLEDGMENTS

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CHAPTER I

INTRODUCTION

Infant dependence on the mother in primates is prolonged compared to most

animals, and the later stages of the mother-infant relationship can vary greatly both

between species and within species in different settings (Kaufman & Rosenblum, 1969).

Differences in maternal interactions related to proximity and contact with infants has

been suggested to indicate individual variation in maternal styles (Berman, 1990).

Physical contact and maternal permissive behavior have been deemed critical

components to the dyadic mother-infant relationship and significant factors in the

attenuation of the bond (Kaufman & Rosenblum, 1969). With described variations in

physical contact and permissive behaviors existing among captive groups (Kaufman &

Rosenblum, 1969; Maestripieri, 1994), it is important to observe free-ranging pigtail

macaque mothers and infants to develop a more complete understanding of mother-infant

interactions in *Macaca nemestrina.* I hypothesized that mother and infant behaviors

would change as infant age increased. In order to fully test the hypothesis, I made several

predictions to examine the pigtail mother-infant relationships from the mother

perspective, infant perspective and all group-member proximities in relation to the pigtail

mothers. From the mother perspective, I predicted that as infant age increased, the

amount of mother permissive behaviors would increase and the amount of contact

between mother and infant would decrease. I predicted that mother permissive behaviors

could be dependent on dominance rank and mother parity. From the infant perspective, as

infant age increased, I predicted that the time spent in contact with the mother would

decrease and mother-directed vocalizations would decrease. I predicted that infant

contact duration with mothers could be dependent on mother dominance rank and parity. I expected that a shift in responsibility for maintaining proximity would occur as infants aged, and that it would shift from mother to infant. I also predicted that group-member proximity to mothers would increase over time, with more group members of more age classes in close proximity of mothers as infants aged.

I used focal animal sampling (Altmann, 1974) to record mother permissive behaviors, mother-infant contact durations and proximity behaviors from a study group of free-ranging pigtail macaques in the Segari Melintang Forest Reserve, Peninsular Malaysia. Mother permissive behavior and contact with infants both showed significant negative correlations with increased infant age, while neither mother dominance rank nor mother parity were significant predictor variables for mother permissive behavior. Infant vocalizations directed toward the mother showed no association with infant age, while infant contact with the mother showed a significant negative correlation with increased infant age. Neither mother dominance rank nor mother parity were significant predictor variables for contact durations with mothers as infants aged. Infants made more breaks in proximity during the period of 100-350 days of age and then were responsible for a greater proportion of contacts made with the mother after 350 days of infant age. Adult females and juveniles had significant positive correlations in the 1 m to 5 m proximity range as infants aged. Mother permissive behaviors, mother-infant physical contact duration and proximity behaviors all were significantly correlated to infant age in the study group of Southern pigtail macaques.

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CHAPTER II

LITERATURE REVIEW

Taxonomy and General Behaviors

The Southern pigtail macaque (*Macaca nemestrina*) is an understudied species within the diverse genus, *Macaca*. This species is classified in the *silenus-sylvanus* lineage, which was the first macaque radiation (Thierry, Singh & Kaumanns, 2004). Southern pigtail macaques are distributed throughout Southeast Asia with populations in Sumatra, Borneo and the southern portion of Peninsular Malaysia (Lang, 2005). In the 1970s there was still some question as to whether *Macaca nemestrina leonina*, *M. n. nemestrina* and *M. n. pagensis* were three different species or were subspecies (Fooden, 1975). *M. nemestrina* and *M. leonina* are currently considered two separate pigtail macaque species, while *M. pagensis* is no longer classified as a pigtail macaque (Lang, 2005). Pigtail macaques have been used in rural communities in Southeast Asia as coconut pickers (Bernstein, 1967; Schmidt-Burbach, Ronfot, & Srisangiam, 2015). There are several Thai and Malaysian venues, or 'monkey schools', that house many captive pigtail macaques, which are currently under investigation for inadequate welfare conditions (Schmidt-Burbach et al., 2015). Pigtail macaques are used as biomedical models in preclinical trials of human vaccines, HIV infections and human susceptibility to diseases (Trist, Tan, Wines, Ramsland, Orlowski, Stubbs & Hogarth, 2014; Kimball, 1998; Adams, Gravett, McAdams, Paolella, Gough, Carl & Heimesaat, 2011; Wood, Iverson-Cabral, Patton, Cummings, Cosgrove Sweeney & Totten, 2013).

M. nemestrina lives in tropical rainforests that include a mix of deciduous and swamp forests, lowland to montane altitudes and varying levels of dipterocarp zones

(Caldecott, 1986a; Sponsel, Ruttanakadul, & Natadecha-Sponsel, 2002). The range in

home range sizes for pigtail macaque groups is 62-828 ha (Sponsel et al., 2002). Species

members live in multi-male and multi-female groups that are matrilineal (Oi, 1990b).

Group sizes range from 6 to 81 individuals, with a group's mean adult sex ratio of 1:6.3

biased towards adult females (Oi, 1990b). Pigtail macaques have a general life span of

26.3 years, and reach sexual maturity at 35 months (Sponsel et al., 2002). Weaning

occurs in pigtail macaques after 12 months (Sponsel et al., 2002). Pigtail macaques are

multiple-mount ejaculators and are sexually dimorphic, with adult males weighing

between 6.2-14.5 kg and adult females weighing between 4.7-10.9 kg (Caldecott, Feistner

& Gadsby, 1996; Fa, 1989). These monkeys eat a wide variety of foods including seeds,

young leaves and leaf stems, insects, fungi and spiders and are highly frugivorous

(Bernstein, 1967; Lang, 2005). Pigtail macaques spend most of their days on the ground

and are more terrestrial than are most other macaque species (Bernstein, 1967; Caldecott,

1986a; Lang, 2005). The daily travel pattern for a pigtail macaque consists of climbing

down to mid-canopy-level from her/his respective sleeping site tree (which is usually

high in the canopy), traveling on the ground or low parts of trees while foraging, and

moving at around sunset to the high levels of the trees to sleep (Bernstein, 1967). This

species is known for being stealthy in an apparent attempt to elude predators and human

observers (Oi, 1990b). This behavioral phenomenon has made it difficult to habituate

wild groups without using food as a means to lure out the monkeys (Oi, 1990b).

As year-round breeders, adult pigtail macaques have visible perineal skin

swellings that researchers have used as indicators of ovarian cycles and pregnancies

(Maninger, Sackett, & Ruppenthal, 2000). Pigtail macaques show diurnal patterns of

behavior where general activity, aggression, passive contact incidence, and grooming are highest during the day, with sleep and contact duration highest at night (Martenson, 1977). During cold and rainy weather, infant pigtail macaques are more likely to be carried by their mothers, and retrieval of an infant with subsequent ventral contact is most common at sunset (Bernstein, 1972). Pigtail mothers regularly spend a great deal of intensive protective attention on their infants (Bernstein, 1972). Younger pigtail macaques seem to prefer to interact with related monkeys rather than unrelated monkeys (Wu, Holmes, Medina, & Sackett, 1980).

Social Behavior

   Affiliation and Dominance.

   Thierry (2004) places pigtail macaques into the Grade two category on his four-grade scale of macaque species based on species-typical patterns of aggression and reconciliation. The longtail macaque, *M. fasicularis*, is the only other species in that grade-level. Caldecott (1986b) also separated macaque species into a grade-system (in this case, a two-grade scale), but he placed the pigtail macaques alongside rhesus (*M. mulatta*), lion-tailed (*M. silenus*), and Japanese macaques (*M. fuscata*) in Group 1 based on these species' general social behaviors. Caldecott (1986b) used free-ranging pigtail macaque data unlike Thierry (2004), who used captive subjects. The varying placement of pigtail macaques as a species in terms of social organization leads to further questions of whether captive and field studies on pigtail macaques should be considered synonymous, as Bernstein suggests (1967). *M. nemestrina*, as a species, shows moderate-to-high rates of conciliatory behaviors compared to other primates, and both dyadic and

triadic reconciliations occur (Judge, 1991). In a study that examined variation in conciliatory tendencies in two captive pigtail macaque groups, members of the more-established group showed more intense ties with fewer partners, which increased the likelihood of reconciliation after a conflict (Castles, Aureli, & de Waal, 1996). Allogrooming and proximity are two distinct affiliative behaviors that indicate mutual preferences between two animals (Troisi, Schino & Aureli, 1989).

Lower-ranked mothers categorized in the first two grades in Thierry's (2004) four-grade scale were found to be protective and frequently retrieved infants and also restricted infant interactions. Species in these two grades have little allomaternal care. Mothers, regardless of dominance rank, in species classified in grades three and four, however, were more permissive, and these species have higher rates of allomaternal care (Thierry, 2004). Allomothering patterns thus appear in macaque species when dominance is less hierarchical (Thierry, 2004). Maternal and allomaternal care patterns can be explained by the varying degrees of protection needed by infants dependent on the social context (McKenna, 1979). Thierry (2000) also attributes covariation between mothering behaviors and dominance patterns to the protection level needed by infants in a social environment. Strict dominance hierarchies will cause the mothers to be more restrictive (Thierry, 2000).

As a multi-male, multi-female and matrilineal species, pigtail macaque males older than four years are commonly seen immigrating into and emigrating from groups (Oi, 1990b). Adult male pigtail macaques protect juveniles from predators, but otherwise do not offer much care to young (Caldecott, 1986b). Pigtail macaque females are year-round breeders, and female estrous cycles are not synchronized (Oi, 1990b). Food

availability and resulting intraspecific competition may dictate the number of males in a group (Caldecott, 1986b). Dominant males are tolerant towards subordinate males within their group in non-resource-oriented contexts in defense of females and offspring against competing males and other predators (Oi, 1990a). High-ranking males and females enforce the social hierarchy (Oi, 1990b). The dominance hierarchy of pigtail macaque groups is stable (Bernstein, 1969). Dominance among female pigtail macaques affects social interactions and observed variability may be attributed to individual responses to conflict (Giacoma & Messeri, 1992). Pregnancies in pigtail macaques do not disrupt female social relationships with other group members (Maestripieri, 1999). In one captive pigtail macaque study, high-ranking matrilines were found to produce more female than male offspring, and low-ranking matrilines produced more male than female offspring (Maestripieri, 2002).

Social behavior can also be studied through communication usage. Gestural forms of communication such as bared-teeth, present and lip-smack were the most common signals observed in *M. mulatta*, *M. nemestrina* and *M. arctoides* (Maestripieri, 2005). These signals were directed up hierarchies from subordinate animals to more dominant ones, while hip-touch and mount gestures were directed down hierarchies (Maestripieri, 2005). A facial expression unique to the pigtail macaque is referred to as the "lips forward-ears back-neck extended" (LEN) (Oettinger, Crockett, & Bellanca, 2007, pg. 293). The pucker face or LEN gesture is the most common and frequent gestural signal in pigtail macaques (Maestripieri, 1996a). While its true meaning(s) is still unknown, the LEN gesture has appeared in affiliative and agonistic interactions in dominance and submission, female-female bonding, juvenile play and in mother-infant contexts

(Maestripieri, 1996a). In most cases, the LEN gesture seems to signal reduction of inter-individual distance or summoning of another individual (Maestripieri, 1996a). Oettinger et al. (2007) suggest the LEN facial expression may have an appeasing function or serves as a rejection signal after a social invitation. As a conspicuous display, the LEN may also have evolved in pigtail macaques as a way to silently coordinate social activities (Oettinger et al., 2007).

Agonistic Behaviors.

Agonistic behaviors, or behaviors that relate to fighting and aggression, vary from species to species. Pigtail macaques are selective when choosing to help another individual and are more likely to aid a close relative than a distantly related individual (Massey, 1977). Older pigtail macaques perform more agonistic aid behaviors than younger individuals, and in mother-infant dyads, there are more agonistic aid behaviors from mothers towards their own offspring than vice versa (Massey, 1977).

Female pigtail macaques participate in more agonistic episodes than males do (Bernstein, 1972). Agonistic screams become more fine-tuned as pigtail macaques age, which shows developmental modification within the species when it comes to recruiting help (Gouzoules & Gouzoules, 1989). Aggression-levels vary among groups, but as aggression levels increase among pregnant females, the probability of a viable and uncomplicated birth decreases (Ha, Alloway & Sussman, 2011). Erwin (1977) was interested in how to arrange captive colony groups of pigtail macaques and found that all-female groups were at high risk for trauma resulting from female-female aggression. He also found that the presence of a male in the group greatly reduced the aggressive interactions between the females.

Infant abuse and neglect are two behaviors seen in pigtail macaque mothers that can occur due to an environment shared with abusive individuals and lack of reproductive experience in mothers, respectively. Neglect in infants is generally seen in first-time mothers, which points to the amount of experience macaque females need to acquire in order to successfully raise an infant (Maestripieri, Wallen & Carroll, 1997). Using longitudinal data, the researchers examined familial records for patterns of past abuse and neglect (Maestripieri et al., 1997). One of the most obvious forms of aggression in nonhuman primates occurs when there are male composition changes or rank shifts in a group. While groups remained at a constant male composition, there were no infant killings attributed to adult male aggression (Clarke, Blanchard, & Snyder, 1995). Infant deaths due to male aggression all occurred within two months of an adult male change in composition (Clarke et al., 1995).

Old World Monkey Mother-Infant Interaction Patterns

Terms like protective, restrictive, and rejecting are commonly used to describe variations in maternal behaviors directed towards their infants (Fairbanks, 1996). A set of maternal behaviors may be determined by the mother's social and ecological circumstances but explanations of these behaviors should also take into account individual differences in maternal care (Fairbanks, 1996). In longitudinal studies, vervet (*Chlorocebus pygerythrus*) mothers show consistent maternal styles across successive infants (Fairbanks, 1996). Between mothers, mother-infant contact varies significantly, while across infants with the same mother, contact is more consistent (Fairbanks, 1989). Berman (1990) also showed consistency in rhesus macaque (*Macaca mulatta*) maternal

styles across infants in such mothering behaviors as contact time, maternally-initiated

contact and maternal rejection. Maternal behaviors varied between mothers depending on

the age and experience of the mothers, the risk an infant was in, the infant's sex, quality

and quantity of available milk and the mother's physiological health (Fairbanks, 1996).

Anxious or protective mothers generally held back their infants from early exploration of

their social and physical world (Fairbanks, 1996). Developing infants used their mothers

as a safe place when they begin to take excursions outside of the mother's reach

(Fairbanks, 1996). Fairbanks (1996) suggested that each primate mother responds

individually to mothering challenges. All monkey mother-infant dyads participate in

interactions, and these interactions need to be presented in a range to investigate

individual maternal differences (Hinde & Simpson, 1975).

Mother-Infant Interactions in Other Macaque Species

According to Thierry's (2004) macaque social grade-level, *Macaca nemestrina*

are similar to *M. fascicularis* in their patterns of aggression and reconciliation. *M.*

nemestrina and *M. fasicularis* are socially similar species that would be expected to show

corresponding mother-infant interaction patterns. As individually-housed longtail infants

age, body contact between mother and infant, mother holding and infant sucking

decrease, while mothers show an increase in aggression towards their infants (Nakamichi,

Cho, & Minami, 1990). These authors also found that macaque infants raised in social

groups were characterized by a gradual decrease in time spent in body contact with the

mother in the first few months of infant life, while mothers were responsible for

maintaining contact and proximity during that time (Nakamichi et al. 1990).

According to Caldecott's (1986b) macaque social grade-system, pigtail macaques are more similar to Japanese macaques (*M. fuscata*), rhesus macaques (*M. mulatta*) and lion-tailed macaques (*M. silenus*), than they are to other species in this genus, so there may be similarities in maternal styles across these four taxa. In a Japanese macaque captive study, researchers found that mother age and matriline size were two crucial components affecting the quality of the mother-infant relationship (Schino, D'Amato, & Troisi, 1995). Older mothers were not as protective of infants and mothers within larger matrilines and showed a greater tendency to reject infants (Schino et al., 1995). In rhesus macaques, mothers initiated mutual gaze more frequently early in an infant's life, and then the infant was seen to initiate mutual gaze after being 'taught' to do so by their mothers (Dettmer, Kaburu, Byers, Murphy, Soneson, Wooddell & Suomi, 2016). In a comparison of free-ranging and captive rhesus macaque mother-infant pairs, small differences in protective behaviors may be attributed to the different environments and not the differences between infants (Berman, 1980). Captive mothers were found to be more protective with less encouragement of infant independence than their free-ranging counterparts (Berman, 1980). In both free-ranging and captive environments, rhesus macaque mothers maintained contact and proximity to infants in the early stages of infant development (Berman, 1980). Gradually, the mother-infant pair spent more time out of contact, until at a certain point the infant was primarily responsible for maintaining contact and proximity to the mother, with an increase in maternal rejections (Berman, 1980). After several years, the captive rhesus macaque mother-infant interactions shifted toward the patterns seen in free-ranging mother-infant interactions in terms of less mother responsibility in maintaining proximity to their infants (Berman, 1980). In a separate

free-ranging rhesus macaque study, differences in maternal interactions related to proximity and contact with infants suggested individual variation in maternal styles (Berman, 1990). The merging of maternal characteristics (e.g., dominance rank, parity), infant characteristics (e.g., age, activity levels) and the surrounding environment (e.g., stress and support from other group members) can account for most variation in mothering styles (Maestripieri, Hoffman, Anderson, Carter & Higley, 2009). Rhesus macaque infants generally play with other group infants when they are not in contact with their mothers, which shows social play and mother-infant body contact as competing variables in an infant's time budget (de Jonge, Dienske, Luxemburg & Ribbens, 1981). In rhesus macaque mother-infant dyads, both individuals are considered social partners. Each partner has a distinct role, such as controlling the amount of time spent in contact or at certain distances from each other. The behavior of both partners must be observed in order to investigate variables influencing durations of time spent in proximity (Brown, 2001).

Some studies were designed to compare pigtail macaque mother-infant behaviors to those of other macaque species. Kaufman & Rosenblum's (1969) study of pigtail and bonnet macaques (*M. radiata*) showed infants of both species initiated breaks in contact early in their lives. Mother and infant behaviors were collected separately and scored to reveal the progression of mother-infant interactions over 15 months. One figure (Kaufman & Rosenblum, 1969 Fig. 17, p.50) showed a distinct drop in time of maximum separation bouts in pigtail macaques, while the bonnet macaques seemed to remain at a constant maximum time. In another study, Rosenblum & Kaufman (1968) focused on maternal permissive behaviors in bonnet and pigtail macaques. Their results highlighted

physical contact as a critical component to the dyadic mother-infant social relationship (Rosenblum & Kaufman, 1968). Bonnet macaques spent a significant amount of time in contact with other members in their group, while pigtail macaques were not in physical contact with each other except to engage in grooming and mating (Rosenblum & Kaufman, 1968). Varying contact patterns in adult pigtail and bonnet macaques may greatly influence the mother-infant dyadic relationship and by extension, the development of the infant (Rosenblum & Kaufman, 1968). In a mother-infant study comparing pigtail, stumptail (*M. arctoides*) and rhesus macaques, Maestripieri (1994) found that pigtail macaque mother-infant pairs spent more time in contact than did rhesus and stumptail pairs. Additionally, pigtail macaque mother-infant pairs showed a gradual decrease over the weeks in the percentage time spent in contact (Maestripieri, 1994). Pigtail macaque mothers were more protective than rhesus macaque mothers and did not encourage infant independence as much as rhesus macaque mothers did (Maestripieri, 1994). Mother scratching was a common behavior seen across all three species, which has been attributed to maternal anxiety and is seen across several macaque species (Maestripieri, 1994). In all three species, the rate of mother scratching while the infant was away decreased as the infant aged (Maestripieri, 1994). The high protectiveness seen in pigtail macaque mothers as compared to rhesus macaque mothers may be related to the rate of infant development and the infant's vulnerability in its environment (Maestripieri, 1994).

Mother-Infant Pigtail Macaque Interactions

There are few captive or field studies of mother-infant interactions in pigtail macaques. In captivity, interindividual variability in mothering styles occurs 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 pigtail macaque mothering style (Maestripieri, 1998). Captive pigtail mothers affiliated more with their infants if the mothers are experiencing hostility from other group members (Maestripieri, 1998). Upon attempts to force separation from their mothers, captive pigtail infants were extremely vocal and clung to the mothers (Jensen & Tolman, 1962). Once reunited, all signs of stress and vocalizations ceased (Jensen & Tolman, 1962). Mothers' behaviors are influenced by the needs of the individual infants (Jensen & Tolman, 1962). Separation increased infant-directed behavior of the mother, and the infant decreased displacement from the mother more during the beginning of the reunion (Jensen & Tolman, 1962). Mother-infant separation led to more differences in infants' physiology and sleep patterns than did peer separation (Boccia, Reite, Kaemingk, Held & Lauenslager, 1989). Captive pigtail macaque mothers showed no differences in vocalization count whether in communication with their own infant or a non-offspring infant (Simons & Bielert, 1973). Mothers initiated the LEN face of pigtail macaques when there was an increase in distance between their infants (Maestripieri, 1996b). 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, 1996b).

Mother-infant pigtail macaque behavioral studies have only been conducted in captive settings. I hypothesized that wild pigtail macaque mother and infant behaviors would change as infant age increased. To test the hypothesis, I made the following predictions:

1. As infant age increases, the amount of permissive behaviors seen from an infant's mother will increase.

2. As infant age increases, time spent in contact with the infant will decrease.

3. Mothers are expected to have varying frequencies of permissive behavior over time, but I predict that permissive behaviors will follow general dominance rank (decrease with rank) and parity trends (decrease with successful offspring) within the study group.

4. As infant age increases, time spent in contact with the mother decreases.

5. As infant age increases, the frequency of mother-directed vocalizations decreases.

6. Infants will have varying amounts of contact duration with their mothers as they age, but I predict that contact time will follow dominance rank and parity trends within the study group.

7. Responsibility for maintaining proximity and contact within the mother-infant dyad will shift from mother to infant as infants age.

8. As infant age increases, group-member proximity to mothers will increase.

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CHAPTER III

METHODS

Study Site

This study took place from April 3, 2016 to September 10, 2016 in the Segari

Melintang Forest Reserve, Perak, Peninsular Malaysia. The forest reserve is

approximately 2,720 ha (Ruppert, 2014). The reserve consists of coastal lowland mixed

dipterocarp forest and freshwater swamp forest zones (Ruppert, 2014). The climate is

fairly stable but is heavily influenced by the northeast monsoon (Ruppert, 2014). The

field site gets an average rainfall of 1,881mm and has an average temperature of 26.8°C

(Ruppert, 2014). The forest is surrounded by oil palm (*Elaeis guineensis*) plantations,

rural settlements and secondary forest (Ruppert, 2014).

Study Subjects

This study group of pigtail macaques (*Macaca nemestrina*), Group "Amy", has

been habituated since November 2014 (Gisbrecht, 2015). All of the individuals in the

group are known and can be separated into age/sex classes using distinguishable physical

characteristics including body size, hair coloration, stage of sexual swellings (females

only), visible presence of testes (males only), canine teeth sizes (males only) and nipple

statuses (females only) as described by Gisbrecht (2015). During the study period, there

were 17 adult females, 10 adult males, nine juveniles and five to six infants within the

study group. I collected focal data on six mothers (Anna, Brienne, Emma, Goldie, Renate

and Sandra) and their six associated 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 used (Gisbrecht, 2015).

Study Ethograms

Through the combination and modification of several published behavioral

ethograms focused on *Macaca nemestrina* and other related macaque species, I

developed two ethograms (one mother-specific, one infant-specific). These ethograms

(see Tables 1 and 2) together describe all mother-infant interactions seen in free-ranging

M. nemestrina mother-infant relationships. The list of mother behaviors includes

permissive behaviors initiated by the mother and affiliative contact/non-contact

behaviors. The infant ethogram has affiliative contact/non-contact behaviors and a

vocalization common to infants separated from their mothers. Each ethogram includes the

LEN face and vocalizations that have been observed from both infants and mothers. The

mother-infant dyads encountered other group members, so proximities (in contact, within

1 m, and 1 m and 5 m) of group-members to the mother-infant dyad were recorded.

Table 1

Mother Ethogram

Behavior	Behavior Code	Definition
Ventral contact	mv	Mother is seated with infant in ventral-ventral contact (4)
Grooming	g	Inspecting or brushing aside fur using one or two hands (3)
Foraging	fo	Mother is actively searching for food while infant is physically separated (4)
Ventral contact with cradle	mcc	Mother is seated with infant in ventral-ventral contact while also holding infant with hands and/or arms (4)
Ventral contact with grooming	mvg	Mother is seated with infant in ventral-ventral contact with grooming (3,4)
Ventral contact with foraging	mvfo	Mother is seated with infant in ventral-ventral contact while foraging
Mother approach	ma	Mother initiates a decrease in the distance between mother and infant (3,4)
Mother leaves vertically	mlv	Mother initiates an increase in the distance between mother and infant in the vertical plane (2,4)

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Table 1 (continued)

Behavior	Behavior Code	Definition
Mother leaves horizontally	mlh	Mother initiates an increase in the distance between mother and infant in the horizontal plane (2,4)
Within proximity	wp	Mother is within proximity to infant (within arm's reach) but physically separated (2)
Out of proximity	oop	Mother is not within arm's reach of infant, mother and infant are separated (2)
LEN	fu	Mother makes LEN face, directed at infant (1)
Play	fp	Playful actions with other group members (4)
Restrain	ir	Mother prevents infant from moving away by holding its limb or tail (3,4)
Bite	ab	Mother bites infant in punitive fashion, not grooming (2)
Rejection	rj	Mother denies physical contact with infant (3,4)
Nipple Removal	iw	Mother removes nipple from infant's mouth while feeding (2)
Weaning Contact Deterrence	id	Mother does not allow infant to reach a nipple with its mouth i.e. blocking nipple (2)
Scratching	ys	Repeated movement of the hand or foot where the finger/toe-tips rub the fur and skin (3)
Retrieval due to group movement	rgm	Mother retrieves infant in order to move with the group (2)
Retrieval due to danger	rd	Mother retrieves infant and places ventrally in reaction to a perceived social or physical danger to the infant by the mother (2)
Cling carriage	cc	Mother actively grasps and supports infant in the ventral-ventral position while in locomotion (2)
Passive carriage	pc	Mother is in locomotion with the infant in ventral-ventral position, but is not actively holding the infant (2)
Groan vocalization	moo	Mother is physically separated from infant and vocalizes a "Moo" sound directed at the infant (1)
Harsh bark	hb	Mother vocalizes a short bark directed at the infant (1)
Out of Sight	oos	Mother is not within observer's view
Other	o	Any behavior that the mother presents but is not listed in the ethogram

Sources: 1.Bobbitt, Jensen, & Gordon, 1964, pp. 73-75, 2.Kaufman & Rosenblum, 1969, pp. 44-46, 3.Maestripieri, 1994, pp. 79-80, 4.Schino et al., 1995, p. 153

Table 2

Infant Ethogram

Behavior	Behavior Code	Definition
Ventral contact with cling	ic	Infant is in contact with the mother ventrally using all four limbs with the head close to her chest (2)
Ventral contact with hold	io	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	g	Inspecting or brushing aside mother's fur using one or two hands (3)
LEN	fu	Infant makes LEN face, directed at mother (1)
Play	fp	Playful actions with other group members (2,4)
Infant Approach	ia	Infant initiates a decrease in the distance between mother and infant (4)
Infant leaves vertically	ilv	Infant initiates an increase in the distance between mother and infant in the vertical plane (2)
Infant leaves horizontally	ilh	Infant initiates an increase in the distance between mother and infant in the horizontal plane (2)
Scratching	ys	Repeated movement of the hand or foot where the finger/toe-tips rub the fur and skin (3)
Within proximity	wp	Infant is within proximity to mother (within arm's reach), but physically separated (2)
Out of proximity	oop	Infant is not within arm's reach of mother, mother and infant are physically separated (2)
Coo vocalization	coo	Infant is physically separated from the mother and vocalizes a "coo" sound directed at the mother (1)
Out of Sight	oos	Infant is not within observer's view
Other	o	Any behavior that the infant presents but is not listed in the ethogram

Sources: 1.Bobbitt, Jensen, & Gordon, 1964, pp. 73-75, 2.Kaufman & Rosenblum, 1969, pp. 44-46, 3.Maestripieri, 1994, pp. 79-80, 4.Schino et al., 1995, p. 153

Sampling Methods

Once I familiarized myself with the study subjects, I scored the dominance rank status of each female adult macaque within the study group through a tally of agonistic interactions and their outcomes. I then assigned a David's Score value (Gammell , Vries, Jennings, Carlin & Hayden, 2003) to each adult female in the study group. Mothers were

assigned to parity groups by their number of successful births since data was first recorded for the study group individuals during my study period. I used focal animal sampling (Altmann, 1974) to record the mother-infant behavioral occurrences during focal animal samples. I collected focal samples daily, between 0700 hr and 1900 hr, for a duration of 30 min per focal individual with a five-minute break between samples to give myself a rest period and time to find the next focal individual. I randomized the mothers and infants during the study period into a combined sequence, which I edited as the study progressed to account for infant births. I randomized the sequence using a random sequence generator. Subsequent sequences were generated upon completion of the previous sequence. I observed all focal subjects before randomizing the sequence again. If a focal subject could not be found after five minutes, I moved on to the next subject in the random sequence list. I then tried to find the missed monkey for at least five minutes before continuing the sequence.

I recorded frequencies and durations of both mother and infant behaviors on an iPad mini in the field, using an animal behavior application (Animal Behaviour Pro). The ethogram behaviors described in the previous section were programmed in the application and used to categorize behavior frequencies and durations in focal samples. I titled each focal sample with the date and subject's name to make it easy to locate each sample. Once a week, my data were added to the project database, which is located on an external hard-drive and cloud storage.

I assessed inter-observer reliability with each of my co-workers before the start of formal data collection with a value of reliability of at least 0.85 for animal identity. For coefficients of reliability below 0.85, observers were given more instruction from me or

practice time until the coefficient was met (Campbell, Crofoot, MacKinnon, & Stumpf, 2011; Martin & Bateson, 2007). I assessed ethogram behaviors using a pre-recorded video focal of a mother pigtail and scored the video at the beginning of the observation period and then once for each subsequent month. Intra-observer reliability with ethogram behaviors were never below 78% (78%, 85%, 94%, 92%).   It is also important to note that none of my data was collected through video observations, but this was the only way to check intra-observer reliability.

Analysis

Using R 3.3.2 (R Core Team, 2016) in R-Studio 1.0.136 (R Studio, 2016), I tested each prediction using various statistical and graphical methods, examining variables such as contact duration, permissive behavior, mother-directed vocalizations, rank parity, self-directed behavior, proximity and infant age. I considered alpha values (p) less than .05 significant and all analysis was conducted under the assumptions of two-tailed tests where relevant.

Mother Perspective.

The null hypotheses for the correlation tests were that there was no change in permissive behavior over time and that there was no change in contact duration over time. I used two Spearman's rank correlation tests to test the prediction of whether mother permissive behavior and mother-infant contact time was associated with infant age. The null hypothesis for the mother-related GLMM was that there was no significant effect from any of the variables to predict mother permissive behavior. I created a GLMM to test the prediction that mother permissive behavior will decrease as dominance rank decreases and decrease as mothers have more successful offspring. I used the lme4

package (Bates, Maechler, Boler & Walker, 2015), EloRating package (Neumann & Kulik, 2014) and the ggplot2 package (Wickham, 2009) to assess the variables of rank, parity, self-directed behavior and infant age as predictors of mother permissive behavior.

Infant Perspective.

The null hypotheses were that there was no change in contact duration over time and that there was no change in mother-directed vocalizations over time. I used two Spearman's rank correlation tests to test the prediction of whether mother-infant contact time and mother-directed vocalizations were associated with infant age. The null hypothesis for the infant-related GLMM was that there was no significant effect from any of the variables to predict mother-infant contact time. I created a GLMM to test the prediction that from the infant's perspective, mother-infant contact duration would increase with maternal dominance rank and decrease with maternal experience (parity). I used the lme4 package (Bates, Maechler, Boler & Walker, 2015), EloRating package (Neumann & Kulik, 2014) and the ggplot2 package (Wickham, 2009) to assess the variables of rank, parity, self-directed behavior and infant age against mother-infant contact duration.

Proximity.

I used a combination of the Hinde index (Hinde & Simpson,1975) and modified Hinde index (Brown, 2001) to measure the responsibility infants and mothers take for changes in proximity as the infant developed. The null hypothesis was that there would be no change in the indices over time. I constructed line graphs to determine changes of proximity responsibility in both mothers and infants. The null hypothesis for group-member proximity was that there would be no significant change in group-member

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frequency as infant age increased. I analyzed group-member proximity relative to the mothers within one meter and more than one but less than five meters using Spearman's rank correlations to test the prediction that as infant age increases, group-member proximity to mothers will increase. I separated group-members into three classes: male, female and juvenile. I weighted each class to create an accurate proportion relative to group size.

CHAPTER IV

RESULTS

I conducted this study over a span of 158 days at the field site in Perak, Peninsular Malaysia, with 96 days of focal observations. Each focal period was 30 min per individual, and I sampled group mothers, infants and adult females. Due to the staggered births within the sampling period, the sample sizes for each of the analyzed groups changed over time. I observed mothers for a total of 3,270 min ($N = 4\text{-}6$ mothers). I observed infants (less than a year old at the beginning of the focal observation period) for a total of 2,880 min ($N = 4\text{-}6$ infants). A total of $N = 19$ adult females were present throughout the entire study period, and I observed them for a total of 2,850 min.

I ran a chi-square goodness-of-fit test to test whether my observation times were evenly distributed across mothers, with the result of $\chi^2(5, N = 6) = 1.33$, $p > .05$, which means the total observation time was evenly distributed across mothers. I ran a chi-square goodness-of-fit test to test for total observation time (minutes) between group infants, with the result of $\chi^2(5, N = 6) = 210.08$, $p < .05$, which showed an uneven distribution in total observation time across infants. A late birth during the study period led to an uneven time distribution for infants, so only one infant did not receive the same observation time. I ran a chi-square goodness-of-fit test to test for total observation time (minutes) between all group adult females, with the result of $\chi^2(18, N = 19) = 3.84$, $p > .05$, which showed an even distribution in observation time across all adult females.

I compiled a table of mothers with associated infants and the categorical variables that I assessed in the GLMMs (Table 3).

Table 3

Female Dominance Rank in Descending Order and Parity Categories in Mothers and

Infants

Mothers	Infants	David Score Value	Parity Category
Anna	Anaconda	31	1
Goldie	Gollum	19	2
Emma	Emanuel	0	2
Sandra	Sausage	-4	2
Renate	Reggie	-4	1
Brienne	Brandy	-9	2

Reliability

To test intra-observer reliability, I scored the same focal video (30 min duration of one of the mothers) at the start of the observation period and every subsequent month throughout the study period. I compared the number of matches for focal animal behavior and ethogram behavior, and my agreement was never less than 62% and never decreased across the observation period. I conducted inter-reliability testing of animal identities every month with the help of project volunteers who had been studying the monkeys for at least one month. Our inter-reliability scores for animal identification were 94%, 97%, 100%, 94%, 100%.

Analyses Conducted from Each Mother's Perspective

I used a Spearman's rank correlation coefficient test to test the prediction that as infants age, the number of permissive behaviors from the infant's mother will increase. The result showed a significant negative correlation $r(5) = -.391, p = < .05$; Figure 1A. I

used a Spearman's rank correlation coefficient test to test the prediction that as infant age increases, the mother's amount of physical contact with the infant will decrease. The result showed a significant negative correlation $r(5) = -.735, p = < .05$; Figure 1B.

I constructed a GLMM to test the prediction that mother permissive behavior was predicted by mother dominance rank, parity, self-directed scratching and infant age. I designated mothers ($N = 6$) as a random effect to take into account inter-individual differences. I transformed permissive behavior frequencies to a binomial distribution in order to incorporate a large number of zero-occurrences. The mother permissive behaviors decreased significantly with increasing age of their offspring (GLMM, $-.006 \pm$ SE .003, $z = -1.978, p < .05$; Table 4).

Analyses Conducted from Each Infant's Perspective

I used a Spearman's rank correlation coefficient test to test the prediction that as infant age increases, the duration of mother-infant contact time from the infant's perspective will decrease. The result showed a significant negative correlation $r(5) = -.733, p = < .05$; Figure 2A. I used a Spearman's rank correlation coefficient test to test the prediction that as infant age increases, the frequency of vocalizations from the infant directed toward her or his mother would decrease. The result showed no linear relationship between the variables and was not significant $r(5) = -.054, p = >.05$; Figure 2B.
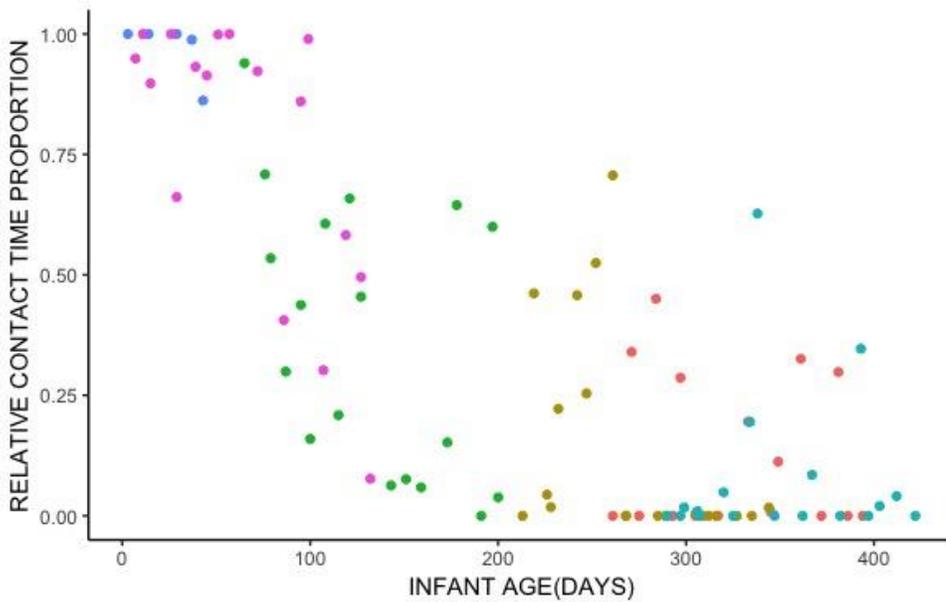
A.
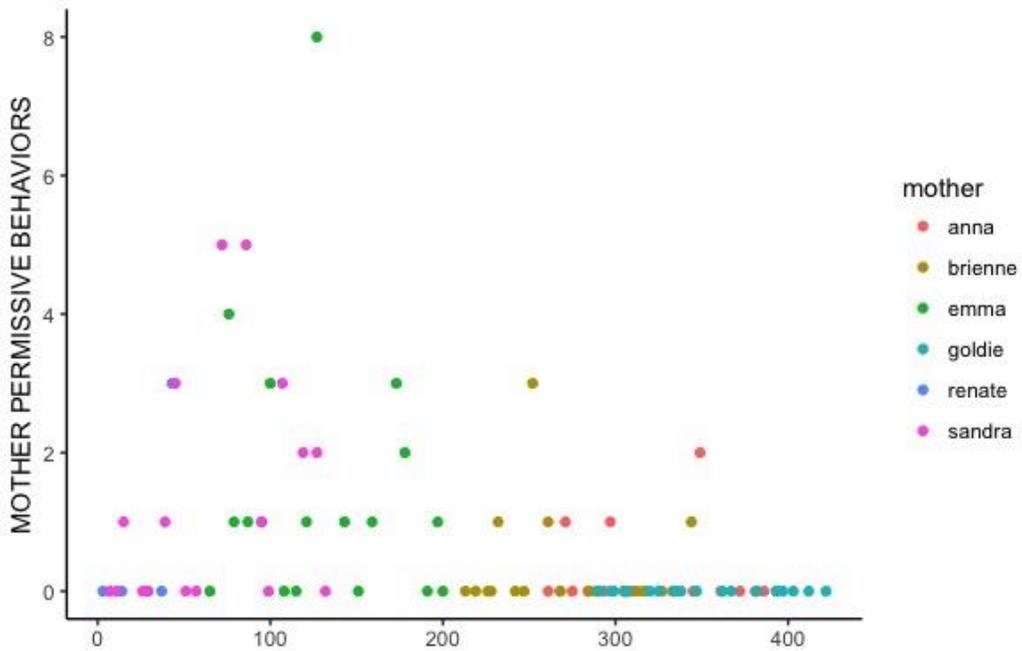
B.

Figure 1. Mother perspective correlations. A) Correlation plot of maternal permissive behaviors and infant age. B) Correlation plot of mother-infant contact time from the mother's perspective and infant age.

I conducted a GLMM to test the prediction that mother-infant contact time (from each infant's perspective) could be predicted through mother dominance rank, mother parity, infant self-directed scratching and infant age. I designated the infants ($N = 6$) as a random effect to take into account any differences seen between individuals. I transformed the response variable using log+1 and then distributed the contact times into categories. The relative mother-infant contact duration per focal decreased significantly with increasing age of the offspring (GLMM, -.005 ± SE .001, z = -9.066, $p < .05$; Table 5).

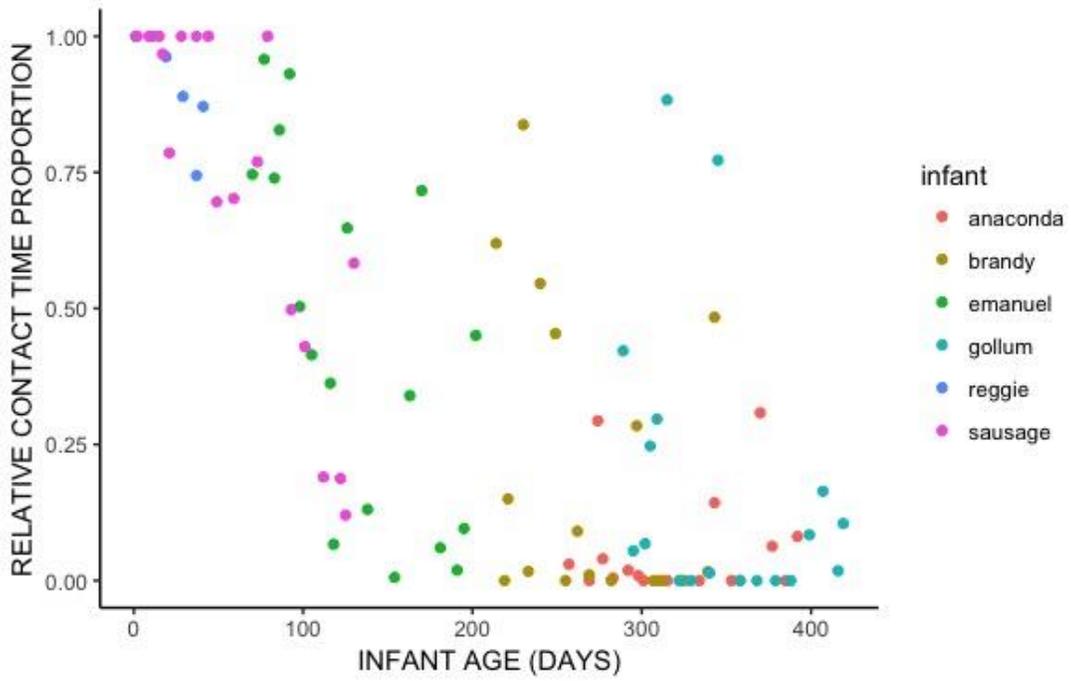**Table 4**

GLMM-Mother Perspective and Permissive Behavior

Predictor variable	Estimate	SE	z-value	p (>|z|)
Intercept	-1.104	1.783	-0.620	.536
Rank	-0.006	0.041	-0.142	.887
Parity	0.715	1.037	0.689	.491
SDB	0.098	0.143	0.683	.495
Infant Age	-0.006	0.004	-1.498	.134
Best Fit Model				
Intercept	0.241	0.781	0.309	.757
Infant Age	**-0.006**	**0.003**	**-1.978**	**.048**

Notes. Table shows initial model and best-fit model after subtracting non-significant variables. Bold lettering indicates significance at $p < .05$.

A.

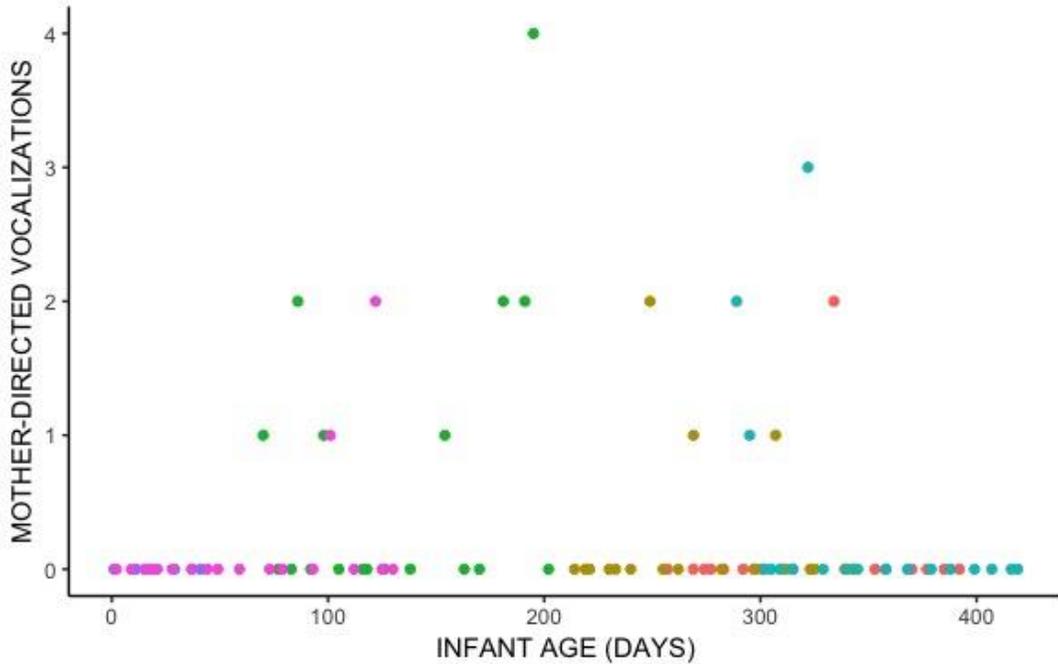B.

Figure 2. Infant perspective correlations. A) Correlation plot of relative contact time from the infant's perspective, based on infant age. B) Correlation plot of infants' mother-directed vocalizations and infant age.

Table 5

GLMM-Infant Perspective and Relative Contact Time

Predictor variable	Estimate	SE	z-value	$p(>|z|)$
Intercept	**1.675**	**.300**	**5.589**	**2.29E-08**
Rank	0.001	.008	0.127	.899
Parity	0.226	.170	1.326	.185
SDB	-0.078	.057	-1.357	.175
Infant Age	**-0.005**	**.001**	**-7.386**	**1.51E-13**
Best Fit Model				
Intercept	**2.071**	**.089**	**23.300**	**<2E-16**
SDB	-0.081	.056	-1.431	.152
Infant Age	**-0.005**	**.001**	**-9.066**	**<2E-16**

Notes. Table shows initial model and best-fit model after subtracting non-significant variables. Bold lettering indicates significance at *p* < .05.

Proximity

Figure 3A shows pigtail mothers' (*N* = 6) Hinde values based on their infants' ages. The X-axes have different ranges due to the age of each associated infant within the observation period. Figure 3B combines all of the individual mothers into one scatterplot to discern any generalizations within the observed individuals (*N* = 6). Figure 3C uses the same plot as Figure 3B for the Hinde index, but also includes the Brown index per focal individual, which I used to determine the total percentage of changes in proximity that resulted from infant movement. From the time period of 100 to 350 days of infant age, the Hinde index in four of the six observed mothers showed the infant as responsible for a greater proportion of contacts broken. I did not run correlations or other statistical tests for these figures.
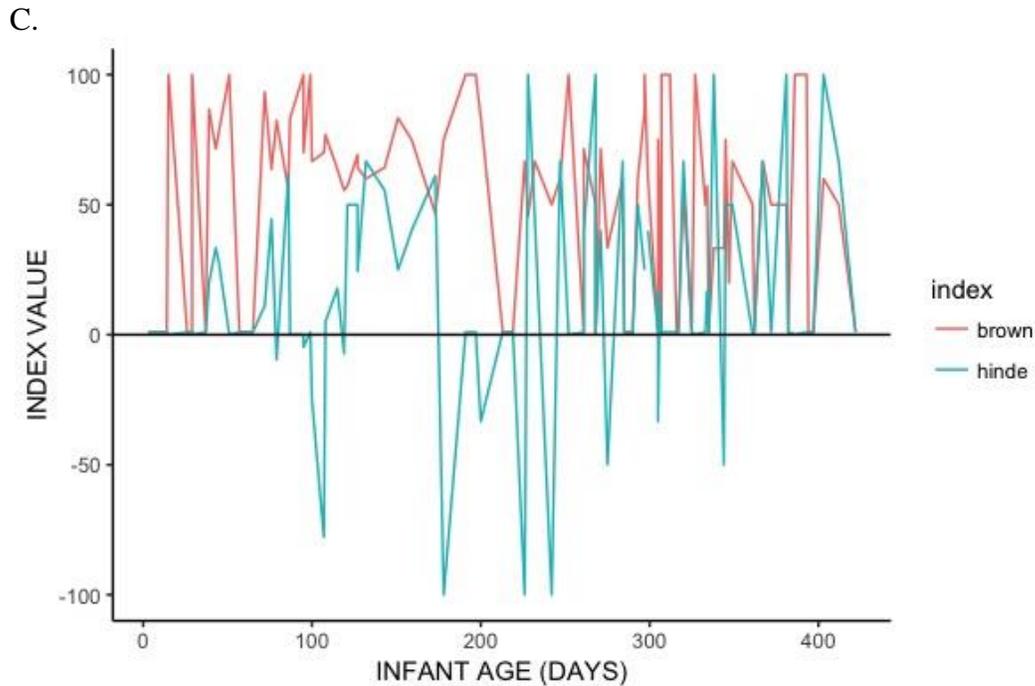
A.

B.

C.
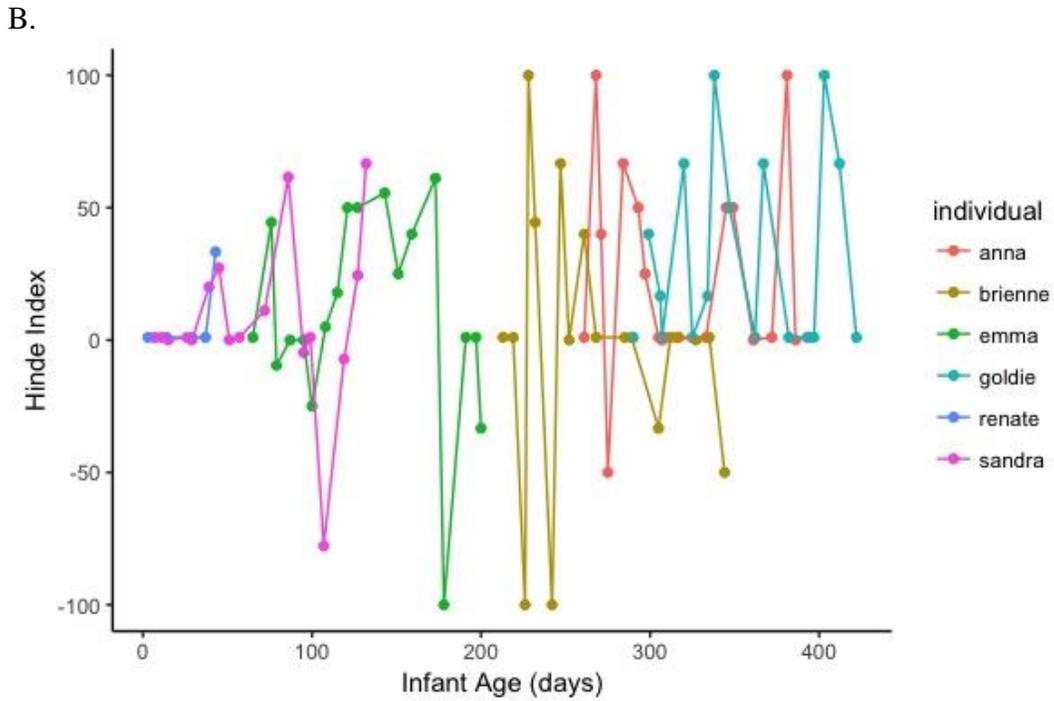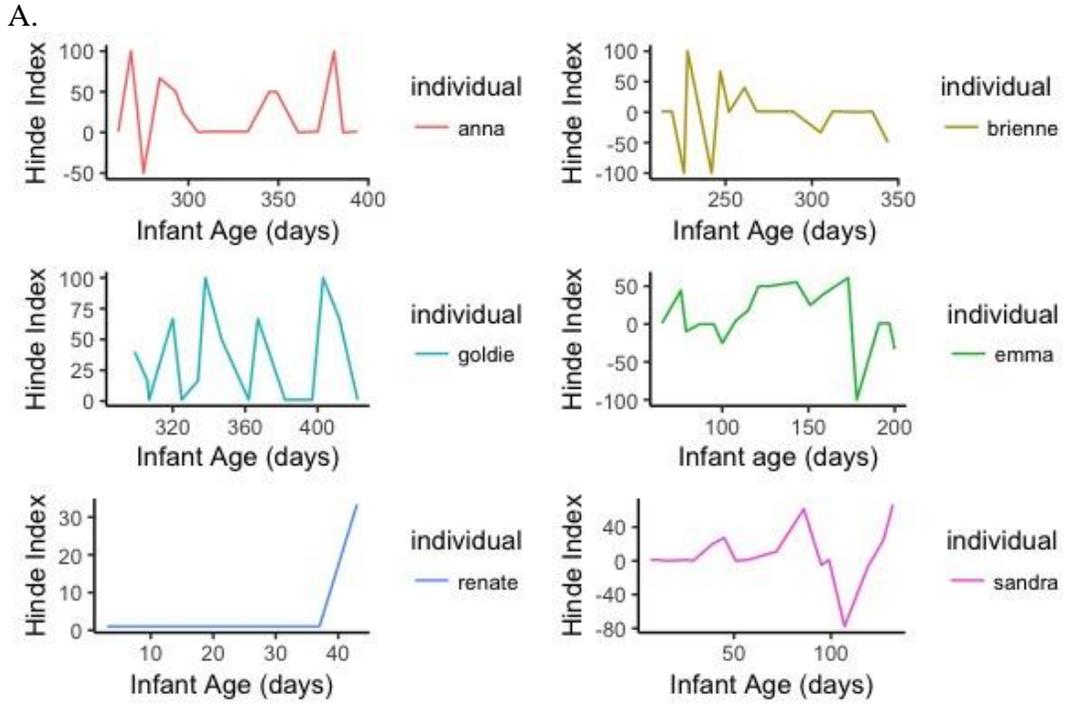
Figure 3. Proximity graphs. A) Each mother's Hinde line graphs. B) Combined mothers' Hinde graphs. C) Hinde (range = -100 to 100) and Brown (range = 0-100) line graph to show proximity responsibility of mother and infant over time.

I used Spearman's rank correlation coefficient tests to test the prediction that as infant age increases, the frequency of group-members from three age/sex classes will increase at both 1m and 5m proximities. The results showed no correlations at 1m: male $r(5) = .101$, $p = > .05$; Figure 4A, female $r(5) = -.155$, $p = > .05$; Figure 4A and juvenile $r(5) = -.156$, $p = > .05$; Figure 4A. The results showed significant correlations in the 1 m to 5 m proximity for adult females $r(5) = .278$, $p = < .05$; Figure 4B and juveniles $r(5) = .274$, $p = < .05$; Figure 4B. The correlation for adult males was close to significant: $r(5) = .197$, $p = .055$; Figure 4B.
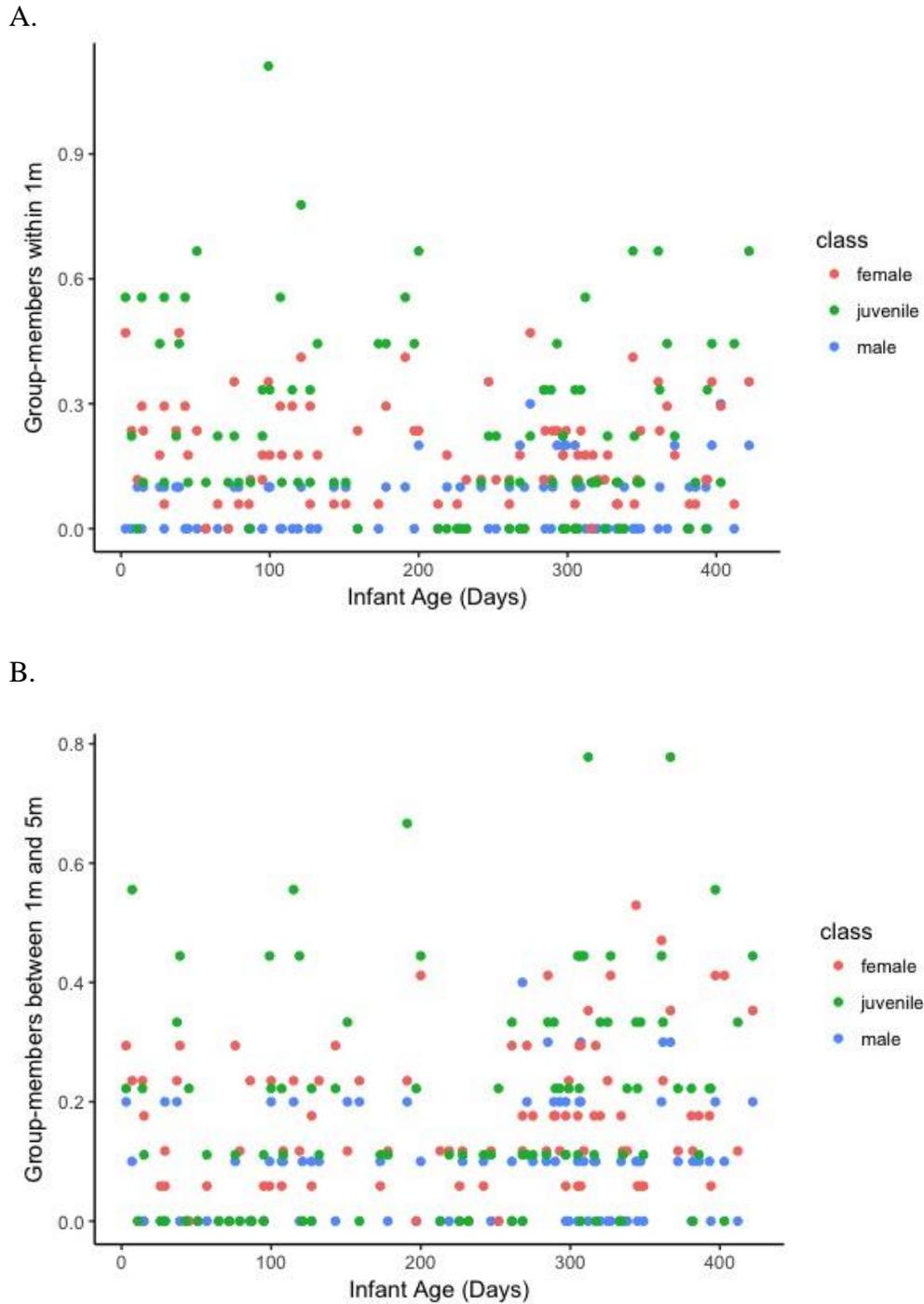
A.

B.

Figure 4. Group-member proximity correlations. A) Scatterplot of adult male, adult female, and juvenile frequency at 1 m plotted against infant age. B) Scatterplot of adult male, adult female, and juvenile frequency at 1 m to 5 m plotted against infant age.

CHAPTER V

DISCUSSION

Mother Perspective

I aimed to explore the mother/infant relationship from the perspective of each

social partner. The mother perspective is the most common of the two perspectives

throughout mother-infant studies. My prediction that as an infant ages, the frequency of

her or his mother's permissive behaviors would increase was not supported by the results

of Spearman's rank correlation tests. Rosenblum and Kaufman (1968) noted that captive

pigtail macaque mothers in their study showed more permissive behavior than did bonnet

macaque mothers. In pigtail macaque mothers, permissive behaviors increased after the

infant reached three weeks of age, regardless of whether the mother was responsible for

maintaining or preventing proximity. In my study, I instead found a negative relationship

between mother permissive behavior and infant age. In another Spearman's rank

correlation test, I found support for my prediction that as infant age increases, the

duration of mother-infant contact time decreases. Maestripieri (1994) found that captive

pigtail mother-infant pairs showed a gradual decrease in percent time spent in contact, a

finding that corresponds to the results in my study. In my dataset, the relationship

between contact duration and infant age is stronger than the relationship between mother

permissive behavior and infant age. As the infants in my study group aged, they spent

less time in contact with their mothers. Captive pigtail macaque mothers were found to

initiate the LEN face when there was an increase in distance with the infant (Maestripieri,

1996b). This species-specific behavior was rarely seen throughout the observation period

and was not used for analysis. The slight decrease in mother permissive frequency I

observed might be explained by the small sample size and my inability to collect data on the infants during the same developmental periods, because infants were born at different times across the duration of my study.

I predicted that the lower ranked mothers in my study group would be more protective of their infants because of Thierry's (2004) placement of this species in grade two of his four-grade scale. Thierry (2000) and McKenna (1979) both attributed variation in quality of maternal care to infants varying in the degree of protection they needed based on their social environment. I created a GLMM to test my prediction that mothers' permissive behavior would decrease with rank and with parity. This prediction was not supported by my data. Infant age was the only significant variable that could be used to predict mother permissive behavior. In captivity, primiparous pigtail macaque mothers often neglect their firstborn (Maestripieri et al., 1997), so I expected that parity would be a predictor of mother permissive behavior. Since most of the previous mother-infant pigtail macaque studies are captive-based subjects, this variable may be more noticeable in captive populations instead of wild populations. In the GLMM model, there was not a strong correlation between mother dominance rank and mother permissive behavior. Self-directed behavior (scratching) was used as a predictor variable to assess maternal anxiety when the infant was separated from the mother. This was a common behavior seen in past captive studies (Maestripieri, 1994), and also common in the wild study group.

Although the study group is free-ranging, adult group members do not have many predation or survival pressures. Infants do have increased survival pressures. It was surprising to see a significant negative correlation between infant age and mother permissive behavior, especially in a free-ranging context. It is noteworthy that during my

study, there was a male dominance hierarchy shift. The alpha and beta males both left the study group, and new alpha and beta males moved in just before I began data collection. This sharp turnover in the male dominance hierarchy may have influenced the female dominance hierarchy and even the behaviors of the mothers. At the time of the male dominance shift, a mother-infant dyad within the study group went missing. Adult females trying to develop relationships with the new dominant males may explain the decline in mother permissive behavior.

Infant Perspective

Usually, studies only observe mother interactions, but I also recorded behavioral observations from the infant's perspective to get the full picture of mother-infant contact. I used Spearman's rank correlation to test the prediction that as infant age increases, the relative contact time between the dyad and from the infant's perspective would decrease. My prediction was supported, with a significant negative relationship between relative mother-infant contact time and infant age. Even though infants can show variability, these infants all followed a similar pattern with respect to their ages and contact time with mothers. When I ran the same correlations from both mother and infant perspectives, I found significant relationships between mother-infant contact time and age. Maestripieri (1994) also found a gradual decrease in contact time between mother and infant in the captive dyads he studied. I used Spearman's rank correlation to test the prediction that as infant age increases, their mother-directed vocalizations would decrease. I made this prediction because Jensen and Tolman (1962) found that when captive pigtail infants were forced to separate from the mothers, they were extremely vocal. My prediction, however, was not supported, and I found no linear relationship between infant

vocalizations and infant age. I predicted that I would see a decrease in vocalizations as the infants aged and grew more independent. If the infants had moved from the mothers by the infants' choice, I thought there might have been a general decrease in this behavior, as the infants grew more independent. Gouzoules & Gouzoules (1989) also found that pigtail agonistic screams/vocalizations became more fine-tuned with age, which made me think that the infants would learn which calls were most effective and only use those calls if they were in trouble and needed their mother's help. However, my study group was generally quiet and adhered to the pigtail macaque stereotype of rarely vocalizing. There is also a lack of information on mother-directed vocalization variation in pigtail macaques, so this may also attribute to the lack of association between infant age and vocalization in my data.

I created a GLMM to further explore the predictors of mother-infant contact time. I predicted that contact time would decrease with decreasing maternal rank and decreasing parity. Maestripieri (1994) found that captive pigtail macaque mother-infant pairs showed a gradual decrease over weeks in percentage of time infants spent in contact with mothers. Neither of my predictions were supported, and infant age was the only significant variable that I could use to predict contact time duration. I used the same predictor variables as the mother GLMM in order to make better comparisons. Contact patterns can greatly influence the mother-infant dyad and ultimately, infant development (Rosenblum & Kaufman, 1968). In rhesus macaques, Berman (1980) found that mother-infant pairs gradually spent more time out of contact until the point of infant independence. In captive longtail macaques, infants spent less time in body contact with their mothers as they aged (Nakamichi et al., 1990). In vervet monkeys, Fairbanks (1989)

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found mother styles to vary significantly between mothers, with each mother showing different contact patterns with infants. A decrease in body contact time with mothers from the infant's perspective could also mean the infant is favoring play opportunities and eventual social independence from the mother (de Jonge et al., 1981). In my study, I found a gradual decrease in contact duration between mother and infant, but I also found similar contact patterns across the six mothers and their infants relative to infant age.

Proximity

Proximity is a distinct affiliative behavior that indicates mutual preference between animals (Troisi et al., 1989). Infants spend most of their early development after birth either in direct contact or in close proximity to their mothers. In free-ranging and captive macaques, mothers are responsible for maintaining proximity and contact to infants in these early life stages (Berman, 1980; Nakamichi et al., 1990). While the Hinde index does not allow a researcher to say that an individual is more responsible for proximity, Berman (1980) showed that infants play a more dominant role in proximity maintenance within the dyad at a certain point. In my dataset, one mother never had a negative Hinde index value, which also happened to be one of the more dominant females of the group. It is not possible to distinguish a trend between mother dominance rank and the proximity indices I 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 then these data shifted back to infants being responsible for a greater proportion of contacts made after 350 days of infant age using the Hinde index. This period of time showed the most variation in mother-infant contact and proximity behaviors and points to the start of infant independence within this study

group. Pigtail macaque weaning age is 12 months (Sponsel et al., 2002), so the shift in maintaining proximity from mother to infant to mother may correspond to the weaning of the infants.

Rosenblum and Kaufman (1968) found that pigtail mothers were reluctant to socially engage with others after birth. All age classes in my dataset showed an increase in frequency of proximity to the mothers at the 1 m to 5 m range. Aggression in the group can play a significant role in shaping mothering styles (Maestripieri, 1998). At my 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 behaviors. Maestripieri (1998) found that pigtail mothers affiliate more with their infants if they are experiencing hostility by other group members. During times of aggression, mothers kept their infants close and away from other group members. While it is surprising that my study group mothers did not appear to be as careful given the change in male dominance rank at the 1 m to 5 m distance, they did not let very many males enter within 1 m proximity, which indicated a select few males were allowed to be in close proximity.

Conclusion

I found that southern pigtail macaque mothers and infants living in a wild population showed changes in mother-infant interactions over time. Mother permissive and contact behaviors both decreased with increasing infant age. Mothers' ranks and parities were not predictors of mother permissive behavior. As infant age increased, the duration of mother-infant contact time decreased (from the infant's perspective). I found no correlation between infant age and mother-directed vocalizations, and infant contact

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time with the mothers did not follow general 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 5m. More research is needed on the entire dominance rank range of mothers to more thoroughly examine any distinct trends. My study can be used as a foundation for future mother-infant interaction studies at this site and used for comparison with other free-ranging groups of pigtail macaques.

Recommendations for Future Research

For future research, I recommend increasing the duration of the study period and increasing the sample size of mother-infant dyads by integrating other free-ranging pigtail groups. I also recommend using other wild, but habituated southern pigtail macaque groups to conduct better comparisons. Lastly, it would be beneficial to compare my results with other macaque species along the macaque aggression-grade scale to further examine dominance rank and its potential effect on mother-infant interactions.

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