1 First-time rhesus monkey mothers, and mothers of sons, preferentially engage in face-to-face

2 interactions with infants

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12 Short title: Parity, infant sex, and mother-infant interactions

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17 **ABSTRACT**
18
19 Face-to-face interactions between mothers and infants occur in both human and non-human

20 primates, but there is large variability in the occurrence of these behaviors and the reason for this

21 variability remains largely unexplored. Other types of maternal investment have been shown to

22 be dependent on infant sex (e.g., milk production and maternal responsiveness) and maternal

23 experience (e.g., symmetrical communication). Thus, we sought to determine whether

24 variability in face-to-face interactions, i.e., mutual gazing (MG), which are hypothesized to be

25 critical for later socio-cognitive development, could be explained by these variables. We studied

26 31 semi-free ranging rhesus monkey (*Macaca mulatta*) mother-infant dyads (6 primiparous; 13

27 male infants) born and reared at the Laboratory of Comparative Ethology field station at the NIH

28 Animal Center in Poolesville, MD, across the first 90 postnatal days. Infant sex (i.e., male) was a

29 significant predictor of maternal grooming ($\beta\pm SE=0.342\pm0.163$, $z=2.1$, $p=0.036$) whereas both

30 parity (i.e. first time mothers) and infant sex (i.e. male) significantly predicted MG (parity:

31 $\beta\pm SE=-0.744\pm0.217$, $z=-3.43$, $p<0.001$; infant sex: $\beta\pm SE=0.383\pm0.194$, $z=1.97$, $p=0.048$).

32 Separation from the mother (outside of arm's reach) was not influenced by parity or infant sex.

33 Together with existing literature, these findings point toward differential maternal investment for

34 sons vs. daughters. Mothers may be investing more in sons, behaviorally, to ensure their future

35 social competence and thus later reproductive success. Collectively, our findings add to the

36 literature that is beginning to identify early life experiences that may lead to sex differences in

37 neurological and behavioral development.

38

40 **INTRODUCTION**
41
42   Face-to-face interactions between mothers and their newborns are known to occur in

43 human and non-human primates [Blehar et al., 1977; Bard et al., 2005; Ferrari et al., 2009].

44 Studies in humans have suggested that these facial interactions facilitate the development of

45 emotion regulation in infants [Feldman, 2007; Tronick, 1989], increase bonding and closeness

46 between infant and mother [Trevarthen, 1998], improve infants' cognitive skills [Murray et al. ,

47 1996], and influence infants' physiological regulation [Feldman et al. , 2009].However, in these

48 documented cases of face-to-face interactions (e.g., mutual gazing, facial expressions, play),

49 there is often large inter-individual variability in their occurrence. The reasons for this

50 variability remain largely unexplored.

51   Mothers are known to differentially engage with their infants in other ways depending on

52 their own experience as well as their infant's sex. For example, first-time rhesus macaque

53 mothers tend to be more protective of their offspring [Hooley & Simpson, 1981; Schino et al.,

54 1995], show higher anxious behaviors towards their infant [Mitchell & Stevens, 1968], produce

55 milk with higher cortisol, which "programs" later infant temperament [Hinde et al., 2014], and

56 provide their sons with richer milk [Hinde, 2007, 2009]. First-time chimpanzee (*Pan*

57 *troglodytes*) mothers nurse, groom, and play with their infants more than experienced mothers

58 [Stanton et al., 2014]. Similarly, in humans (*Homo sapiens*) first-time mothers engage in more

59 social and caretaking behavior with their first child than with their second child [Jacobs & Moss,

60 1976] and are more likely to maintain symmetrical communication (i.e., mutually coordinated

61 actions) for longer periods of time before transitioning to asymmetrical communication [i.e., one

62 active and one passive partner; Hsu & Fogel, 2003]. In addition, human mothers are more

63 responsive [Lewis, 1972], and engage in more physical play [MacDonald & Parke, 1986] with

64   their sons than with daughters. In chimpanzees, mothers with sons are more gregarious and

65   spend more time in parties containing males compared to mothers of daughters especially in the

66   first six months of life, probably as a way to influence their sons' social environment in a male-

67   bonded society [Murray et al., 2014].

68   A wide variety of studies have demonstrated how variations in mother-infant interactions

69   can influence offspring development at a genetic [reviewed in Meaney, 2001], cognitive [Olson

70   et al., 1986; Murray et al., 1996], physiological [Feldman, 2012] and behavioral level [Mitchell

71   & Stevens, 1968]. For example, pups of high licking/grooming-arched-back nursing (LG-ABN)

72   rat mothers show reduced physiological and behavioral reactivity to stressful situations, and are

73   themselves better mothers than low LG-ABN mothers [Meaney, 2001]. Most of the literature

74   concerns naturally occurring variations in physical aspects of maternal care, yet little is known

75   about the influences of less obvious aspects of care such as face-to-face communication.

76   Given the potential for mother-infant face-to-face communication to also exert

77   downstream socio-cognitive effects, and the fact that other types of mother-infant interaction are

78   experience- and sex-dependent, we tested the hypothesis that these variables would also

79   influence the occurrence of a particularly salient form of face-to-face communication, mutual

80   gazing (MG), in rhesus monkeys (*Macaca mulatta*). In this species, newborns (< 7 days of life)

81   stay in close physical contact with their mother, who carries them ventrally, and tends to protect

82   him/her from other group members. Infants start wandering off their mothers from the second

83   week of life, although locomotor skills reach a good level of development at 6 weeks of life

84   [Lindburg and Rosenblum, 1971]. Although infant rhesus macaques start eating solid food at two

85   weeks of age, it is at about four months that mothers start rejecting infant's attempts to nurse,

86   while full weaning is reached by the birth of the next sibling [Fooden, 2000]. Face-to-face

87   interactions between mother and infants (e.g. mutual gaze) are less intense in the first week of

88   life, while they start becoming more frequent as the infant grows up [Ferrari et al. , 2009]. We

89   predicted that first-time mothers, and mothers of sons, would engage in MG more frequently

90   than experienced (i.e., multiparous) mothers or mothers of daughters. We also compared rates of

91   grooming and mother-infant proximity, which are more hands-on indicators of maternal care, to

92   determine if rates of these behaviors differed based on parity and infant sex. We expected to see

93   consistent decreases in all three behaviors across the first three months of life as infants became

94   more independent of their mothers.

95   **METHODS**

96   **Subjects and housing**

97   Rhesus monkey mother-infant dyads (N=31; n=13 male infants; n=6 primiparous

98   mothers; see Table I) were born and raised at the Laboratory of Comparative Ethology's 5-acre

99   field station at the NIH Animal Center near Poolesville, MD. Dyads were studied in the spring

100   and summer of 2013 and 2014. Mothers ranged in age from 4-16 years (mean$\pm$SEM: 7.6$\pm$0.5),

101   and all infants were carried to term without complications. Twenty-three individual mothers

102   were represented in this sample; thus, five mothers gave birth in 2013 and 2014. This semi-free

103   ranging population of rhesus monkeys has been well characterized [Dettmer et al., 2014, 2015],

104   and a small sample of this population (n=6 dyads) has previously been confirmed to exhibit some

105   of the face-to-face interactions described previously [Ferrari et al., 2009] and studied here.

106   Monkeys were fed twice daily (Purina High Protein Monkey Chow #5038, St. Louis, MO), and

107   given fresh fruit or foraging items (e.g., seeds, nuts) daily. Water was available *ad libitum*.

108   Importantly, mothers and infants were undisturbed for the duration of the study; i.e.,

109   infants were never removed from their mothers. In previous studies of MG in nonhuman

110   primates, infants were routinely separated from their mothers [Ferrari et al., 2009], which may

111   account for at least some of the rates of gazing observed [Bard et al., 2005].

112

113   [Table I here]

114

115   **Social rank**

116   Because dominance status has been associated with aspects of maternal behavior [Schino

117   et al., 1999; Berman, 1992], we quantified each mother's social rank to determine whether high

118   or low social status varied by parity or infant sex. We used Elo-rating [Elo, 1978], a recently

119   proposed method in behavioral research [Neumann et al., 2011], which has several advantages

120   over conventional matrix-based analyses including the ability to detect changes in rank dynamics

121   [Neumann et al., 2011; Wooddell et al., 2015]. A total of 3,567 *ad libitum* [Altmann,1974]

122   agonistic (supplants, threats, chases, attacks) and submissive (fear grimaces) interactions were

123   collected between February 2013 and April 2015. All agonistic interactions between 93

124   individuals in the troop were entered into a database. Using R software (v3.1.2), Elo-ratings were

125   generated after each sequential interaction using the *elo.sequence* function devised by Neumann

126   et al. [2011]. In brief, each individual's initial Elo-rating of 1,000 increased for wins and

127   decreased for losses. The amount of points won or lost in each interaction depended on the

128   expected outcome, so that higher rated individuals obtain, after winning, fewer points (because

129   the expectation of winning is high), than lower-rated individuals whose expectation of winning is

130   low [Neumann et al., 2011]. Therefore, an individual's Elo-rating reflected not only the winning

131   success rate, but also the relative strength of dominated opponents. At the end of the two-year

132   observation period, average Elo-ratings were generated for each of the 23 mothers (range: 524 to

133   1640). A median split (=955) then divided the Elo-ratings into low (N=13) or high (N=13)

134   dominance rank. High-ranking females were those who rarely received agonistic behaviors from

135   others and instead directed much of the agonistic behaviors (thus reflecting higher Elo-ratings),

136   and lower ranking monkeys rarely directed aggressive behaviors, but most often received these

137   behaviors.

138   **Mother-infant interactions**

139   Monkeys were observed by five different observers, who were blind to the aim of the

140   research (as to avoid any bias during data collection), according to previously published

141   procedures for this species [Ferrari et al., 2009]. Focal animal observations [Altmann, 1974]

142   were conducted between 900 and 1700, 1-2 times per day, 5 days per week for the first 30 days

143   of the infant's life; 3 times per week during days 31-60; and once per week during days 61-90.

144   A total of 649 observations were collected (mean$\pm$SEM per focal: 20.9$\pm$0.8). Data collection

145   began only if both the mother and infant had their eyes open and if they were alert [Ferrari et al.,

146   2009]. If the dyad moved out of sight or if the mother or infant fell asleep for more than 50% of

147   the session, the session was aborted. Sessions were 15 minutes long and were coded from the

148   infant's perspective. Frequencies of the following behaviors in each 15-minute session were

149   recorded: gazes (initiated, received, and mutual), lipsmacking (initiated, received, and mutual),

150   grooming (received), and separate from mother (within arm's reach and outside of arm's reach).

151   Each bout (i.e., behavior lasting at least 3 seconds) was recorded once, and the end of a bout

152   occurred when the behavior ceased for 3 or more seconds. For gazing, lipsmacking, and

153   grooming, the social partner (mother, adult female, adult male, juvenile, or infant) was recorded.

154   Table II presents an ethogram for all behaviors.

155   Of the 649 observations, 61 (9.4%) were coded by two or more observers to establish

156   reliability. We calculated Gwet's AC1 coefficient to assess inter-rater reliability [Gwet, 2014]

157   using the function *gwet.ac1.raw* implemented in R 3.1.2. This method is more robust than

158   Cohen's κ, as it is not sensitive to infrequent behaviours (such as MG), which can result in high

159   observed agreement (most probably due to chance, given the high probability of having zeros)

160   but low κ values [Gwet, 2002a; Gwet, 2002b; Gwet, 2014; Wongpakaran et al. , 2013]. Since we

161   aimed to assess the presence of MG, social grooming between mother and infant as well as

162   infant's out of arm's reach (lipsmacking was observed so rarely that it was not included in this

163   dataset), we calculated inter-rater reliability on the basis of the number of bouts each rater

164   observed for each behaviour. We found moderate agreement for grooming (AC1: 0.57, SE:

165   0.068, P < 0.001), substantial agreement for out of arm's reach (AC1: 0.72, SE: 0.062, P <

166   0.001), and almost perfect agreement for MG (AC1: 0.84, SE: 0.051, P < 0.001). In those cases

167   in which instances of MG were recorded by both observers, the agreement on the identity of the

168   initiator of MG (i.e. whether it was the mother or the infant) was almost perfect (AC1: 0.89, SE:

169   0.04, P<0.001).

170

171   [Table II here]

172

173   **Data analysis**

174   In order to determine whether rank should be included in all following analyses, we used

175   chi-square analysis to assess whether social rank (high and low) was evenly distributed across

176   parity (primiparous and multiparous) and infant sex (male and female), and Spearman's rank

177   correlation test to test whether mean rates of mutual gazing (MG), grooming and outside of

178   arm's reach significantly correlated to mother's dominance rank.

179   MG, grooming, and outside of arm's reach of the mother were analyzed for this study.

180   For each behavior, we calculated the mean frequency across three consecutive days in the first 30

181   days of life [Ferrari et al., 2009], then weekly thereafter, resulting in a mean frequency per 15-

182   min session for each dyad for days 0-2, 3-5, 6-8, 9-11, 12-14, 15-17, 18-20, 21-23, 24-26, and

183   27-30, and for weeks 5, 6, 7, 8, 9, 10, 11, and 12.

184   Across the entire study period, average rates of MG, grooming, and outside of arm's

185   reach were calculated for each mother and Spearman correlation was used to determine if the

186   occurrence of these behaviors was correlated. We then assessed whether mean frequencies of

187   these behaviors varied between age groups using a polynomial contrast analysis, with LSD post-

188   hoc test to assess whether adjacent ages significantly differed in the frequencies of those

189   behaviors. In addition, we tested the effects of infant age, infant sex, mother parity and their

190   interactions on the frequency of MG, grooming, and separation from the mother using

191   Generalized Linear Mixed Model analysis (GLMM), in order to account for multiple sampling of

192   the same mother-infant dyads across multiple time points. We used the *glmmadmb* function

193   [Bolker et al. 2012] with Gaussian distribution implemented in R 3.1.2 as this function handles

194   zero-inflated data sets, and we have some days in which mother-infant dyads were not observed

195   engaging in mutual gazing or grooming, or infants were not recorded to be outside of arm's

196   reach. The data were square root transformed to more closely approach a Gaussian distribution.

197   Rates of MG, grooming and outside of arm's reach were entered as dependent variable with

198   continuous distribution while female's parity (binary) and infant's sex (binary), as well as their

199   interactions with age (continuous) set as fixed factors, with both female's and infant's identity

200   included as random factors with crossed structure. Age was entered in these models by assigning

201   to the age groups described above a cardinal number in ascending order from 1 to 18.

202   Analysis of variance (ANOVA) was used to examine the proportion of MG initiated by

203   the mother vs. by the offspring calculated for each dyad in the first 30 days, since MG occurs

204   most frequently in this time (Ferrari et al., 2009; this study: $t_{(460)}=1.99$, P<0.05). This test was

205   completed using parity x sex (e.g., primiparous-male, primiparous-female, multiparous-male,

206   multiparous-female) as the grouping variable to determine the influence of each partner on this

207   behavior. This analysis was first run with the 31 original subjects, then with the three newer

208   mothers included.

209   This research adhered to the American Society of Primatologists principles for the ethical

210   treatment of primates. All procedures had prior approval from the NICHD Animal Care and Use

211   Committee, and were conducted in accordance with the NIH Guide for the Care and Use of

212   Laboratory Animals.

213

214   **RESULTS**

215   **Social rank**

216   Mothers did not differ in rank based on parity ($\chi^2=0.07$, P=0.79) or infant sex ($\chi^2=0.41$,

217   P=0.52). Additionally, none of the behaviors examined was significantly related to mother's

218   dominance rank (Spearman's rank correlation test, MG: N = 23, r_s = 0.073, P = 0.742; grooming:

219   N = 23, r_s = - 0.305, P = 0.157; out of arm's reach: N = 23, r_s = 0.136, P = 0.535). Thus, we did

220   not include this variable in any further analyses.

221   **Correlation of behavior**

222   The average frequencies of MG, grooming, and outside of arm's reach were not

223   correlated ($-0.11 \leq r_s \leq 0.13$; $0.48 \leq P \leq 0.80$).

224   **Mutual gazing (MG)**

225   The polynomial contrast test revealed that there was no significant difference in means

226   across the different age groups ($F_{(1,16)}$=1.001, P=0.456, $\eta^2 = 0.037$, Figure 1A).

227   Rates of MG were significantly predicted by both parity and infant sex (GLMM, parity:

228    $\beta \pm SE$=-0.744±0.217, Z=-3.43, P<0.001; infant sex: $\beta \pm SE$=0.383±0.194, Z=1.97, P=0.048)

229   although the interaction between the two variables was not significant (parity x infant sex:

230    $\beta \pm SE$=-0.301±0.432, Z=-0.70, P=0.486). Primiparous females engaged more frequently in MG

231   with their infants (mean±SE=1.31± 0.27 per session) than multiparous mothers

232   (mean±SE=0.22±0.08 per session; Figure 2A), and MG occurred more frequently with sons

233   (mean±SE=0.79±0.15 per session) than with daughters (mean±SE=0.20±0.04 per session; Figure

234   2B). No significant interaction was found for infant sex and age ($\beta \pm SE$=0.0003±0.018, Z=0.02,

235   P=0.987), or for parity and age, although there was a trend for the latter ($\beta \pm SE$=-0.041±0.022,

236   Z=-1.88, P=0.06). MG decreased over time for multiparous females ($\beta \pm SE$=-0.013±0.004, Z=-

237   3.54, P<0.001), while age did not predict frequencies of MG for primiparous females ($\beta \pm SE$=-

238   0.011±0.019, Z=-0.60, P=0.547).

239   [Figures 1 and 2 here]

240

241   **Grooming**

242   We found a significant difference in grooming rates by mothers between the different age groups

243   ($F_{(1,16)}$=6.574, P<0.001, $\eta^2 = 0.201$, Figure 1B), with both quadratic ($F_{(1,16)}$= 7.251; p = 0.002)

244   and cubic relationships ($F_{(1,16)}$= 31.859; p < 0.001) between grooming and infant's age. Rates of

245   grooming significantly increased from weeks 5-8 before returning to levels seen from days 15-30

246   (Figure 3).

247   The GLMM analysis showed that whereas parity did not have an effect on frequencies of

248   grooming ($\beta\pm$SE=0.073$\pm$0.220, Z=0.33, P=0.74), grooming was significantly predicted by infant

249   sex ($\beta\pm$SE=0.352$\pm$0.165, Z=2.13, P=0.033), with sons receiving significantly more grooming

250   (mean $\pm$ SE: 3.29$\pm$0.32) than daughters (mean $\pm$ SE: 2.01$\pm$0.15 Figure 3). No significant

251   interaction between parity and infant sex was found ($\beta\pm$SE=-0.094$\pm$0.421, Z=-0.22, P=0.823).

252   We did find a significant interaction between parity and infant age ($\beta\pm$SE=-0.078$\pm$0.031, Z=-

253   2.52, P=0.012; Figure 4A), with primiparous mothers significantly increasing grooming rates

254   over time ($\beta\pm$SE=-0.119$\pm$0.024, Z=-5.03, P<0.001; Figure 4A). This interaction was not

255   significant for multiparous mothers ($\beta\pm$SE=0.022$\pm$0.012, Z=1.76, P=0.078; Figure 4A). We also

256   found a significant interaction between infant sex and age for grooming ($\beta\pm$SE=0.058$\pm$0.021,

257   Z=2.72, P=0.006; Figure 4B), whereby sons received increasingly more grooming over time

258   ($\beta\pm$SE=0.055$\pm$0.023, Z=2.40, P=0.016; Figure 4B) but no such pattern was found among

259   daughters ($\beta\pm$SE=0.020$\pm$0.013, Z=1.50, P=0.13; Figure 4B).

260   [Figures 3 and 4]

261

262   **Separation from mother**

263   Mean frequencies of outside of mother's arm's reach varied with infant's age ($F_{(1,16)}$=

264   16.756, P < 0.001, η^2 = 0.037) with a linear relationship ($F_{(1,16)}$=143.907, P<0.001): they steadily

265   rose from birth through 30 days, peaked from weeks 5-8, then dropped to 30-day levels

266   thereafter (Figure 1C). No effect of parity or infant sex on outside of arm's reach was found

267   (parity: $\beta\pm$SE=-0.056$\pm$0.176, Z=-0.32, P=0.75; infant sex: $\beta\pm$SE=-0.02$\pm$0.149, Z=-0.13, P=0.89),

268   nor was their interaction (β±SE=0.541±0.363, Z=1.49, P=0.14). Interactions between parity and

269   infant age and between infant sex and age were not statistically significant (parity x infant age:

270   β±SE=0.004±0.027, Z=0.16, P=0.87; infant sex x infant age: β±SE=0.015±0.02, Z=0.72,

271   P=0.47).

272   [Table IV here]

273   **Initiation of mutual gazing**

274   Five of the 31 dyads never engaged in MG (three multiparous mothers of females, two

275   multiparous mothers of males). Across the first month of life, dyads did not differ in the

276   proportion of MGs initiated by the infant ($F_{(3,23)}$=0.097, P=0.96).

277   When adding in the three additional primiparous mothers from 2015, results remained

278   unchanged ($F_{(3,26)}$=0.183, P=0.91).

279
280
281   **DISCUSSION**
282
283   We sought to determine whether some of the variability in the observed face-to-face

284   interactions between macaque mothers and their newborn infants could be explained by maternal

285   history and infant sex and age, as has been the case for other types of mother-infant interactions

286   in both human and nonhuman primates [Mitchell & Stevens, 1968; Lewis, 1972]. Our study of

287   semi-free ranging rhesus monkeys afforded us the opportunity to study these interactions in a

288   naturalistic environment without the possible confound of human caregivers or interactions

289   influencing these behaviors. In addition, our large sample of dyads was not subjected to routine

290   separations as in earlier studies [Ferrari et al., 2009]. We found that first-time mothers were

291   much more likely to engage in MG with their infants, as were mothers of sons. Interestingly, we

292   also found a negative relationship between rates of MG and infant age only among multiparous

293   females but not among primiparous mothers, suggesting that first-time mothers and their infants

294   continued to engage in this form of face-to-face communication over time without decreasing in

295   frequency as infants grew.

296   Our findings that primiparous mothers engage in MG with their infants more frequently

297   than experienced mothers may simply be due to the fact that multiparous mothers have multiple

298   offspring and thus less time to devote to each. This study could not address this question

299   directly, as we did not study the amount of time mothers spent grooming, gazing, or providing

300   other types of care for their older offspring. Our future work will be able to incorporate these

301   variables.

302   Another possible explanation for the high MG in primiparous mothers is that with

303   subsequent offspring, the "novelty" of the first infant wears off and mothers become less

304   preoccupied with their infants. "Maternal preoccupation," a term coined for human mothers by

305   Winnicott in 1956 to describe "a very special psychiatric condition of the mother" which lasts for

306   the first months of the infant's life in which she experiences a stated of "heightened sensitivity"

307   and is deeply focused on the infant almost to the exclusion of all else [Winnicott, 1956; Leckman

308   et al., 2002]. Winnicott posited that mothers must experience this state in order to create and

309   sustain an environment that can meet their infants' physical and psychological needs [Winnicott,

310   1956]. Subsequent research has shown that first-time human parents experience heightened

311   preoccupation compared to experienced parents [Kim et al., 2013], and that first-time mothers

312   and their infants maintain symmetrical communication for longer periods of time than

313   experienced mothers [Hsu & Fogel, 2003]. Moreover, experienced mothers feel more effective

314   at parenting [Fish & Stifter, 1993] and thus may not feel the need to employ MG in order to

315   regulate their infants' attention or affect. Although this idea is only speculation at this point and

316   requires further study, we may be observing a similar phenomenon in our macaque mothers, as

317   evidenced by the six-fold increase in mutual gazing by our primiparous mothers compared to our

318   multiparous mothers. These findings are consistent with previous accounts showing that first

319   time mother rhesus macaques tend to be more protective of their infants than multiparous

320   females [Hooley & Simpson, 1981].

321   Another possible explanation for the effect of parity on MG is that infants of primiparous

322   mothers initiate MG with their mothers more frequently, and this difference may be driving our

323   results. However, we found that dyads did not differ in the proportion of MG initiated by the

324   infant, which means they also did not differ in the proportion of MG initiated by the mother.

325   Thus, it appears that MG is a behavior that relies equally on both partners in the mother-infant

326   dyad. It is still unclear why first-time mothers, and mothers of sons, engage in MG more

327   frequently. Future studies could explore in more detail the sequential nature of this behavior.

328   Perhaps mothers initiate MG more frequently very early in the infant's life, and the infant then

329   becomes the primary initiator after having received this special type of attention from its mother.

330   In other words, some mothers (first-time and mothers of sons) may "teach" their infants to

331   engage in and initiate this behavior. Further research is needed to test this hypothesis directly.

332   Hooley and Simpson [1981] found that primiparous mothers show more protective

333   behaviors towards their daughters than their sons. In this study, we observed that mothers of

334   sons engaged in more frequent mutual gazing and also increased the rates of grooming they

335   directed to their infants over time. This sex-specific maternal care may be due to the fact that

336   females ultimately remain in their natal group and thus might eventually pose a higher threat

337   than males, thereby becoming a target of other adult females' aggression, whereas males

338   naturally emigrate to join new troops and must be socially savvy in order to be accepted. In

339   primate societies, social grooming is crucial for the maintenance of social bonds [Nakamichi &

340   Yamada, 2007; Schino et al., 2007; see Dunbar & Shultz, 2010 for a review], which are in turn

341   critical for survival [Silk et al., 2010; Archie et al., 2014] and fitness [Silk et al., 2003, 2009;

342   Silk, 2007]. It is also known that more socially competent adult male primates enjoy greater

343   reproductive success [Schülke et al., 2010; Langergraber et al., 2013], but that males are at a

344   greater risk for mortality across the lifespan, particularly when they emigrate from the troop

345   [Small & Smith, 1986; Isbell et al., 1993; Fedigan & Zohar, 1997]. Thus, if mothers can "teach"

346   their young sons the fundamentals of proper social engagement early in life, they may be

347   providing them with an advantage later in life that makes them more likely to survive their

348   emigration and integration into a new troop. As such, mothers of sons can improve their own

349   inclusive fitness.

350   Hinde and colleagues have shown that mothers produce richer milk for sons than for

351   daughters [Hinde, 2007, 2009]. As such, Hinde et al [2007, 2009] have hypothesized that

352   mothers of sons in particular may be using lactation to signal to their infants that they should

353   prioritize growth above all else during the critical newborn period. Our data showing that

354   mothers of sons engage in significantly more MG with their infants, and groomed sons more than

355   daughters, during lactation merge with the findings by Hinde et al. [2007, 2009] and suggest that

356   they may be investing more in their sons socially, as they do lactationally. It is possible that

357   richer milk given to sons encourages more frequent nursing, and more frequent nursing

358   encourages more mutual gazing. However, this hypothesis could not be directly tested in this

359   study. The enhanced engagement by mothers of sons may enhance the development of sons'

360   social cognition about social partners, which would further optimize the infants' chances for

361 survival and future success in a new troop. In this way, mothers of sons may also be ensuring

362 their own reproductive fitness.

363   Bard et al. [2005] suggested that, in chimpanzees, MG may be part interchangeable with

364 tactile forms of mutual engagement, e.g., cradling. In fact, they found that cradling was

365 inversely related with MG. Bard et al. [2005] place compare this interchangeable relationship in

366 chimpanzees with that in humans, emphasizing that in Western societies, mutual engagement

367 between mothers and infants is more often visual as a result of reduced physical contact. This

368 idea is supported by studies of tribal cultures in Africa. In particular, the Gusii, a minority tribe

369 living in densely populated highlands of southwestern Kenya, engage in very little gazing

370 overall, and mothers rarely look at their infants [Dixon et al., 1981]. One likely reason for this is

371 that mothers hold their infants less than half the time after 5 months of age, and most of this

372 holding is on the hip or on the back [Dixon et al., 1981], thus allowing for very little face-to-face

373 interaction. Another reason posited by Dixon et al. [1981] for low rates of mother-infant

374 engagement is that "these practices may be protective for both partners in a culture where infant

375 mortality has been high. Mothers may have needed a ritualized method to dampen the intensity

376 of their feelings for infants they may lose [Dixon et al., 1981, p. 153]. This reasoning is

377 intriguing in the context of our captive colony, as well as for other captive nonhuman primate

378 populations for which MG has been recorded [Bard et al., 2005; Ehardt & Blount, 1984], as the

379 animals are well provisioned and infant mortality rates are likely much lower than those of wild

380 populations.

381   Whether or not face-to-face interactions such as MG do indeed influence an infant's later

382 social and emotional development remains to be determined. There is some evidence that

383 firstborn humans, who tend to receive greater care from the parents than siblings, are more

384   sociable [Lees, 1952]. Further, we know that in humans early face-to-face interactions are

385   predictive of later mother-infant attachment [Blehar et al., 1977; Belsky et al., 1984], and that

386   maternal sensitivity (but not face-to-face interactions *per se*) during mother-infant interactions is

387   predictive of infant cognitive development [Olson et al., 1986; Murray et al., 1996], but whether

388   or not infants who engage in more mutual gazing (or similar types of face-to-face interactions) or

389   are also more social later in development remains to be determined. We have preliminary data

390   indicating that this may indeed be the case [Dettmer et al., 2015], and we are now systematically

391   studying this in current and future cohorts in our laboratory.

392   Collectively, our data along with other studies showing effects of maternal experience

393   and infant sex on maternal investment are identifying early life experiences that may lead to later

394   sex differences in neurological and behavioral development. These studies point toward a

395   crucial window for development for both infants and mothers, and give us a greater

396   understanding of the changes that mothers undergo as they transition to first-time motherhood

397   and, subsequently, to experienced motherhood. Such information will be invaluable to

398   understanding the complexities surrounding development across the lifespan.

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529

530   Table I. Breakdown of subjects by parity and infant sex.

	Female Infant	Male Infant	Total
Primiparous Mother	2	4	6
Multiparous Mother	16	9	25
Total	18	13	31

531

532

533   Table II. Ethogram of behaviors for this study.
534

Behavior	Definition
Gazing	Infant looks at the face of another monkey, or another monkey looks at infant's face, within one meter. Coded as mutual gaze if one subject reciprocated the gaze of another.
Lipsmacking	Rapid movement of the lips directed toward another monkey
Grooming	One monkey picks at and sweeps the hair of another monkey
Separation from Mother	Infant moves off of the mother's ventrum to within or outside an arm's distance, or mother puts infant down within arm's distance, or mother walks away from infant.

535

536   Figure Legends
537
538   Figure 1. Changes in the frequencies of mutual gaze (A), grooming by mother B), and outside of
539   mother's arm's reach (C) across the first three postnatal months.
540
541   Figure 2. Mutual gaze was higher in primiparous mothers (A) and mothers of sons (B).
542
543   Figure 3. Mothers of sons groomed their infants more than did mothers of daughters.
544
545   Figure 4. Primiparous mothers (A) and mothers of sons (B) increase rates of infant grooming as
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