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Intraspecific Variability in Parenting Styles of Rhesus Macaques (*Macaca mulatta*): The Role of the Social Environment

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Abstract

This study tested the hypothesis that differences in parenting styles between two captive populations of rhesus macaques, one living in the UK (Madingley) and the other in the USA (Yerkes), are associated with differences in the degree to which social interactions with other group members pose a risk to infants. Twenty-eight mother–infant dyads, 17 living at Madingley and 11 at Yerkes, were observed for 24 h during the first 12 wks of infant life. Mother–infant dyads living at Madingley spent a higher percentage of time in contact than those living at Yerkes. The Madingley mothers also restrained and retrieved their infants more often, and rejected them less often than the Yerkes mothers. Consistent with the prediction, the protective parenting style of the Madingley mothers was associated with higher frequency of infant kidnapping and higher risk of infant harassment from other group members. Interpopulation differences in risks to infants and parenting styles are likely to be the result of differences in social density in the two environments rather than differences in the matrilineal structure of the two populations.

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Introduction

Variability in behavior is often the result of adaptation to the environment and behavioral adaptation can be studied at three different levels of analysis. At one level, conspecifics living in the same social group or population may show differences in many aspects of their behavior in relation to biological (e.g. sex), demographic (e.g. age), social (e.g. dominance rank) or psychological (e.g.

personality) characteristics (Clark & Ehlinger 1987). At the next level, groups or populations of conspecifics may show differences in social structure and behavior in relation to variation in local ecological conditions (Lott 1991). Finally, variation in social and ecological conditions may also account, at least in part, for differences in behavior between closely related species (e.g. Tinbergen 1959). Understanding the proximate determinants and adaptive value of differences in behavior at one level of analysis may also help in the understanding of variation at the other levels. In some cases, the same explanatory principles that account for behavioral differences among individuals can be successfully extrapolated to variation among populations or species.

The validity of this argument can be illustrated by the study of variability in maternal behavior in Old World monkeys. In macaques (genus *Macaca*) and vervet monkeys (*Cercopithecus aethiops*), variability in maternal behavior occurs along the two orthogonal dimensions of Protectiveness and Rejection (Simpson & Howe 1980; Tanaka 1989; Schino et al. 1995; Fairbanks 1996; Maestripieri 1998). In other words, maternal behaviors reflecting protection and control over the infant's behavior tend to be correlated with each other and to vary independently from behaviors such as breaking contact, increasing distance and rejecting the infant's attempts to make contact and nurse. Variation along the two dimensions of Protectiveness and Rejection can result in four different types of parenting styles: Controlling (high in both Protectiveness and Rejection), Protective (high in Protectiveness and low in Rejection), Rejecting (low in Protectiveness and high in Rejection), and Laissez-Faire (low in both Protectiveness and Rejection).

In Old World monkeys, variability in parenting style has been investigated by comparing individuals living in the same social group or population, in different populations of the same species, and also in closely related species. Studies focusing on individual differences have suggested that the extent to which the social environment is a source of stress or support to the mother (or the mother's subjective perception of the environment as stressful or supportive) is an important determinant of variability in parenting style, particularly in the dimension of Protectiveness (for reviews, see Nash & Wheeler 1982; Fairbanks 1996). Comparative studies investigating two or three species of macaques have shown that this general principle can also account for some interspecific differences in parenting styles (Rosenblum & Kaufman 1967; Thierry 1985; Mason et al. 1993; Maestripieri 1994a, b). For example, the Protective and Controlling parenting styles of pigtail macaque (*Macaca nemestrina*) and rhesus macaque (*Macaca mulatta*) mothers are associated with a relatively high risk of infant harassment and kidnapping in these species, while the more relaxed parenting styles of bonnet macaque (*Macaca radiata*) and stumptail macaque (*Macaca arctoides*) mothers are associated with more benign interactions between infants and other group members (Rosenblum & Kaufman 1967; Maestripieri 1994a, b).

Variability in parenting styles among different populations of the same species is poorly understood and only a few comparative studies have been conducted to date. Berman (1980) compared her data on mother-infant

relationships among food-provisioned rhesus macaques living on the island of Cayo Santiago, Puerto Rico, with those previously collected by Hinde and others in the captive colony of Madingley, England (Hinde & Spencer-Booth 1967). Johnson & Southwick (1984, 1987) compared data obtained from free-ranging rhesus populations living in three different habitats in India and Nepal. The data collected by Berman on Cayo Santiago and by Johnson & Southwick in India and Nepal were later compared with a new set of data collected at Madingley by Simpson et al. (1986). Finally, in a study of vervet monkeys, Hauser & Fairbanks (1988) compared data on mother–infant relationships obtained in captivity with those obtained in two different habitats in the field.

These studies reported two main sets of findings. The first one is that the developmental changes in mother–infant interactions during the first few months of infant life are remarkably similar across different populations and environments. For example, the decrease in time spent in contact by mother and infant, the decrease in maternal protectiveness, and the increase in maternal rejection occurring in the first 3 mo were very similar among the rhesus macaque populations of Madingley, Cayo Santiago, and India and Nepal (Simpson et al. 1986). These developmental curves are also similar to those observed in other captive populations of macaques (Maestriperi 1994a). Thus, it appears that there are modal developmental curves for mother–infant interactions that are characteristic of macaques and perhaps of all Old World monkeys that are little influenced by environmental variation.

The second set of findings reported by comparative studies of different groups or populations involves quantitative differences in mother–infant interactions. Berman (1980) reported that mothers and infants living at Madingley spent more time in contact than those living on Cayo. Furthermore, the Madingley mothers played a larger role in maintaining proximity to their infants and rejected them less than the Cayo mothers. Although the cause of these differences in maternal behavior was not immediately apparent, Berman (1980) noted that the data collected at Madingley in later years had greater similarity to the Cayo data than those collected in earlier years. Because in earlier years most of the Madingley mothers were unrelated to each other, Berman suggested that a well-established matrilineal structure favors a relaxed parenting style and that the differences in parenting styles between the two populations could be accounted for by the limited presence of kin groups at Madingley relative to Cayo. In a subsequent study, Simpson et al. (1986) confirmed that rhesus mothers and infants at Madingley spent more time in contact than mothers and infants on Cayo but unlike Berman (1980), they reported that the Madingley mothers were less responsible for maintaining contact with their infants than the Cayo mothers.

The study of rhesus macaques in India and Nepal conducted by Johnson & Southwick (1984, 1987) reported few or no interpopulation differences in maternal protectiveness and rejection. In the authors' view, the few observed differences in mother–infant interactions were unlikely to be caused by differences in the matrilineal structure of the three populations but were likely to be associated with differences in habitat structure and the risk of infant mortality at

each site. Differences in food availability and quality rather than in the risk of infant mortality, however, seemed to account best for the differences in mother–infant interactions among free-ranging vervet monkeys living in a dry woodland habitat and in a swamp habitat (Hauser & Fairbanks 1988). Hauser & Fairbanks (1988) also reported that vervet mothers living in captivity were more protective of their infants than those in the wild and suggested that this difference in parenting style may be result from the higher risk of infant kidnapping in captivity (see also Silk & Kraemer 1978 for a similar suggestion for chimpanzees).

The overall findings of these studies are generally consistent with the hypothesis that differences in the extent to which the social environment poses a risk to infants (along with other ecological variables) play an important role in determining differences in parenting styles among groups or populations of Old World monkeys. Unfortunately, none of the above studies reported data on social interactions between mother–infant dyads and other group members. Therefore, this hypothesis remains to be formally tested.

In the present study, I compared the parenting styles of rhesus macaques living in two captive populations and tested the hypothesis that differences in parenting styles, if any, should be associated with differences in the degree to which the social environment poses a risk to infants. Specifically, I predicted that in populations in which infants are at higher risk of being harassed or kidnapped by other group members, mothers should be more protective, and perhaps also less rejecting, than mothers living in populations in which risks for infants are lower. Differences in the risk of infant harassment/kidnapping and parenting style may or may not also be accompanied by differences in aggressive interactions between mothers and other group members.

Methods

Subjects and Housing

Subjects of this study were 17 rhesus macaque mother–infant dyads housed at the Sub-department of Animal Behaviour of the University of Cambridge in Madingley, UK, and 11 rhesus mother–infant dyads housed at the Field Station of the Yerkes Regional Primate Research Center of Emory University in Lawrenceville, GA, USA. At Madingley, the subjects lived in five captive social groups, each inhabiting an outdoor pen ($8 \times 3 \times 4$ m) connected to an indoor room ($2.5 \times 1.5 \times 2$ m). Each group consisted of a single adult male with three to eight adult females and their subadult, juvenile, and infant offspring (group size = 14–30 individuals). In two of the five groups, all individuals with the exception of the adult male belonged to the same matriline. In the other three groups, individuals from two matriline were present. Five mothers were primiparous and 12 multiparous. At Yerkes, the subjects lived in one social group housed in an outdoor compound (38×38 m) with attached indoor quarters. The group was composed of three adult males and 35 adult females with their subadult, juvenile,

and infant offspring (group size = 92 individuals). At least 10 different matriline were present in the group. Four mothers were primiparous and seven were multiparous. At both Madingley and Yerkes, all animals were fed early in the morning with Purina monkey chow and for a second time in the afternoon with fresh fruit or vegetables. Water was freely available.

Procedure

I collected the data at Madingley from Apr. to Oct. 1991 and those at Yerkes from Apr. to Oct. 1993, using similar procedures. The subjects selected for this study were the first individuals to give birth during the birth season (Apr.–Aug.). I began behavioral observations of the mother–infant dyad the day after the birth of the infant. I observed each mother–infant dyad in four-weekly 30-min observation sessions for the first 12 wks of lactation and collected a total of 672 h of observation (24 h for each mother–infant dyad). Observation sessions were randomly distributed between 08.00 and 19.00 hours. At Madingley, I made observations from the indoor rooms using two-way glass windows that allowed a clear view of each group’s outdoor pen and indoor room. The animals were free to be inside or outside during observation time and were well habituated to observers. At Yerkes, I made observations from a tower that provided an unrestricted view of the entire outdoor compound. The monkeys were locked outside during observation time. In both cases, I collected data using portable computers programmed to allow the collection of frequencies, durations, and sequences of behavior. Data collection included interactions between mothers and offspring as well as interactions between mothers or infants and other group members.

I used the following measures of mother–offspring interactions: (1) percentage of time spent in contact; (2) number of contacts made and broken by mothers and infants; (3) percentage of contacts made by mothers; (4) number of maternal restraining episodes, defined as maternal attempts to prevent infants from breaking contact by pulling them by their tail or legs; (5) percentage of restraining, defined as the percentage of all infant attempts to break contact that were prevented by mothers; (6) number of rejections, defined as maternal attempts to prevent infants from making contact by turning, running away, or holding the infant at a distance with an arm; (7) percentage of rejection, defined as the percentage of all infant attempts to make contact that were prevented by the mother; (8) number of maternal retrieval episodes, defined as instances in which the mother rushed to pick up her infant; and (9) maternal grooming, calculated as the percentage of time spent in contact in which the mother groomed her infant.

In addition to mother–offspring interactions, I recorded the following behavioral measures: (1) number of aggressive acts (threats, bites, and chases) shown and received by mothers; (2) number of infant handling episodes, defined as interactions in which an infant was gently touched, groomed or carried by another individual; (3) number of infant harassment episodes, defined as interactions in which an infant was roughly pulled, dragged, hit or bitten by

another individual and where the infant displayed a clear sign of distress such as screaming or jerking; (4) percentage of harassment, defined as harassment/(handling + harassment) \times 100; and (5) number of kidnapping episodes, defined as interactions in which an individual prevented an infant from returning to its mother (e.g. by holding it by the tail or leg) for more than 1 min while the infant was actively trying to return to its mother. I also recorded the number of times mothers scratched themselves and the scratching rate (number of scratching episodes \times 1000 s) when the infant was out of contact with its mother. Scratching was recorded to obtain information about maternal anxiety (Maestriperi 1993a). Dominance rank of all mothers relative to other adult females in their group was assessed on the basis of aggressive interactions. High, middle, or low rank was assigned depending on whether the mothers' rank fell into the top, middle or bottom third of their group's hierarchy. Of the Madingley mothers, four were classified as high ranking, seven as middle ranking, and six as low ranking. Of the Yerkes mothers, three were classified as high ranking, five as middle ranking, and three as low ranking.

The frequencies and durations of behaviors recorded in the four-weekly observation sessions were summed and then averaged across the 12 wks. Comparisons between data collected at Madingley and Yerkes were conducted with the Mann–Whitney *U*-test and the χ^2 test. All tests were two-tailed unless otherwise specified and probabilities ≤ 0.05 were considered statistically significant.

Results

Preliminary analyses showed that the five captive groups at Madingley did not differ significantly in any of the behavioral measures considered in this study (one-way analysis of variance, all results are nonsignificant; see Simpson & Howe 1986 for similar findings). The Madingley mothers did not differ significantly from the Yerkes mothers in their age (Madingley, mean \pm SEM = 7.41 \pm 0.86 yr; Yerkes, mean \pm SEM = 6.54 \pm 0.56 yr; $z = -0.19$, ns), parity ($\chi^2 = 0.15$, $df = 1$, ns), dominance rank ($\chi^2 = 0.2$, $df = 2$, ns) or infant sex (Madingley, 12 males, five females; Yerkes, seven males, four females; $\chi^2 = 0.15$, $df = 1$, ns).

The Madingley mothers spent a higher percentage of time in contact with their infants than the Yerkes mothers (Madingley = 75.29 \pm 2.07; Yerkes = 61.65 \pm 1.84; $z = -3.27$, $p = 0.001$). The Madingley mothers also displayed a higher number of restraining episodes ($z = -2.28$, $p < 0.05$) as well as a lower number of rejection episodes than the Yerkes mothers ($z = -2.50$, $p < 0.01$; Fig. 1). Because the number of restraining and rejection episodes could be influenced by differences in infant activity, the percentage of restraining and rejection were also compared. Again, the Madingley mothers displayed a higher percentage of restraining and a lower percentage of rejection than the Yerkes mothers (% restraining, $z = -2.18$, $p < 0.05$; % rejection, $z = -2.04$, $p < 0.05$; Fig. 1). Thus, differences in maternal restraining and rejection occurred irrespective of possible differences in the infants' tendency to make or break

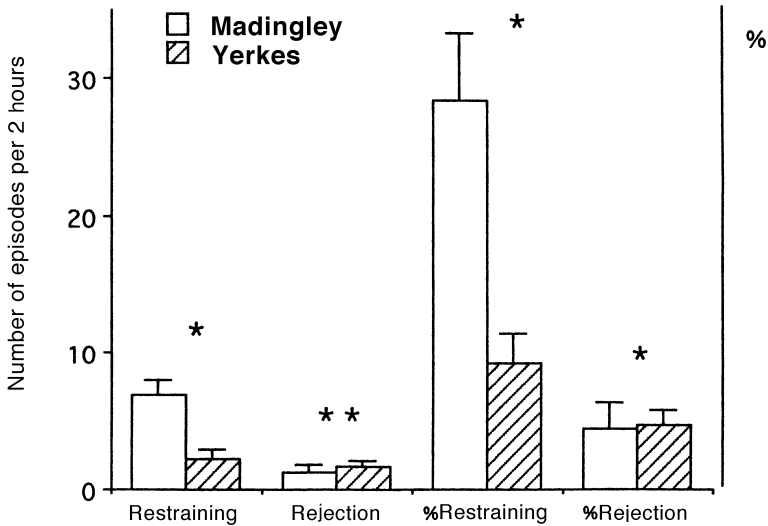


Fig. 1: Mean number (\pm SEM) of restraining and rejection episodes and mean (\pm SEM) percentage of restraining and rejection per individual per week (2 h of observations) in the Madingley and Yerkes populations. The two Y axes have the same scale; * $p \leq 0.05$; ** $p \leq 0.01$

contact with their mothers. In addition to differences in restraining and rejection, the Madingley mothers also retrieved their infants more frequently than the Yerkes mothers (Madingley = 6.17 ± 1.01 ; Yerkes = 2.36 ± 10.37 ; $z = -2.92$, $p < 0.01$). No significant differences, however, between the Madingley and the Yerkes mothers were found for the percentage of contacts made by mothers (Madingley = 36.39 ± 3.67 ; Yerkes = 27.35 ± 1.16 ; $z = -1.62$, ns) and the percentage of time spent grooming the infant (Madingley = 4.39 ± 0.94 ; Yerkes = 3.95 ± 0.76 ; $z = -0.02$, ns).

To test the hypothesis that the higher levels of maternal protectiveness and lower levels of maternal rejection observed at Madingley relative to Yerkes were associated with differences in the social environment, some social interactions between mother-infant dyads and other group members were compared between the two locations. There were no significant differences in aggression shown (Madingley = 2.55 ± 0.47 ; Yerkes = 2.72 ± 0.38 ; $z = -0.78$, ns) or received by mothers (Madingley = 1.76 ± 0.28 ; Yerkes = 1.42 ± 0.23 ; $z = -0.77$, ns). Infants were handled by other individuals more frequently at Yerkes (17.67 ± 1.67) than at Madingley (8.08 ± 0.96 ; $z = -3.88$, $p = 0.0001$), while the number of infant harassment episodes was not significantly different (Madingley = 2.08 ± 0.32 ; Yerkes = 1.86 ± 0.47 ; $z = -0.8$, ns). The percentage of harassment, however, was significantly higher at Madingley (26.59 ± 3.30) than at Yerkes (9.86 ± 2.23 ; $z = -3.41$, $p = 0.0006$). In other words, when an infant was handled by another individual, there was a much greater probability that the infant would be harassed at Madingley than at Yerkes. The number of

kidnapping episodes was also significantly higher at Madingley (0.72 ± 0.14) than at Yerkes (0.44 ± 0.12 ; $z = -1.98$, $p < 0.05$). Moreover, at Madingley, it was necessary to intervene and return the infant to its mother on at least three occasions, when an infant had been held by a kidnapper for several hours. At Yerkes, external intervention was never necessary. Data analyses reported elsewhere showed that adult females were responsible for most episodes of infant harassment and kidnapping at both Madingley and Yerkes (Maestriperi 1993d, e, 1994b).

The frequency with which mothers scratched themselves was significantly higher at Madingley (31.41 ± 3.17) than at Yerkes (20.28 ± 1.48 ; $z = -2.70$, $p < 0.01$). Because infant handling was more likely to involve harassment at Madingley than at Yerkes and because most infant harassment occurs when the infant is out of contact with its mother, it was expected that the rate of scratching when the infant was out of contact would be higher at Madingley than at Yerkes. Although the scratching rates differed in the direction predicted, the difference was not statistically significant (Madingley = 10.05 ± 1.23 ; Yerkes = 7.80 ± 0.58 ; $z = -0.73$, one-tailed test, ns).

Discussion

This study revealed several quantitative differences in mother–infant interactions between two captive populations of rhesus macaques, one living at Madingley, Cambridge, UK, and the other at the Yerkes Primate Center in Lawrenceville, GA, USA. Developmental changes in mother–infant interactions were not directly compared between these two populations because they were already known to be remarkably similar (Maestriperi 1993a, 1994a).

Mother–infant dyads living at Madingley spent a higher percentage of time in contact than those living at Yerkes. This is consistent with Berman's (1980) and Simpson et al.'s (1986) finding that Madingley mothers and infants spent more time in contact than those living on Cayo Santiago, Puerto Rico. Differences in time spent in contact could result from differences in maternal behavior, infant behavior, or both. One possible explanation for the difference in mother–infant contact time is that it simply reflects a difference in ambient temperature. Macaque mothers and infants may be expected to spend more time in contact at lower temperatures than at higher temperatures (Dahl et al. 1986; but see Schino & Troisi 1998) and temperature is generally lower in the UK than in the Southern USA or Puerto Rico (e.g. when rhesus infants are born at Madingley the temperature is, on average, 10–15°C lower than at Yerkes). Although an effect of temperature on mother–infant contact is plausible, other differences in mother–infant interactions are unlikely to be the result of climatic factors.

In the present study, the Madingley mothers restrained and retrieved their infants more often, and rejected them less often, than the Yerkes mothers, even when potential differences in infant activity were taken into account (differences in rejection, however, were less marked than those in protectiveness and statistical significance may have been an artifact of the nonparametric test). Thus, the

Madingley mothers were generally more protective than the Yerkes mothers. Again, these data are consistent with those reported by Berman (1980) showing that rhesus mothers living at Madingley were more protective than those living on Cayo. Although Berman (1980) speculated that interpopulation differences in parenting styles may have resulted from differences in matrilineal structures of the two populations, this study suggests a different explanation.

At the time when the Madingley data presented here were collected, the rhesus groups had strong matrilineal structure. Except for the adult males, two groups consisted of a single matriline, and three groups consisted of two matrilines. Therefore, the average degree of relatedness between mothers and other group members was higher at Madingley than at Yerkes, where at least 10 different matrilines were present in the social group. Berman (1980) hypothesized that being surrounded by close kin promotes a relaxed parenting style. However, this study reported differences in parenting styles between the Madingley and the Yerkes populations that are opposite to those predicted by this hypothesis. The differences in parenting styles between vervet monkeys living in captivity and in the wild reported by Hauser & Fairbanks (1988) were also in the opposite direction to that which would be predicted from differences in matrilineal structure. Therefore, differences in matrilineal structure are unlikely to be the main determinant of differences in parenting style between populations of Old World monkeys.

The interpopulation differences in maternal protectiveness and rejection reported here are consistent with the hypothesis that differences in parenting styles are associated with differences in the degree to which the social environment poses a risk to infants (Maestripieri 1993b, c, 1994b). Although the frequency of infant handling was generally lower at Madingley than at Yerkes (perhaps because of differences in the number of individuals that had the opportunity to interact with infants or differences in maternal protectiveness), infant handling was more likely to involve harassment at Madingley than at Yerkes. Moreover the number of kidnapping episodes, and in some cases also their duration, was also higher at Madingley than at Yerkes. Therefore, interactions between infants and other individuals were potentially more dangerous to infants at Madingley than at Yerkes, thus explaining the protective parenting style of the Madingley mothers. These findings lend support to Hauser & Fairbanks's (1988) suggestion that higher risk of infant kidnapping in captivity may have been responsible for differences in maternal protectiveness between captive and free-ranging vervet monkeys.

The higher frequencies of scratching observed at Madingley also provide indirect evidence that the mothers in this population lived in a riskier or more stressful social environment than the Yerkes mothers. Scratching is a good indicator of anxiety in macaques (Maestripieri 1993a) and interpopulation differences in scratching rates suggest either that these populations are exposed to different levels of anxiety-eliciting situations or that they differ in emotional reactivity to the environment (i.e. in their temperament). In this study, the Madingley and Yerkes mothers did not differ significantly in the frequency of

aggression received from other group members. Thus, differences in scratching rates probably reflected differences in the risk of infant harassment and/or kidnapping. This is likely to be the case even though the rates at which mothers scratched themselves when infants were out of contact were not significantly different at Madingley and Yerkes. It is possible that the Madingley infants were at higher risk from other group members than the Yerkes infants not only when they were out of contact with their mothers but also during contact time. For example, in many cases the infants at Madingley were pulled away from their mothers and kidnapped while still in contact with their mothers (see Maestripieri 1993a for rates of infant harassment when infants were in or out of contact with their mothers).

Although the present data support the hypothesis linking variability in parenting style and risks to infants, a question arises as to why such risks were higher at Madingley than at Yerkes. Since infant kidnapping and harassment are probably best viewed as a form of competition among adult females (Silk 1980; Maestripieri 1993c), it may be surprising that infants were at higher risk from other group members in smaller groups composed of closely related females than in a larger group with many individuals unrelated to each other. This finding is not surprising, however, if we consider that in rhesus macaques aggression is often most frequent between closely related individuals (although aggression between kin can be of relatively low intensity; Walters & Seyfarth 1987), and that aggression may increase under conditions of high social density (Southwick 1969).

The limited availability of space for social interactions for the rhesus macaques living at Madingley relative to those living at Yerkes or on Cayo Santiago, perhaps coupled with structural differences in space, may ultimately have been the main factor responsible for the observed differences in parenting styles. In fact, density was about 10 times higher at Madingley (about 0.5 individuals/m²) than at Yerkes (about 0.06 individuals/m²). Thus, it is possible that infants were more accessible to potential harassers or kidnappers under the higher density population. Alternatively, it is possible that individuals under high-density conditions were less tolerant of the annoying behavior that infants sometimes exhibit, and therefore more likely to behave roughly to them. For example, Judge & De Waal (1993) reported that rhesus infants tended to be the targets of more rough behavior during short-term crowding and suggested that this may have been the result of lower tolerance for infant rambunctious behavior at close quarters. Although adult individuals cope with the increased risk of aggression under high-density conditions by increasing the frequency of grooming (Judge & De Waal 1997), such coping strategies are not available to infants. Thus, if restriction of space increases the risk of infant harassment, it is the infants' mothers that must reduce such an increased risk by adjusting their parenting style. The findings of this study suggest that this may indeed be the case. Therefore, this study provides an example of how variation in an ecological parameter (social density) may be responsible for a change in behavior (parenting style) and highlights the need to take social density into account when comparing the behavior of different populations of the same or different species.

Clearly, the hypothesis that interpopulation differences in parenting styles result from differences in density and their consequences for infant safety needs to be further investigated in a more systematic fashion. The results of this study and their interpretation must also be confirmed by further interpopulation comparisons in which data are obtained from more than one social group for each population. This will ensure that the observed differences in behavior reflect true differences between populations and not just between groups. Indeed, the investigation of intergroup variability can complement the study of interindividual, interpopulation, and interspecific differences and make an important contribution toward a comprehensive understanding of the determinants of different parenting styles in primates and their consequences for development.

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