

**Dario Maestriperi**

Animal Behavior Research Group  
The University of Chicago  
5730 S. Woodlawn Avenue  
Chicago, IL 60637  
E-mail: dario@uchicago.edu

Yerkes National Primate Research Center  
Emory University  
Atlanta, GA 30322

# Similarities in Affiliation and Aggression between Cross-Fostered Rhesus Macaque Females and Their Biological Mothers

**ABSTRACT:** In female-bonded primate species, there is cross-generational consistency in female affiliative and aggressive behavior. This consistency could be the result of maternal effects, offspring learning, shared environment, and/or direct genetic inheritance of behavioral or psychological traits. In this study, I investigated possible similarities in affiliation and aggression between cross-fostered rhesus macaque females and their biological mothers. Ten female infants were cross-fostered at birth, and selected aspects of their affiliative and agonistic behavior over the course of their first 3 years of life were compared to the behavior of their foster and biological mothers. Average offspring rates of social contact and aggression across the 3 years, and in particular in Years 2 and 3, resembled those of their biological mothers whereas no clear behavioral similarities between offspring and foster mothers were observed at any age. Heritable variation in female social behavior may be maintained by natural selection and leads to adaptation to different socioecological niches within macaque populations.

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**Keywords:** parent–offspring resemblance; cross-fostering; behavioral development; affiliation; aggression; rhesus macaques

Many species of nonhuman primates, and in particular of Old World monkeys, live in social systems characterized by female philopatry and male migration (Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987). As a result of this sex-biased dispersal, these “female-bonded” species live in groups with a strong matrilineal structure, in which female relatives from several generations live together (Wrangham, 1980). In these societies, female social networks and dominance ranks are transmitted across generations so that the social preferences and dominance ranks

of young females are remarkably similar to those of their mothers (e.g., Chapais, 1983; de Waal, 1996). Although the social processes underlying the maintenance and intergenerational transmission of dominance ranks are well understood (e.g., Chapais, 1992; Holekamp & Smale, 1991), little is known about the mechanisms underlying the intergenerational transmission of female affiliative and aggressive tendencies.

Affiliative and aggressive behavior in primates may have a direct genetic heritable basis or may be affected by temperamental and personality traits that are heritable. Conversely, shared environment between mothers and daughters or the effects of maternal behavior on offspring development can be responsible for intergenerational consistencies in female behavior. Finally, it is possible that daughters learn specific styles of social interaction by observing their mothers and reproducing their behavior. Investigating cross-generational consistencies in the social behavior of female primates living in matrilineal societies

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Correspondence to: D. Maestriperi

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can elucidate the dynamics of social evolution in these primates and the mechanisms by which behavior becomes adapted to the social and ecological environment.

Cross-fostering studies are one way to investigate parent–offspring resemblance and the mechanisms underlying cross-generational consistencies in behavior. For example, recent cross-fostering studies conducted in gregarious birds have demonstrated that parents and offspring maintain substantial similarities in aspects of sociality such as choice of colony size and nearest neighbor distance even when offspring are reared by foster parents in different environments (Brown & Brown, 2000; Møller, 2002). In these studies, parent–offspring similarities appeared to be due to genetic similarity rather than to maternal effects or shared environment.

Cross-fostering experiments are difficult to perform in nonhuman 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 the intergenerational transmission of behavior, and these studies typically involved very small sample sizes (e.g., Owren, Dieter, Seyfarth, & Cheney, 1993; Suomi, 1987).

In this study, I investigated possible cross-generational consistencies in female affiliative and agonistic tendencies among rhesus macaques (*Macaca mulatta*) using a cross-fostering procedure and parent–offspring regression analyses. Ten female infants were successfully cross-fostered at birth, and selected aspects of their behavior over the course of their first 3 years of life were compared to the behavior of their foster and biological mothers. Specifically, I investigated whether the social behavior of infant and juvenile offspring was more similar to the social behavior of their foster mothers or to that of their biological mothers during the first 3 months of lactation.

If similarities between mothers and daughters in basic measures of affiliation and agonism such as rates of contact, grooming, aggression, and submission are the product of maternal effects, shared environment, or offspring observational learning, then offspring behavior should be similar to the behavior of the foster mothers. Conversely, if behavioral similarities between mothers and daughters are the product of direct genetic inheritance or inheritance of temperamental and personality traits that affect social behavior, then offspring behavior should be similar to the behavior of the biological mothers.

## METHODS

### Subjects

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 to 5 adult males and 30 to 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 to 5 years.

Study subjects were 10 female infants born in 1998 to 1999. These infants were cross-fostered within 24 to 48 hr 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. Foster mothers were chosen among adult females who gave birth within a few hours or days of the birth of the study subjects. Six of the subjects' biological mothers served as foster mothers in this study. All mothers were multiparous.

On the day of the cross-fostering experiment, 2 mothers were captured with their newborn infants and housed indoor in a standard squeeze cage. The infants were gently removed from their biological mothers, wrapped in a towel, and placed into the cage of the other female. The foster mother and the infant were observed for a minimum of 10 min to a maximum of 4 hr. If the mother continuously held the infant on her chest and showed no instance of rejection, the adoption was considered successful, and both mother and infant were released into the group (see Maestripieri, 2001, for further details on the cross-fostering procedure). All infants included in this study were successfully adopted and reared by their foster mothers.

All adult females in this study had been involved in previous behavioral studies, and their dominance ranks were assessed using data on unidirectional aggression and submission collected during these studies. Adult females were classified as high, middle, or low ranking depending on whether they fell into the upper, middle, or bottom third of the dominance hierarchy within their group. Dominance ranks were stable and did not change over the course of the study.

### Procedure

During the first 3 months of life, the 10 infants and their foster mothers were observed once a week for 1 hr. Data collection included observation of mother–infant interactions, interactions between infants and other group members, and interactions between mothers and other group members.

After the first 3 months, the adopted infants were observed once a month for 1 hr until the end of their third year of life. Data collection included the subjects' interactions with other group members. The 4 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. 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. Interobserver reliability was considered to have been achieved when percent agreement in recording behavior exceeded 90% and Cohen's kappa (Cohen, 1960) exceeded 0.8. Observation sessions were randomly distributed between 0800 and 1900 hr.

Behavioral data analyses focused on two measures of affiliation and two measures of agonistic behavior for the 10 subjects and their foster and biological mothers. The rates of contacts and grooming exchanged (done and received) with other group members (any individual in the group except the subjects' mothers) were used as measures of affiliation. Contact was defined as any bodily contact between 2 individuals except brief touching or hitting. The rates of aggression (threats, slaps, bites, and chases) and submission (bared-teeth displays) done and received with other group members (any individual in the group except the subjects' mothers) were used as measures of agonistic behavior. All measures were analyzed as number of events per hour. For both foster and biological mothers, data analysis involved the mean hourly rates of behavior during the first 3 months of lactation; for the 10 offspring, data analysis involved the mean hourly rates of behavior in each of their first 3 years of life.

Behavioral similarities between offspring and their foster and biological mothers were assessed with linear regression analyses (Falconer & Mackay, 1996). Correlations between behavioral variables were assessed with the Pearson's product-moment correlation coefficient. Other behavioral comparisons involved the Student's *t* test for paired samples. Whenever the data were nonnormally distributed or the variances were nonhomogeneous, the data were log transformed. All tests were two-tailed, and probabilities  $\leq 0.05$  were considered statistically significant.

## RESULTS

### Behavior of Biological and Foster Mothers

To control for possible effects of the cross-fostering procedure on the behavior of foster mothers, interactions between foster mothers and adopted infants were compared to those of 10 mother-infant pairs observed in 1993 in the same environment. No significant differences were found, suggesting that the foster mothers interacted with their adopted infants as if they were their biological offspring.

To control for the possibility that rates of social interactions between mothers and other group members may be unusually high due to the presence of dependent infants, rates of contact, grooming, and aggression for 6 mothers were compared to similar data collected from the same individuals during the last 8 weeks of pregnancy the year prior to this study (Data were collected by the same observers with similar procedures.) Pregnancy data

on contact, grooming, and aggression were not available for the other mothers involved in this study, and pregnancy data on submissive behavior were not available for any of the mothers. Rates of contact and aggression were not significantly different during pregnancy and lactation, contact:  $t = -1.26$ ,  $df = 5$ ,  $p = 0.26$ ; aggression:  $t = 1.63$ ,  $p = 0.16$ , whereas rates of grooming were significantly lower during lactation than during pregnancy,  $t = -3.81$ ,  $p = 0.01$ . The correlation between rates of contact, grooming and aggression during pregnancy and lactation were all positive, but none was statistically significant, probably because of the small sample size.

There were no significant differences in age between biological and foster mothers, biological:  $8.30 \pm 0.75$  years, foster:  $9.10 \pm 0.86$  years;  $t = 0.85$ ,  $df = 9$ ,  $p = 0.42$ , or in dominance rank, biological: high rank = 2, middle rank = 4, low rank = 4, foster: high rank = 1, middle rank = 4, low rank = 5;  $\chi^2 = 0.44$ ,  $df = 2$ ,  $p = 0.80$ . This is not surprising given that 6 biological mothers also served as foster mothers. To assess whether the biological and foster mothers for each particular infant were similar or dissimilar in their rates of affiliative and aggressive behavior, their data were compared with tests for paired samples. There were no significant differences between biological and foster mothers in rates of social contact,  $t = 0.94$ ,  $df = 9$ ,  $p = 0.37$ , grooming,  $t = 0.52$ ,  $df = 9$ ,  $p = 0.62$ , aggression,  $t = -1.1$ ,  $df = 9$ ,  $p = 0.30$ , or submission,  $t = -0.23$ ,  $df = 8$ ,  $p = 0.83$  (Table 1). There also was no significant correlation between biological and foster mothers for any of these measures, suggesting that, for example, infants born to mothers with high rates of grooming or aggression were not reared by foster mothers with high rates of grooming or aggression. Finally, there was no significant correlation between the rates of social contact, grooming, aggression, and submission for biological mother, foster mothers, or the offspring, suggesting that these behavioral measures were independent from each other.

### Developmental Changes in Offspring Rates of Behavior

Developmental changes in offspring behavior were different for different behaviors (Table 1). Offspring's rates of

**Table 1. Mean ( $\pm$ SEM) Hourly Rates of Behaviors for Foster Mothers, Biological Mothers, and Offspring in Year 1, 2 and 3**

	Foster Mother	Biological Mother	Offspring 1	Offspring 2	Offspring 3
Contact	$8.73 \pm 1.27$	$10.71 \pm 1.03$	$4.14 \pm 0.62^{a,b}$	$7.67 \pm 0.88^a$	$8.22 \pm 1.61$
Grooming	$5.59 \pm 0.50$	$5.09 \pm 0.54$	$0.76 \pm 0.20^{a,b}$	$1.62 \pm 0.19^{a,b}$	$2.08 \pm 0.35^{a,b}$
Aggression	$1.51 \pm 0.36$	$2.14 \pm 0.36$	$0.26 \pm 0.07^{a,b}$	$0.71 \pm 0.08^{a,b}$	$0.96 \pm 0.17^a$
Submission	$0.75 \pm 0.13$	$0.82 \pm 0.12$	$0.03 \pm 0.02^{a,b}$	$0.23 \pm 0.09^{a,b}$	$0.11 \pm 0.05^{a,b}$

<sup>a</sup>Significantly lower than Biological mothers.

<sup>b</sup>Significantly lower than Foster mothers (see Results).

social contact in the first year were significantly lower than those of both their biological,  $t=5.42$ ,  $df=8$ ,  $p<0.001$ , and their foster mothers,  $t=3.67$ ,  $df=7$ ,  $p<0.01$ . In the second year, offspring's rates of social contact were lower than those of their biological mothers,  $t=4.35$ ,  $df=9$ ,  $p=0.001$ , but not different from those of their foster mothers,  $t=0.52$ ,  $df=9$ ,  $p=0.61$ . In the third year, there were no significant differences in contact between offspring and biological mothers,  $t=1.40$ ,  $df=9$ ,  $p=0.20$ , or foster mothers,  $t=0.28$ ,  $df=9$ ,  $p=0.78$ . Thus, offspring reached adult rates of social contact in their second or third year.

Offspring rates of grooming increased steadily over the 3 years, but in the third year the rate of offspring grooming was still about half the adult rates. Therefore, there were significant differences in all 3 years between offspring grooming rates and those of both the biological mothers, first year:  $t=5.74$ ,  $df=8$ ,  $p<0.001$ ; second year:  $t=5.62$ ,  $df=9$ ,  $p<0.001$ ; third year:  $t=4.99$ ,  $df=9$ ,  $p<0.001$ , and the foster mothers, first year:  $t=9.60$ ,  $df=8$ ,  $p<0.0001$ ; second year:  $t=7.46$ ,  $df=9$ ,  $p<0.0001$ ; third year:  $t=4.62$ ,  $df=9$ ,  $p=0.001$ .

In the first and second years, aggression by offspring was less frequent than aggression by biological mothers, first year:  $t=4.72$ ,  $df=8$ ,  $p=0.001$ ; second year:  $t=4.60$ ,  $df=9$ ,  $p=0.001$ , and foster mothers, first year:  $t=3.22$ ,  $df=8$ ,  $p=0.01$ ; second year:  $t=2.17$ ,  $df=9$ ,  $p=0.05$ . In the third year, offspring aggression rates were still less than half the aggression rates of biological mothers,  $t=3.85$ ,  $df=9$ ,  $p<0.01$ , but not significantly different from those of foster mothers,  $t=1.25$ ,  $df=9$ ,  $p=0.24$ .

Finally, offspring submission rates appeared to develop more slowly than other behaviors. They increased in the second year, then decreased the third year. In all 3 years, offspring submission rates were significantly lower than those by biological mothers, first year:  $t=5.40$ ,  $df=7$ ,  $p=0.001$ ; second year:  $t=3.61$ ,  $df=8$ ,  $p<0.01$ ; third year:  $t=5.65$ ,  $df=8$ ,  $p<0.001$ , and foster mothers, first year:  $t=4.86$ ,  $df=8$ ,  $p=0.001$ ; second year:  $t=3.80$ ,  $df=9$ ,  $p<0.01$ ; third year:  $t=5.45$ ,  $df=9$ ,  $p<0.001$ . In particular, in the third year, they were still several orders of magnitude lower than those of both mothers (Table 1).

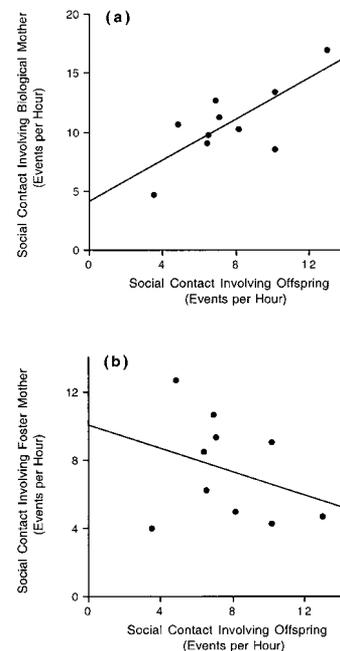
Rates of offspring social contact, grooming, or aggression were not significantly correlated across the 3 years. Submission rates were positively correlated in the second and the third years,  $r=0.86$ ,  $df=8$ ,  $p<0.01$ .

### Mother–Daughter Similarities in Affiliative and Aggressive Tendencies

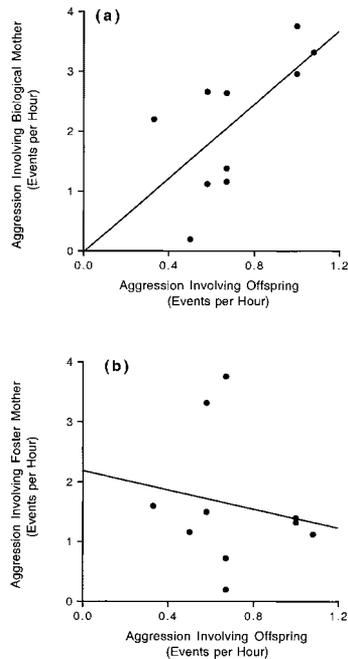
In the first year, offspring affiliation and aggression rates were very low, and linear regression analyses did not reveal any significant association between offspring

behavior and the affiliative and aggressive behavior of their foster or biological mothers. In the second year, offspring resembled their biological mothers in their rates of contact,  $F(1, 9)=10.02$ ,  $r^2=0.56$ ,  $p=0.01$ , and aggression,  $F(1, 9)=6.24$ ,  $r^2=0.44$ ,  $p<0.05$  (Figures 1a and 2a). Offspring rates of contact and aggression tended to be negatively associated with those of their foster mothers in the second year (Figures 1b and 2b), but the linear regressions were nonsignificant. There was no significant association between offspring's and mothers' grooming or submission in the second year.

In the third year, there was no significant relationship between any measures of offspring affiliation or aggression and the correspondent measures for their biological or foster mothers. However, 2 subjects lost their foster mothers in their third year (They died following a short illness period.), and for these subjects, the third year was associated with a sharp change in interaction with other group members, including a reduction in the rate of contact (from about 7–8 events/hr in the second year to about 4–5 events/hr in the third year) and an increase in aggression and submission (They doubled or tripled in the third year for both individuals.) When these 2 individuals were excluded from the analysis, offspring rates of contact and aggression during the third year were significantly predicted by those of their biological mothers, contact:



**FIGURE 1** Linear regression of rate of contact involving offspring in Year 2 and the rate of contact involving biological mothers (a). Linear regression of rate of contact involving offspring in Year 2 and the rate of contact involving foster mothers (b).



**FIGURE 2** Linear regression of rate of aggression involving offspring in Year 2 and the rate of aggression involving biological mothers (a). Linear regression of rate of aggression involving offspring in Year 2 and the rate of aggression involving foster mothers (b).

$F(1, 7) = 7.59$ ,  $r^2 = 0.56$ ,  $p < 0.05$ ; aggression:  $F(1, 7) = 8.71$ ,  $r^2 = 0.59$ ,  $p < 0.05$ , but not by those of their foster mothers. No significant association was found between offspring rates of grooming and submission and those of their biological or foster mothers in the third year after the subjects that lost their mothers were excluded from the analysis.

Finally, when offspring average rates of behavior across the 3 years were calculated (For the 2 offspring that lost their mothers in the third year, part of the third year was excluded from the analysis.), offspring rates of social contact and aggression were still significantly associated with those of their biological mothers, contact:  $F(1, 9) = 6.62$ ,  $r^2 = 0.45$ ,  $p < 0.05$ ; aggression:  $F(1, 9) = 6.42$ ,  $r^2 = 0.45$ ,  $p < 0.05$ , but not with those of their foster mothers, contact:  $F(1, 9) = 0.45$ ,  $r^2 = 0.05$ ,  $p = 0.52$ ; aggression:  $F(1, 9) = 0.16$ ,  $r^2 = 0.02$ ,  $p = 0.70$ . Therefore, despite developmental fluctuations in offspring behavior across the 3 years, some aspects of their affiliative and aggressive behavior in this period were significantly predicted by the behavior of their biological mothers. There was no significant association between offspring rates of grooming or submission across the 3 years and those of their biological mothers, grooming:  $F(1, 9) = 1.04$ ,  $r^2 = 0.11$ ,  $p = 0.34$ ; submission:  $F(1, 9) = 0.04$ ,  $r^2 = 0.01$ ,  $p = 0.85$ , or their foster mothers, grooming:

$F(1, 9) = 0.77$ ,  $r^2 = 0.09$ ,  $p = 0.41$ ; submission:  $F(1, 9) = 0.76$ ,  $r^2 = 0.09$ ,  $p = 0.41$ .

## DISCUSSION

This study showed that cross-fostered young female rhesus macaques resembled their biological mothers in their rates of social contact and aggression in their first 3 years of life, and in particular, in their second and third years. There were no significant associations between offspring behavior and the behavior of their foster mothers in any year. These findings represent the first evidence that primate affiliative and aggressive behavior may be heritable (see Suomi, 1987, for evidence of heritable emotional reactivity), and suggest that biological predispositions for social and agonistic behavior may contribute to intergenerational consistencies in female social preferences and dominance ranks observed in female-bonded primate species.

The sample size of this study ( $n = 10$ ) and the amount of observations per individual were relatively small relative to similar cross-fostering studies of birds (e.g.,  $N > 100$  in Møller, 2002). However, cross-fostering experiments are far more difficult with nonhuman primates than with birds, and previous primate studies using this procedure had an even smaller sample size (e.g.,  $N = 4$ ; Owren et al., 1993). Although, ideally, offspring should have been tested when they reached the same age as their mothers, in practice this is difficult to do in long-lived species such as rhesus macaques (e.g., in this particular study, it would have involved waiting up to 15 years since offspring were born). Furthermore, if offspring had been tested at the same age as their mothers, the comparison might have been confounded by gross differences in the social environment in which mothers and offspring lived (e.g., because group composition in a captive environment such as that of a primate research center may change dramatically in a 10- to 15-year period due to issues of colony management and researchers' needs).

In addition to the difference in age between mothers and offspring, there also was a difference in reproductive condition, as the mothers' social behavior was recorded during the lactation period and in the presence of dependent infants. This was necessary because one of the hypotheses being tested was that similarities between the behavior of mothers and offspring may result from early experience, including early maternal effects, shared environment, or offspring observational learning. Therefore, it was important to document differences in the mothers' behavior during the early lactation period and the early environment to which infants were exposed. If anything, the use of these lactation data for the mothers' behavior biased the data analysis toward finding behavioral

correlations between offspring and foster mothers. However, no such correlations were found. Therefore, it is noteworthy that behavioral similarities between offspring and their biological mothers occurred despite differences in age and reproductive condition. These similarities may have been even more marked if the offspring had been observed as adults and if their mothers had been observed in a period without dependent infants.

Offspring were not similar to their biological mothers in grooming and submission. This raises the possibility that these behaviors are more flexible and dependent on individual or social learning than contact and aggression. However, grooming and submission appeared to be the behaviors with the slowest rates of maturation among those considered in this study. In fact, in the third year of life, offspring rates of grooming and submission were still significantly lower than those of both their biological and foster mothers. Thus, it cannot be ruled out that similarities between mothers and daughters in these social behaviors are more likely to emerge later, when these behaviors reach adult levels of expression. Offspring submissive behavior, in particular, is likely to become similar to that of foster mothers because submission is an important expression of dominance rank, and dominance rank is socially inherited through maternal effects (e.g., Chapais, 1992; Holekamp & Smale, 1991).

The resemblance in rates of social contact and aggression between offspring and their biological mothers could not have resulted from postnatal environmental and experiential factors because offspring and biological mothers lived in different social groups and had no further interactions after birth. Prenatal maternal effects, however, cannot be excluded by the analyses conducted in this study. Paternal genetic contributions to affiliative and aggressive tendencies also are possible, but were not investigated. In addition, it also is possible that the behavioral correlations between offspring and biological mothers resulted from genetically correlated physical characteristics that affect behavior rather than from direct genetic control of behavior itself. The most parsimonious explanation for the findings of this study, however, is that some aspects of female affiliative and agonistic behavior are genetically heritable.

Evidence that some aspects of the affiliative and aggressive behavior of female rhesus macaques are transmitted across generations through genetic inheritance can help us understand the sources of behavioral variability within rhesus macaque groups and how this variability is maintained over time. Because rhesus macaque mothers and daughters usually share the same social microenvironment, evidence for the genetic heritability of affiliative and aggressive behavior raises the possibility that female social behavior may become adapted, by means of natural selection, not only to the ecological environment in which

most rhesus macaques live but also to the specific socio-ecological niche occupied by matriline and individuals within a population or social group. For example, individuals that exhibit “rank-appropriate” behavior (e.g., subordinates who never fight back when attacked by dominants) may have higher chances of survival and reproductive success than individuals that exhibit “rank-inappropriate” behavior (e.g., subordinates with the tendency to be impulsive and to fight back).

The matrilineal structure of macaque societies is quite stable so that there may be consistencies in female dominance and access to resources over long periods of time (e.g., Bernstein, 1969; Chapais, Girard, & Primi, 1991; Sade, 1972; Sade et al., 1977). Thus, it is possible that the behavioral predispositions of particular individuals (e.g., the members of the same matriline) represent adaptations to the social circumstances these individuals will encounter during their lifetime. It also is important that mechanisms be in place to allow fine tuning of behavior or flexible adjustments in relation to environmental changes, whenever they occur. Such mechanisms may include direct maternal encouragement or discouragement of offspring behavior and/or offspring observational learning from the mother’s behavior (e.g., Boesch, 1991; Maestriperieri, Ross, & Megna, 2002). Although studies of other mammalian species have shown that mothers may have long-term effects not only on offspring behavior but also on physiological responses to stress (e.g., in rats; Francis, Diorio, Liu, & Meaney, 1999), maternal effects have been poorly investigated in primates, with the exception of transmission of dominance rank (Chapais, 1992). Thus, it is not clear how possible biological predispositions for affiliation or aggression such as those suggested by this study interact with social learning processes or other maternal and environmental effects to produce the adult phenotype.

Clearly, an individual’s social and reproductive success within a primate society is the result of a complex process involving many environmental and experiential variables. Longitudinal and cross-generational studies including accurate information about kinship can provide crucial information to understand primate social dynamics and the evolution of primate social behavior.

## NOTES

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