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ORIGINAL ARTICLE

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Genetic aspects of mother-offspring conflict in rhesus macaques

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Abstract This study investigated the occurrence of mother-offspring conflict in rhesus macaques and possible genetic correlations between maternal and offspring conflict-related behavior, using a cross-fostering procedure and a developmental approach. Ten female infants were cross-fostered at birth and observed with their foster mothers during their 1st year of life. Data on the infants' biological mothers were also available. In the 1st 3 months of infant life, there was little or no mother-infant conflict over time spent in contact. Correlations between infant behavior and the behavior of foster mothers in this period likely resulted from individual differences in infant activity levels and maternal concerns for safety or maternal attempts to encourage infant independence. During the mating season, when infants were 7–9 months old, conflict over time spent in contact became apparent. Infant conflict-related behavior was not predicted by their foster mothers' behavior but by the behavior of their biological mothers. These findings concur with those of recent studies in other animal taxa in suggesting that conflict-related behavioral traits may be genetically correlated in mothers and offspring and that the latter may be engaged in a runaway selection process that would result in the escalation of conflict.

Keywords Mother-offspring conflict · Cross-fostering · Genetic correlation · Mother-offspring coadaptation · Rhesus macaques

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Introduction

Trivers's evolutionary theory of parent-offspring conflict assumes that behavioral conflict reflects an underlying genetic conflict of interest because parents and offspring share only 50% of their genes, and therefore have different optimum levels of parental investment (Trivers 1974). Although the genetic basis of parent-offspring conflict is assumed by a number of theoretical models (e.g., Godfray 1995), most empirical work has concentrated on the phenotypic expressions of conflict rather than on its underlying genetic assumptions (Kölliker and Richner 2001). Some recent studies, however, used cross-fostering procedures to demonstrate a genetic correlation between offspring solicitations for food and the parental responses to such solicitations. For example, a study of great tits (*Parus major*) reported that there is genetic variation in the intensity of begging calls of nestlings and that the size of the maternal response was positively related to the begging-call intensity of their biological offspring (Kölliker et al. 2000). Similarly, a study of burrower bugs (*Sehirus cinctus*) reported a negative correlation between the amount of provisioning by a mother to her foster clutch and the number of nutlets elicited by her biological clutch from an unrelated foster mother (Agrawal et al. 2001). Finally, a cross-fostering study involving different strains of mice reported that offspring were more efficient in eliciting food from foster mothers of the same strain as their biological mothers (Hager and Johnstone 2003), suggesting positive coadaptation of maternal and offspring effects on resource transfer (or some form of kin discrimination by the mothers). Taken together, these studies provide genetic evidence that offspring solicitations have coevolved with parental responses.

Evolutionary aspects of parent-offspring conflict have been thoroughly investigated, both theoretically and empirically, in only a few animal taxa, especially birds (e.g. Mock and Forbes 1992; Kilner and Johnstone 1996; Mock and Parker 1997; Budden and Wright 2001). Behavioral conflict between parents and offspring, however, is widespread in other taxa as well, and in particular among mammals. In non-human primates, behavioral conflict between mothers and offspring is intense and often prolonged. In the vast majority of primate species, mothers are the only caregivers, and milk production and transfer to the offspring represent the main form of maternal investment. Nursing occurs when mothers and offspring are in ventro-ventral contact and physical stimulation of the nipple above a certain threshold level triggers a chain of neuroendocrine events that result in inhibition of ovulation (Aso and Williams 1985). In other words, by being in contact with their mothers and sucking their nipples, infants may not only obtain more milk for themselves but also inhibit their mothers' reproduction.

Behavioral conflict between mothers and infants in non-human primates is often manifested as conflict over time spent in contact (Maestripieri 2002). Mothers break contact and reject their infants with increasing frequency as infants grow older, and infants respond with further attempts to make contact, distress calls or tantrums (Hinde and Spencer-Booth 1967). In seasonally breeding species such as rhesus (*Macaca mulatta*) and Japanese macaques (*M. fuscata*), mother-infant conflict intensifies during the mating season (e.g., Worlein et al. 1988; Berman et al. 1993). Mothers who spend less time in contact with their infants and reject them at high rates are more likely to conceive than mothers who spend more time with their infants and reject them at low rates (Simpson et al. 1981). Although the phenotypic aspects of mother-infant conflict in primates seem to be consistent with the predictions of Trivers's evolutionary hypothesis (Maestripieri 2002), the possible genetic correlation between maternal and infant conflict-related behavior has not been investigated.

Cross-fostering is the experimental procedure used by recent studies investigating the genetic aspects of parent-offspring conflict in animals (see references above). Cross-fostering experiments are difficult to perform in non-human primates because mothers adopt unrelated infants only under very restricted circumstances (e.g., Smith 1986; see Maestripieri 2001, for a review). As a result, very few studies have used this procedure to investigate genetic aspects of behavior, and these studies typically involved very small sample sizes (e.g., n=4, Owren et al. 1993). In this study I used data from ten successfully cross-fostered rhesus macaque infants to investigate the hypothesis that maternal and infant responses to conflict over time spent in contact may have coevolved. To this end, I investigated behavioral interactions aimed at making or breaking contact between infants and their foster mothers in two time-different periods: the 1st 3 months of infant life, and 3 months during the subsequent mating season. I hypothesized that in the 1st 3 months of life, there would be variability in both infant and maternal behavior but little or no conflict over the maintenance of contact. Based on previous studies (e.g. Worlein et al. 1988; Berman et al. 1993), I hypothesized that mother-infant conflict would intensify during the mating season. I also hypothesized that a genetic correlation between infant demands for contact and concomitant maternal behaviors would be most likely to be expressed when mother-infant conflict is most intense, i.e., during the mating season. Thus, I predicted that infant contact-making and contact-breaking behavior during the mating season would be more likely to be predicted by the behavior of their biological mothers during the same period than by the behavior of their foster mothers.

Methods

This study was conducted with female rhesus macaques living in several different social groups at the Field Station of the Yerkes National Primate Research Center in Lawrenceville, Ga. (USA). The groups were housed in 38×38 m outdoor compounds with attached indoor areas, and consisted of 2–5 adult males and 30–35 adult females with their immature offspring. All groups had a stable matrilineal structure and a linear dominance hierarchy. The adult males were unrelated to the adult females within their groups and were replaced by other males every 4–5 years.

Study subjects were ten female infants born in 1998–1999. These infants were cross-fostered within 24–48 h after birth and reared by unrelated foster mothers in social groups different from the group of origin (there was no visual or physical contact between monkeys living in different groups, but in most cases, monkeys could hear conspecific vocalizations from other groups). Foster mothers were chosen from adult females who gave birth within a few hours or days of the birth of the study subjects. This study was part of a larger project that involved 25 infant cross-fostering procedures and had an 80% success rate (the 10 infants included in this study were those for whom data on their biological mothers were available). Six of the subjects' biological mothers served as foster mothers in this study. All biological and foster mothers were multiparous. To control for possible effects of the cross-fostering procedure on maternal behavior, interactions between foster mothers and adopted infants were compared to those of ten mother-infant pairs observed in 1993 in the same environment (Maestripieri 1994). No significant differences were found for any mother-infant interactions, including contact-making or breaking, time spent in contact, or maternal grooming, restraining, and rejection. Thus, the cross-fostering procedure did not appear to have significant effects on maternal behavior.

The ten infants and their foster mothers were observed once a week for 1 h during the 1st 3 months of life, and once a month for 1 h until the end of their 1st year of life. Behavioral data were collected by three observers using a portable computer. The three observers were tested for reliability prior to the beginning of data collection. Inter-observer reliability was considered to have been achieved when percent agreement in recording behavior exceeded 90% and Cohen's Kappa exceeded 0.8. Cohen's Kappa is calculated as Po–Pc/1–Pc, where Po is the observed percentage of agreements between observers and Pc is the probability that agreements occur by chance (Lehner 1996). Observation sessions were randomly distributed between 0800 and 1900 hours.

For the purposes of the present study, interactions between infants and their foster mothers were analyzed in two 3-month periods: the 1st, 2nd, and 3rd month of life (Birth Season, BS; all infants were born within a 2-month period, between early April and early June) and the 7th, 8th, and 9th month of life (Mating Season, MS; in this rhesus population the mating season begins in September and ends in February). Data analysis involved the mean hourly rates of behavior in each of the two periods. The four biological mothers that did not serve as foster mothers in this study were observed with their own infants and with similar procedures the year before or the year after the cross-fostering experiment. Data for the BS period were available for all of these four mothers, but data for the MS were available for only two of them. Therefore, data analysis concerning the biological mothers included ten individuals during the BS period and 8 individuals during the MS period. Six of these individuals were observed with adopted infants and four of them (two in the MS season) with their biological infants.

Data collection included observations of mother-infant contact made and broken, as well as maternal restraining and rejection. Contact involved any bodily contact between mother and infant except brief touching or hitting. Breaking contact was recorded whenever the mother or the infant interrupted bodily contact for more than 5 s. Maternal restraining involved the mother preventing the infant from breaking contact by holding it or pulling its tail or leg. Maternal rejection involved the mother preventing the infant from making contact by holding the infant at a distance with an arm or turning and walking away from the infant. All measures were analyzed as number of events per hour.

Rates of contact-making and contact-breaking by mothers and infants were used to calculate the Hinde's Index of Contact (Hinde and Atkinson 1970). This index is calculated by subtracting the percentage of contacts broken by infants from the percentage of contacts made by infants, and provides information on the relative role played by mothers and infants in the maintenance of contact. Negative values of the Hinde's Index indicate that the mother is primarily responsible for maintaining contact, whereas positive values indicate that the infant is primarily responsible. Another index proposed by Brown (2001) to assess whether the mother or the infant is responsible for the majority of changes in contact was also used. The Brown Index is calculated as the percentage of contacts made and broken by infants relative to all the contacts made and broken by mothers and infants (see Brown 2001, for a discussion of this index in relation to the Hinde's Index).

Associations between behavioral variables within or between subjects were assessed with the Pearson's product moment correlation coefficient or with linear regression analysis. Comparisons in rates of behavior between individuals and time periods were made with analysis of variance (ANOVA) for repeated measures. Whenever the data were non-normally distributed or the variances were non-homogeneous, the data were log-transformed. All tests were two-tailed and probabilities <0.05 were considered statistically significant.

Results

Maintenance of contact and conflict of interests between infants and foster mothers

Infant rates of making contact were significantly positively correlated with infant rates of breaking contact during both the BS (r=0.9, n=10, P=0.0004) and the MS (r=0.9, n=10, P=0.0004). In contrast, the positive correlation for the foster mothers was significant in the MS (r=0.77, P<0.01) but not in the BS (r=0.22, P=0.54). These correlations suggest that, particularly for infants, individual differences in rates of making and breaking contact reflect, at least in part, differences in baseline activity levels.

There was no significant correlation between the rates of infants making contact (r=0.04, P=0.91) or breaking contact (r=0.09; P=0.40) recorded in the BS and those recorded in the MS. No significant correlations were found for the foster mothers either (making contact: r=0.35, P=0.32; breaking contact: r=0.59; P=0.07). The rates of maternal rejection in the BS and the MS were positively correlated (r=0.68, P<0.05) but this correlation was due to one individual with very high rates of rejection, and without this individual the correlation was not significant (r=0.12, n=9; P=0.75). No maternal restraining was observed in the MS.

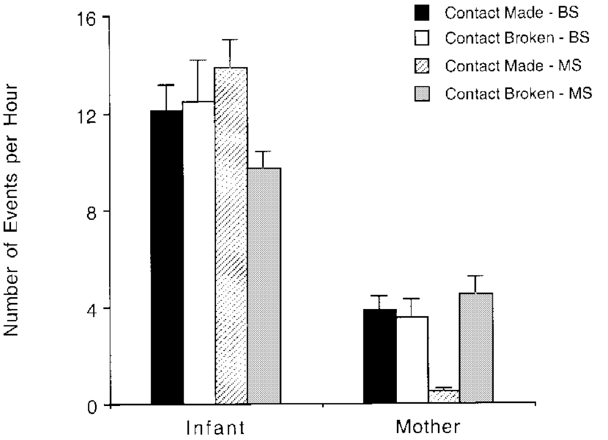

Fig. 1 Mean (+SEM) number of contacts made and broken by infants and foster mothers in the birth season (*BS*) and the mating season (*MS*)

When rates of contact-making were compared between foster mothers and infants across the two time periods, ANOVA revealed both a significant main effect for subjects, with infants having higher rates than mothers ($F_{1,18}$=154.16, P<0.0001) and a significant interaction between subject and season ($F_{1,18}$=9.98, P<0.01). This significant interaction reflected the fact that infant contact-making increased in the MS whereas maternal contact-making decreased (Fig. 1). Similar results were found for contact-breaking. Infant rates of contact-breaking were higher than those of their foster mothers across the two seasons ($F_{1,18}$=25.9, P<0.0001) and there was a significant interaction between subjects and season ($F_{1,18}$=5.52, P<0.05). In this case, infant contact-breaking decreased during the MS whereas maternal contact-breaking increased (Fig. 1). Thus, relative to the BS, the MS was characterized by increased motivation by infants to be in contact with their mothers and decreased motivation by their mothers to be in contact. This suggests an intensification of conflict of interests between mothers and infants during the MS.

The Hinde's Index of Contact was −2.33 in the BS and +28.20 in the MS, suggesting that responsibility for maintenance of contact shifted from mothers to infants. The Brown's Index was 76.68 in the BS and 82.45 in the MS. Thus, infants were generally responsible for the majority of changes in contact in both seasons due to their higher activity levels, and their role slightly increased in the MS.

Behavioral correlations between infants and their foster and biological mothers

In the BS, the infant rates of contact-making and contact-breaking were positively correlated with the rate of

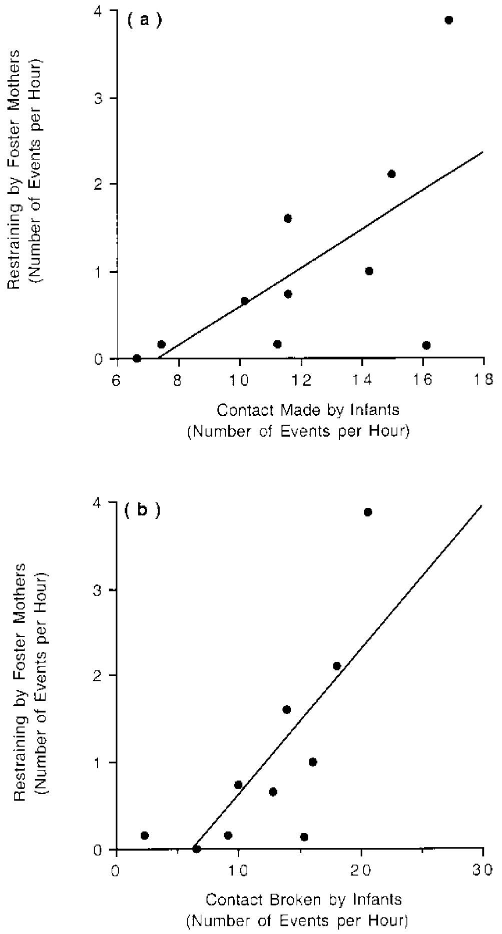

Fig. 2 a Correlation between rate of contact-making by infants and rate of restraining by foster mothers during the birth season. **b** Correlation between rate of contact-breaking by infants and rate of restraining by foster mothers during the birth season

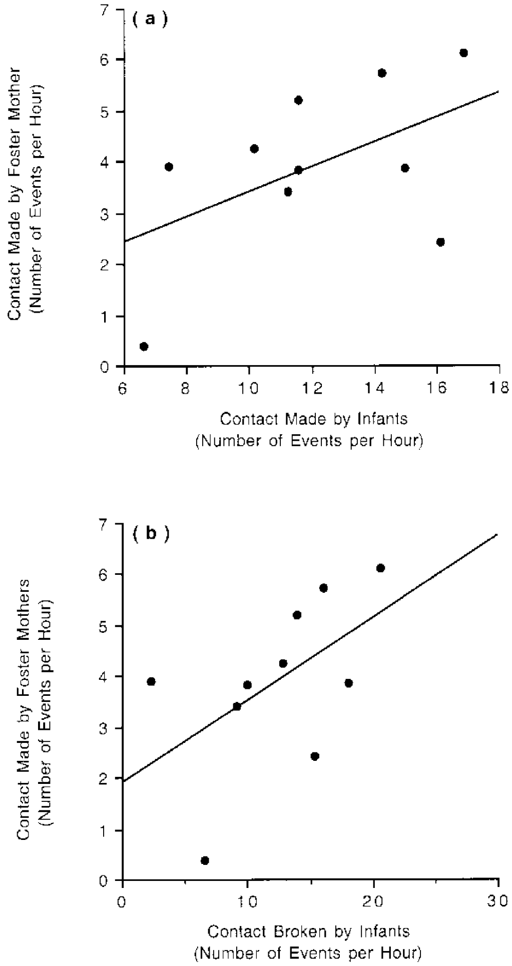

Fig. 3 a Correlation between rate of contact-making by infants and rate of contact-making by foster mothers during the birth season. **b** Correlation between rate of contact-breaking by infants and rate of contact-making by foster mothers during the birth season

restraining by their foster mothers (contact-making: r=0.64, P<0.05; contact-breaking: r=0.76, P<0.01; Fig. 2). Thus, infants with higher activity levels were restrained more by their foster mothers. Infant rates of contact-breaking, but not contact-making, were negatively correlated with rates of rejection by their foster mothers (contact-breaking: r=0.72, P=0.01; contact-making: r=0.50, P=0.14). Thus, infants who broke contact less were rejected more by their foster mothers. Infant rates of contact-making and contact-breaking were also positively correlated—but not significantly—with rates of contact-making by their foster mothers (contact-making: r=0.52, P=0.1; contact-breaking: r=0.54, P=0.1; Fig. 3). Taken together, these findings suggest that the behavioral correlations between infants and their foster mothers in the BS resulted from individual differences in infant activity levels and maternal attempts to protect infants or encourage their independence.

Infant rates of contact-making and contact-breaking in the BS were not significantly correlated with the rates of contact-making (infant contact-making: r=0.18, P=0.61; infant contact-breaking: r=0.10, P=0.77) or contact-breaking (infant contact-making: r=0.31, P=0.38; infant contact-breaking: r=0.42, P=0.23), or with the rates of restraining (infant contact-making: r=0.15, P=0.68; infant contact-breaking: r=0.10, P=0.79) or rejection (infant contact-making: r=0.40, P=0.26; infant contact-breaking: r=0.46, P=0.18) by their biological mothers in the same season. Thus, during the 1st 3 months of life, there was no apparent relation between infant behavior and the behavior of their biological mothers.

In the MS, the infant rates of contact-making and breaking were not significantly correlated with the rates of contact-making (infant contact-making: r=0.38, P=0.28; infant contact-breaking: r=0.10, P=0.78) or contact-breaking (infant contact-making: r=0.05, P=0.88; infant contact-breaking: r=0.36, P=0.31), or with the rates of rejection (infant contact-making: r=0.14, P=0.69; infant contact-breaking: r=0.15, P=0.68) by their foster mothers in the same period. Similarly, there was no significant correlation between the infant rates of contact-making and contact-breaking in the MS and their foster

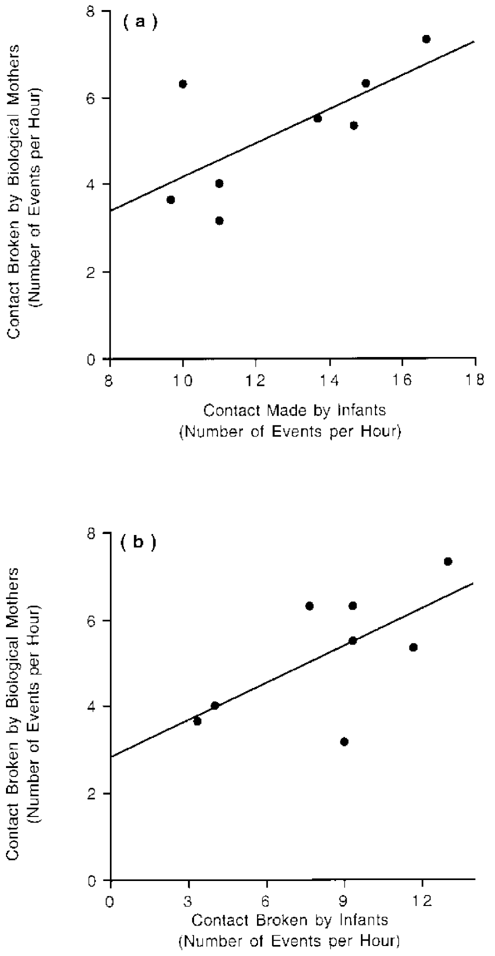

Fig. 4 a Linear regression of rate of contact-making by infants and rate of contact-breaking by biological mothers in the mating season. **b** Linear regression of rate of contact-breaking by infants and rate of contact-breaking by biological mothers in the mating season

mothers' behaviors in the BS (infant contact-making-mother contact-making: r=0.22, P=0.53; infant contact-making-mother contact-breaking: r=0.15; P=0.67; infant contact-breaking-mother contact-making: r=0.11, P=0.75; infant contact-breaking-mother contact-breaking: r=0.40; P=0.25; infant contact-making-rejection: r=0.08, P=0.83; infant contact-breaking-rejection: r=0.28, P=0.42). These findings suggest that infant behavior in the MS was not significantly predicted by current or earlier interactions with their foster mothers.

The infant rates of contact-making during the MS, however, were predicted by the rates of contact-breaking by their biological mothers in the MS (infant contact-making; r^2=0.48, n=8, P=0.05; Fig. 4a). Thus, infants whose biological mothers broke contact at a high rate made contact with their foster mothers at a high rate. Infant rates of contact-breaking were associated with the rates of contact-breaking by their biological mothers, but the regression was not statistically significant (r^2=0.42, n=8, P=0.08; Fig. 4b). Infant rates of contact-making or breaking in the MS were not predicted by the rates of contact-making (infant contact-making: r=0.08, P=0.84; infant contact-breaking: r=0.17; P=0.68) or the rates of rejection (infant contact-making: r=0.55, P=0.16; infant contact-breaking: r=0.23; P=0.59) by their biological mothers in the same period. All foster and biological mothers except one conceived another offspring during the mating season in which they were observed.

Discussion

The study documents the occurrence of mother-infant conflict over the maintenance of contact during the mating season in rhesus macaques and provides suggestive evidence for a genetic correlation between infants' and mothers' conflict-related behavior.

In both the birth and the mating seasons, there was considerable variability in both infants' and mothers' behaviors related to contact regulation. The significant correlation between rates of contact-making and contact-breaking that emerged in the birth and the mating seasons across individuals, and in particular across infants, suggests that these rates reflect, at least in part, baseline activity levels. Infants had much higher rates of contact-making and contact-breaking in both seasons, suggesting that their activity levels were higher than those of their mothers. Accordingly, the high scores of the Brown's Index of contact in both seasons suggested that infants were responsible for the majority of changes in contact with their mothers (see Brown 2001). The rates of contact-making and contact-breaking by infants and mothers, however, were not correlated between the birth and the mating seasons, suggesting that contact-making and contact-breaking behavior were influenced by changes in age and/or season to a different extent for different individuals and dyads.

As predicted, the 1st 3 months of infant life were characterized by little or no mother-infant conflict over contact regulation. Both infants and their foster mothers had similar rates of contact-making and contact-breaking, and the Hinde's Index of Contact had a low negative value, suggesting that mothers were only slightly more responsible than infants for the maintenance of contact. The first few months of infant life in rhesus macaques are typically associated with high levels of maternal protectiveness (e.g., restraining) and increasing levels of maternal rejection (Hinde and Spencer-Booth 1967). In this study, the infants with higher rates of contact-making and contact-breaking in the birth season, i.e., the infants with higher activity levels, were restrained more by their foster mothers. Furthermore, the infants who broke contact less frequently were encouraged more by their mothers. Previous studies have shown that both maternal and infant characteristics contribute to variability in early mother-infant interactions (Fairbanks 1996) and the correlations reported in this study suggest that mothers and infants influenced and adjusted their behavior reciprocally, probably on the basis of observation and previous interaction.

When rhesus infants were 7–9 months old and their mothers resumed mating, their conflict of interest over the maintenance of contact became apparent from changes in their contact-making and contact-breaking behavior. Relative to the earlier months, infants increased contact-making and decreased contact-breaking whereas their mothers did the opposite (see also Maestripieri 2002, for similar evidence). Thus, there appeared to be a concomitant increase in infant demands for contact and a decrease in the mothers' willingness to be in contact. Mother-infant contact may interfere with mating activity and, when associated with frequent nipple stimulation, may also inhibit ovulation (Aso and Williams 1985). Infants, however, have evolutionary reasons for demanding more investment in themselves rather than in their future siblings (Trivers 1974). Therefore, the optimum amount of time spent in contact during the mating season should be different for mothers and infants.

A previous study reported a significant positive correlation between infant contact-making and maternal contact-breaking in rhesus macaque mothers with their biological offspring during the mating season (Maestripieri 2002). In other words, infants with high levels of contact demands had mothers with high levels of rejection. The present study suggests that this phenotypic correlation reflects a genetic correlation between mothers and offspring. In fact, in this study, the same significant correlation was found between infants and their biological mothers (with whom they never interacted after the cross-fostering procedure) and not between the infants and the foster mothers that reared them.

Although other variables, such as prenatal maternal effects (e.g., nutritional or hormonal) or heritable differences in activity levels, may account for some of the observed individual differences in maternal and infant behavior, this study generally concurs with previous research in suggesting that parent-offspring conflict is influenced by genes expressed in both the parent's and the offspring's genome (e.g., Haig 1993; Keverne 2001; Kölliker and Richner 2001). In particular, this study is consistent with the findings of Agrawal et al. (2001) in indicating that mothers that are genetically predisposed to be "stingy" with their resources produce offspring that are strong elicitors of parental effort. For example, genes that influence competitiveness and persistence in conflict situations and are expressed in both mothers and daughters may be responsible for the behavioral correlation between female rhesus macaque infants and their biological mothers reported in this study. Correlations between cross-fostered infants and their biological mothers in other measures of behavior, such as rates of affiliation and aggression towards other individuals (Maestripieri 2003), suggest that genetic similarities between rhesus macaque mothers and daughters extend above and beyond the context of parent-offspring conflict.

The possibility of a genetic correlation between maternal and infant responses to conflict over parental care has several important implications. First, while this possibility is consistent with Trivers's evolutionary theory of parent-offspring conflict, it is not consistent with other interpretations of mother-infant behavioral conflict in primates that explain this phenomenon in terms of behavioral contingencies and rescheduling of activities (Altmann 1980; Barrett et al. 1995). Second, the dynamics of parent-offspring conflict in primates and other animals have traditionally been interpreted as the product of maternal investment strategies and offspring condition (e.g., Gomendio 1991; Lee 1996). However, the existence of a correlation between conflict-related behavioral traits in cross-fostered offspring and their biological mothers suggests that the maternal and infant sources of variation in the negotiation of parental investment are not independent but are, at least in part, the result of mother-offspring coevolution and coadaptation (e.g., Wolf and Brodie 1998; Agrawal et al. 2001; Kölliker and Richner 2001). Therefore, mother-offspring coevolution must be taken into consideration by both theoretical models and empirical studies of parent-offspring conflict. Finally, a genetic correlation between conflict-related behavioral traits in mothers and offspring may favor a runaway selection process that would further escalate the intensity or duration of conflict (Stamps et al. 1978; Kölliker and Richner 2001). Therefore, understanding the genetic aspects of parent-offspring conflict may help us understand the intense and prolonged forms of behavioral conflict that occur in many species of primates, including humans.

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