Social and Demographic Influences on Mothering Style in Pigtail Macaques

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Abstract

This study represents the first investigation of variability in mothering styles in pigtail macaques, *Macaca nemestrina*. Fifteen group-living mother-infant pairs were focaly observed during the first 12 wk of infant life and several measures of maternal and infant behavior were recorded. Variability in mothering styles occurred along the three dimensions of maternal protectiveness, rejection, and warmth. Maternal parity and aggression received by mothers were the best predictors of variability in protectiveness and warmth, whereas variability in rejection was not predicted by any of the variables considered. This study provides clear evidence that aggression towards mothers and previous maternal experience have an important influence on mothering styles in pigtail macaques.

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Introduction

In recent years, there has been a growing interest in studying individual differences in animal behavior. Animals that share the same environment with other conspecifics may show striking differences in many aspects of their behavior, including foraging, aggression, affiliation, mating, and parenting (see CLARK & EHLINGER 1987 for a review). Although many researchers have concentrated their efforts on understanding the adaptive value of individual differences in behavior, there has also been a growing interest in understanding the determinants of this variability.

In Old World monkeys such as macaques and vervet monkeys, individual differences in maternal behavior are remarkably consistent with successive infants and across generations (FAIRBANKS 1989, BERMAN 1990). Several studies in which data were analyzed with multivariate statistics have demonstrated that variation in mothering styles occurs mainly along the two dimensions of protectiveness and rejection (SIMPSON & HOWE 1980, FAIRBANKS & MCGUIRE 1987, TANAKA 1989, SCHINO et al. 1995). In other words, maternal behaviors reflecting protection and control over the infant’s behavior tend to be correlated with each other and vary independently from behaviors such as breaking contact, increasing distance, and rejecting the infant’s attempts to make contact. In addition
to protectiveness and rejection, Hinde & Simpson (1975) identified a third dimension of mothering style, which they labeled 'warmth': this consisted of maternal behaviors such as cradling and grooming. In Hinde & Simpson's study, however, maternal warmth partly overlapped with protectiveness because maternal cradling and grooming were positively correlated with the mother's tendency to make contact with her infant.

Characteristics of mother–infant pairs such as maternal age, parity, dominance rank, infant sex, and presence and sex of siblings or other relatives have been shown to affect interindividual variability in mothering styles (Fairbanks 1996). The effects of these variables, however, are often highly correlated with each other, thus making it difficult to identify the primary source of variation in mothering style. For example, older mothers are also likely to be more experienced than young mothers, and their infants are more likely to have siblings or other relatives than the infants of young mothers. Moreover, part of the variation in mothering styles is not accounted for by any demographic characteristics of mothers and infants. For example, in a study of rhesus macaques, maternal anxiety measured with visual monitoring and scratching rates was a better predictor of variation in maternal protectiveness than demographic characteristics of mothers and infants (Maestripieri 1993).

The aim of this study was to investigate the determinants of interindividual variability in mothering styles in a captive group of pigtail macaques. This study provides an original contribution to the existing literature on mothering styles in monkeys in two main ways: 1. it is the first investigation of variability in mothering styles in pigtail macaques; and 2. the effects of different maternal characteristics on mothering styles could be independently investigated more fully than in any other previous studies. Specifically, the characteristics of the study subjects allowed the analysis of the effects of maternal parity and dominance rank, infant sex, and the presence and sex of siblings without the confounding effects of maternal age and family size.

Methods

Subjects and Housing

The subjects were 15 pigtail macaque mother–infant pairs living in a social group. The group was housed in a large outdoor compound (25 x 25 m) with attached indoor quarters at the Field Station of the Yerkes Regional Primate Research Center in Lawrenceville, Georgia, USA. The group consisted of five adult males, one subadult male, and 32 adult females, half of which had one yearling offspring. All 32 adult females in the group were caught in the wild when reproductively immature and their genetic relationships were unknown. All females were within the same age range (5–7 yr), thus excluding the presence of mother–daughter pairs among the adult females. Preliminary genetic analysis and phenotypic similarities suggested that there were one or two pairs of sisters or cousins in the group. The group was formed 2 yr before the study and, when observations began, there was already a linear dominance hierarchy among all females which remained stable throughout the study period. Among the 15 study subjects, eight females were primiparous, six had one yearling offspring (three males, three females), and one had given birth in the previous year but her infant had not survived. Five subjects were classified as high ranking, six as middle ranking, and four as low ranking because they fell into the upper, middle, and lower third of the group's dominance hierarchy. Six subjects gave birth to a male infant and nine to a female.

Procedure

Mother–infant pairs were focaly observed (Martin & Bateson 1986) in 4-weekly 30-min observation sessions randomly distributed between 08.00 and 19.00 hours. Observations began the day after infants were
born and continued until the end of the week 12 of infant life. A total of 24 h of observation per mother-infant pair were available. Observations were made from a platform that provided unrestricted view of the entire compound. Data were collected using binoculars and a portable computer.

Since the aim of this study was to investigate individual differences in maternal behavior, most behavioral measures considered are percentage measures so as to control for differences in infant activity. The following eight measures of maternal behavior were considered: 1. percentage cradling = the percentage of mother-infant contact time in which the mother kept her arms around the infant; 2. percentage grooming = the percentage of contact time in which the mother groomed her infant; 3. percentage contacts made by mother = the percentage of all mother-infant body contacts made by mothers; 4. percentage contacts broken by mother = the percentage of all mother-infant body contacts broken by mothers; 5. percentage approaches made by mother = the percentage of all mother-infant approaches made by mothers (an approach is a reduction of mother-infant distance from more than 60 cm to less than 60 cm without making contact for at least 5 s); 6. percentage leaves made by mother = the percentage of all mother-infant leaves made by mothers (a leave is an increase in mother-infant distance from less than 60 cm to more than 60 cm); 7. percentage restraining = the percentage of all infant attempts to break contact that were prevented by the mother pulling the infant by its tail or leg; 8. percentage rejection = the percentage of all infant attempts to make contact that were prevented by the mother turning, running away, or holding the infant at a distance with an arm. The following measures were also considered: percentage time in contact = the percentage of observation time mother and infant spent in body contact; aggression received = the number of aggressive acts (threats, bites, chases) received by mothers from other individuals; infant harassment = the number of acts of harassment (rough pulling, dragging, slapping, or biting) received by infants from other individuals; scratching rate = the rate at which mothers scratched themselves (number of episodes per 1000 s) when their infants were out of contact.

Data Analysis

Interindividual variability in maternal behavior was analyzed in two steps: first, the 8 measures of maternal behavior were analyzed with the principal components analysis (PCA) to investigate correlations between different measures and to obtain composite measures of mothering style. Second, step-wise multiple regression analyses were used to investigate the role of several factors as predictors of variability in the composite measures of mothering style. For purposes of analysis, each subject's average score of maternal behavior over the first 12 wk of infant life was used.

The PCA is a statistical technique used to identify a small number of factors, or principal components, that can be used to represent relationships among sets of many variables (Norusis 1985). The assumption of this analysis is that correlations between variables result from their sharing these factors. In PCA, linear combinations of the observed variables are formed. The first factor is the combination that accounts for the largest amount of variance in the sample. The second factor accounts for the next largest amount of variance and is not correlated with the first. Successive factors explain progressively smaller portions of the total variance and are not correlated with each other. Factor loadings are coefficients of correlation between the factors and the variables and, usually, coefficients of correlation greater than +0.30 or less than -0.30 are arbitrarily chosen as a criterion for loading. Eigenvalues are the sum of the squares of the factor loadings and reflect the total variance explained by each factor. To determine the number of factors considered in the analysis, only factors whose eigenvalue is greater than 1 are included. Because the factors are not correlated, the total proportion of variance explained is just the sum of the variance explained by each factor.

Stepwise multiple regression analysis is a statistical technique that allows one to examine the effects of any number of quantitative or categorical independent variables (predictors) upon a single dependent variable (Pedhazur 1973). In this analysis, the correlations of all the independent variables with the dependent variables are calculated. The independent variable that has the highest zero-order correlation with the dependent variable is entered first into the analysis, followed in subsequent stages by the other independent variables. Because predictors that were entered into the regression equation at an early stage can lose their usefulness when additional predictors are brought into the equation, tests are performed at each step to determine the contribution of each predictor already in the equation if it were to enter last. Linear regression, one-way ANOVAs, and Student's t-tests for unpaired samples were also used in data analysis. All probabilities are two-tailed with $\alpha \leq 0.05$ considered statistically significant.

Results

The developmental changes of maternal and infant behavior over the first 12 wk of infant life, as well as the social interactions between mothers, infants and other individuals
are presented elsewhere (MAESTRIPieri 1994a,b). The PCA applied to the eight measures of maternal behavior identified three factors that accounted for 70.9% of the total variance. Table 1 shows factor loadings and eigenvalues.

In the first factor, percentage contacts made by mother, percentage approaches made by mother, percentage cradling time, and percentage restraining had significant positive loadings. The individual scores of these four measures were thus added to obtain a composite measure of maternal protectiveness. In the second factor, percentage contacts broken by mother and percentage leaves by mother had significant positive loadings. Their scores were added to obtain a measure of maternal rejection. Percentage grooming time and percentage cradling time were positively loaded on the third factor and their scores were added to obtain a measure of maternal warmth. The low frequency and low variability of rejection behavior among the subjects of this study were probably responsible for percentage rejection not being loaded on any of the three factors. Some measures of maternal behavior were highly variable but the results of the PCA did not change when outliers were excluded from the analysis.

The measures of protectiveness, rejection, and warmth served as dependent variables in stepwise multiple regression analyses in which the following variables were used as predictors: maternal rank (high, middle, or low), age (5, 6, or 7 yr), and parity (primiparous, multiparous), sex of the infant (male, female), presence and sex of a sibling (no sibling, brother, or sister), aggression received, and scratching rate. Quantitative information on these variables for all study subjects is presented elsewhere (MAESTRIPieri 1994a,b). There was no statistically significant association between any of these variables. In particular, age did not differ significantly between primiparous and multiparous females (mean age in year ± SE, primiparous: 6.0 ± 0.4; multiparous: 6.7 ± 0.2; t = 0.13, df = 13, ns).

Variability in protectiveness was best explained by parity (R = 0.49, F 1,13 = 4.09, p < 0.05) followed by aggression received (R = 0.69, F 2,12 = 5.63, p < 0.05). Primiparous mothers were more protective (mean score ± SE = 153.97) than multiparous mothers.

**Table 1:** Factor loadings and eigenvalues of PCA applied to eight measures of maternal behavior

<table>
<thead>
<tr>
<th>Behavioral measures</th>
<th>Factor 1 Protectiveness</th>
<th>Factor 2 Rejection</th>
<th>Factor 3 Warmth</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Cradling</td>
<td>0.64*</td>
<td>-0.13</td>
<td>0.51*</td>
</tr>
<tr>
<td>% Grooming</td>
<td>0.44</td>
<td>0.35</td>
<td>0.71*</td>
</tr>
<tr>
<td>% Contacts made</td>
<td>0.70*</td>
<td>0.48</td>
<td>-0.21</td>
</tr>
<tr>
<td>% Approaches made</td>
<td>0.74*</td>
<td>0.37</td>
<td>-0.28</td>
</tr>
<tr>
<td>% Restraining</td>
<td>0.72*</td>
<td>-0.38</td>
<td>0.29</td>
</tr>
<tr>
<td>% Rejection</td>
<td>-0.35</td>
<td>-0.35</td>
<td>-0.45</td>
</tr>
<tr>
<td>% Contacts broken</td>
<td>0.04</td>
<td>0.65*</td>
<td>0.45</td>
</tr>
<tr>
<td>% Leaves</td>
<td>-0.31</td>
<td>0.81*</td>
<td>0.06</td>
</tr>
<tr>
<td>Eigenvalues (% variance)</td>
<td>2.39</td>
<td>1.87</td>
<td>1.39</td>
</tr>
<tr>
<td></td>
<td>(30.0)</td>
<td>(23.4)</td>
<td>(17.5)</td>
</tr>
</tbody>
</table>

*, statistically significant.
(109.18 ± 11.39), and protectiveness increased as a function of aggression received by mothers. Variability in rejection was not significantly predicted by any of the predictors considered, although infant sex had the highest partial correlation with rejection (R = -0.42), with male infants being rejected by their mothers (mean score ± SE = 63.99 ± 6.97) more than female infants (49.83 ± 5.17). Aggression received was the best predictor of maternal warmth (R = 0.53, F 1,13 = 5.10, p < 0.05), the higher the aggression received the warmer the mother with her infant.

To assess whether different mothering styles had significant consequences for infant safety, linear regression analyses were run using infant harassment data and measures of mothering style. Infant harassment, however, was not significantly associated with protectiveness (R = 0.39, F 1,13 = 2.31, ns), rejection (R = 0.16, F 1,13 = 0.35, ns), or warmth (R = 0.06, F 1,13 = 0.05, ns). Infant harassment was inversely related to percentage time in contact (R = -0.57, n = 15, p < 0.05), suggesting that infants that spent less time in contact with their mothers were harassed more by other individuals. Infant harassment did not differ significantly in relation to maternal rank (F 2,12 = 0.77, ns) or parity (t = 0.02, df = 13, ns). There was a tendency for male infants to be harassed more than females (t = 2.05, df = 13, p = 0.06), but this difference was mainly due to one male infant that received unusually high levels of harassment.

Discussion

Variability in the mothering styles of pigtail macaques mainly occurred along the three dimensions of maternal protectiveness, rejection, and warmth. Protectiveness consisted of behaviors reflecting the mother's effort in maintaining proximity and contact with her infant such as approaching, making contact, cradling, and restraining. Pigtail macaque mothers have been shown to be very protective relative to other species of macaques (ROSENBLUM & KAUFMAN 1967, MAESTRIPIERI 1994a), and variation in protectiveness accounted for 30% of total variation in the maternal behavior data. Variation in the mothers' tendency to break contact with their infants and increase distance from them accounted for 23% of the variance. In other Old World monkeys, these behaviors are highly correlated with maternal rejection (FAIRBANKS & McGUIRE 1987, SCHINO et al. 1995), but in this study rejection was relatively infrequent. This study focused only on the first 3 mo of infant life when most pigtail macaque mothers have not yet started to reject their infants (MAESTRIPIERI 1994a). Variability in maternal warmth, reflected by cradling and grooming behavior, accounted for 17% of the variance.

Although the factor analysis of maternal behavior was conducted with a small sample size relative to the number of variables considered, the results of this analysis were generally consistent with the findings reported for other species of Old World monkeys (FAIRBANKS 1996). Maternal age and matriline size have been identified as an important source of variation in macaque mothering styles (BERMAN 1988, SCHINO et al. 1995) and it is noteworthy that variability in the mothering styles of pigtail macaques could be reliably detected despite the fact that all subjects were in the same age range and lived in a group without a typical matrilineal structure.

This study clearly indicates that primiparity has an important effect on mothering style. Parity was the best predictor of variation in maternal protectiveness although the
only difference in parity among the study subjects was that some of the subjects had one previous infant while others did not. The data suggested that it was maternal experience associated with parity, rather than the presence or sex of a sibling, that accounted for variability in protectiveness. Furthermore, the fact that aggression received was the second best predictor of variation in protectiveness suggests that maternal experience may influence the perception of infant safety in relation to danger in the environment (MAESTRIPIERI 1995). Variation in the rejection dimension of mothering style was not significantly associated with any of the predictors considered, while maternal warmth increased as a function of aggression received by mothers. Thus, it appears that when mothers are treated with hostility by other group members they affiliate more with their infants.

Infant sex, maternal age (though only variable between 5 and 7 yr) and scratching rate did not affect any dimensions of mothering style. The lack of an association between scratching and mothering style is somewhat surprising because in rhesus macaques scratching rate was a good predictor of maternal protectiveness (MAESTRIPIERI 1993). Although the reason for this discrepancy is not entirely clear, it may be related in part to the different mothering styles of rhesus and pigtail macaques. Scratching primarily reflects a component of anxiety associated with uncertainty and motivational conflict (MAESTRIPIERI et al. 1992). Rhesus macaques have both high maternal protectiveness and rejection, whereas pigtail macaque mothers have a more marked tendency toward protectiveness (MAESTRIPIERI 1994a). Thus, it is possible that rhesus mothers experience more conflict-related anxiety than pigtail mothers and, as a result, scratching behavior is more strictly associated with mothering style in rhesus than in pigtail macaques.

Individual differences in maternal protectiveness, rejection, or warmth were not significantly correlated with differences in harassment received by infants. Thus, the consequences for infant safety of different mothering styles were not clear. Infants that spent less time in contact with their mothers were harassed more by other group members than infants that spent more time in contact, suggesting that contact with the mother reduced the probability of infant harassment. Time in contact, however, is the result of both maternal and infant behavior and it is unclear from this data set whether high levels of infant harassment resulted from low levels of maternal protectiveness or high levels of infant activity and independence.

Understanding the relationship between danger for the mother–infant pair in the social environment and mothering style is complicated by the difficulty in establishing a clear cause–effect relationship between these two variables. In other words, with observational studies and correlational analyses alone, it is difficult to assess whether levels of aggression and harassment received by mothers and infants are the cause or the consequence of different mothering styles. Research in which mothering style or the social environment are experimentally manipulated is needed to resolve this issue. More research is also needed to better understand the determinants of variability in maternal rejection and the role played by infant characteristics other than their sex.

Acknowledgements

This research was supported by grants from the LEAKY Foundation, the Biomedical Resources Foundation, the Harry Frank GUGGENHEIM Foundation, and NIMH (MH56328). Support was also received from NIH
grant RR-00165 awarded to the Yeager Regional Primate Research Center. The Yeager Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care. I thank Kim Wallen for comments on the manuscript.

Literature Cited


Received: April 14, 1997

Accepted: October 3, 1997 (J. Bruckmann)