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Long-Term Effects of Infant Rearing Condition on the Acquisition of Dominance Rank in Juvenile and Adult Rhesus Macaques (*Macaca mulatta*)[†]

ABSTRACT: *We examined the effects of early rearing experience on the development of dominance status in 53 juvenile (age 3) and then in 38 adult (ages 5–8) rhesus macaques. Based on previous research investigating the behavioral outcomes of nursery-rearing, we predicted that mother-reared (MR) monkeys would outrank peer-only reared (PR) monkeys, which would in turn outrank surrogate/ peer-reared (SPR) subjects. Juvenile MR and PR subjects did not differ in ranks, but monkeys from both rearing backgrounds outranked SPR cage-mates at age 3. Independent of rearing condition, high-ranking juveniles gained the most weight between ages 1–3, suggesting that low status may be associated with decreases in early weight gain. Adult MR subjects outranked both PR and SPR subjects, with PR animals occupying intermediate ranks. These results indicate that impoverished early experiences, such as adult absence and limited social interaction, are useful predictors of future social success in rhesus macaques. Published 2003 Wiley Periodicals, Inc.[†] Dev Psychobiol 42: 44–51, 2003.*

Keywords: *rhesus monkey; rearing condition; aggression; dominance; weight gain*

The quality and nature of early experience and physical attachment play essential roles in the acquisition of skills necessary for the development of competent social behavior and alliances in groups of socially-living primates (Bowlby, 1982). In both human and non-human primate species, an individual's dominance status and survival may depend heavily on its ability to function socially (Sameroff & Suomi, 1996). Previous research

suggests that the ability to form stable social alliances and to appropriately express aggression is critical to the acquisition of social status, lifetime reproductive success, and ultimate survivorship (Fairbanks & McGuire, 1984; Higley, Linnoila, & Suomi, 1994).

The mother–infant bond is the most fundamental early relationship in primates and is critical to developing the social skills necessary to succeed in securing mates, physical resources, and long-lasting bonds and alliances. The mother's primary role during this period is to facilitate the development of emotional stability (Alexander & Harlow, 1965; Sameroff & Suomi, 1996). Primate infants spend their first weeks of life either in constant physical contact or within arm's reach of their mothers, who provide nourishment, protection, and comfort. By the second month of life, the infant has established a strong bond with its mother and uses her as a "secure base" from which to explore its immediate environment (Suomi, 1995; Sameroff & Suomi, 1996). As Bowlby notes, young non-human primate infants continue to seek secure

attachment to their mother or other primary attachment figure throughout infancy (Bowlby, 1982).

Monkeys reared without conspecifics for the first few months of life initiate and reciprocate lower rates of play later in life when compared to their mother-reared peers (Harlow & Suomi, 1970). Results of one of the few early studies that investigated the long-term outcomes of early social isolation revealed that physical contact, either with peers prior to adulthood or with their own infants immediately after birth, decreases the possibility that monkeys reared without mothers will develop inadequate maternal behavior themselves (Ruppenthal, Arling, Harlow, Sackett, & Suomi, 1976). Several investigators have reported results that indicate an inadequate development of aggressive, affiliative, play, and sexual behavior in monkeys reared on surrogates but without access to either adults or age-mate peers (Alexander & Harlow, 1965; Capitanio, 1986; Higley et al., 1994; Mitchell, 1970).

Infant monkeys removed from their mothers shortly after birth will establish attachment bonds with age-mate peers or even with artificial surrogates or other inanimate objects (Champoux, Shannon, Airoso, & Suomi, 1999; Higley, Hopkins, Thompson, Byrne, Hirsh, & Suomi, 1992; Suomi & Harlow, 1972). Peer-rearing compensates for many of the deficits seen in infants raised without conspecifics (Harlow & Harlow, 1965). As infants, however, these subjects display high levels of anxiety-like ventral-ventral clinging, behavior withdrawal, and high levels of stress hormones (Champoux, Coe, Schanberg, Kuhn, & Suomi, 1989; Clarke, Wittwer, Abbott, & Schneider, 1994; Fahlke, Lorenz, Long, Champoux, Suomi, & Higley, 2000; Higley, Hasert, Suomi, & Linnoila, 1991).

For young primates, obtaining the skills necessary to interact socially with peers and to use aggression appropriately is a major developmental task. Because overly aggressive monkeys may risk social ostracism from their conspecifics, the appropriate use of aggression is critical for both acquiring and maintaining social status throughout development. Previous studies show that rhesus monkeys reared for the first 6 months of life with unrestricted access to other age-mate peers but without mothers or other adults in a peer (only)-reared condition (PR) display inappropriate aggression and disturbed social relationships relative to monkeys reared by their mothers. (Alexander & Harlow, 1965; Higley et al., 1992; Mitchell, 1970; Suomi, 1982). PR monkeys are also more likely than their mother-reared (MR) counterparts to be removed from their social groups for excessive aggression and to display signs of psychopathology, including excessive alcohol intake when tested later in life for differences in voluntary alcohol consumption (Fahlke et al., 2000; Higley et al., 1991; Higley & Suomi, 1996),

antisocial behaviors, and impaired social competence (Higley, Suomi, & Linnoila, 1996a,b).

Both the theory and methods of measuring social dominance have been widely explored (Bernstein, 1981; Boyd & Silk, 1983; Zumpe & Michael, 1986). Numerous studies report evidence of social deficits in young primates reared in the absence of their mothers or other adults (Capitanio, 1984; Ruppenthal et al., 1976; Sackett, 1967). Yet few have reported data that directly investigated the longer-term effects of alternative rearing conditions on behaviors such as social dominance status. This paper explores the impact of alternative infant rearing conditions on the acquisition of dominance status in rhesus monkeys from three different rearing backgrounds and two different age groups to determine the long-term effects of early experience on social functioning and impairment. Subjects were reared for the first 6 months of life with their mothers in social groups (MR condition), with unrestricted access to peers (PR condition), or with continual access to artificial surrogate "mothers" and 2–3 h of exposure to peers in a surrogate/peer-reared (SPR) condition. Thereafter, all three groups were combined and received identical treatment.

We hypothesized that infant rearing condition would significantly affect relative dominance rank in both juvenile and adult subjects. While both PR and SPR monkeys display regressive, infantile behaviors (Higley et al., 1992), previous casual observations suggest that SPR monkeys exhibit a particularly high incidence of rocking and other abnormal stypic and stereotypic behaviors that may interfere with competent social functioning as these animals mature. We therefore predicted that both early in life and through adulthood, MR monkeys would outrank their PR and SPR counterparts and PR subjects would rank higher than their SPR cage-mates. This developmental assessment of subjects at different life stages also allowed us to assess how dominance may affect such biological variables as weight gain. While other researchers have assessed reproductive outcomes and survival rates in high- and low-ranking monkeys, we know of no previous studies that have investigated how having high or low rank might affect growth rates in nonhuman primates. This question is ideally suited for study in the laboratory, where food availability is controlled and weight gain can be measured repeatedly. We expected that low-ranking monkeys would show slower growth than high-ranking monkeys.

METHODS

Subjects and Housing

Study I. Fifty-three juvenile rhesus macaques (25 males, 28 females), selected from 2 separate birth-year cohorts (N = 26–27

subjects in each cohort), were studied during their third year of life at the NIH Animal Center's rhesus colony. Of these, ten subjects were "mother-reared" (MR), raised in social groups either by their biological mothers or by unrelated, multiparous foster mothers. Preliminary analyses showed no difference between the relative dominance ranks of subjects reared by either their biological or foster mother. They were, therefore, combined for the purposes of analysis. Twenty-one infants were reared without adults but with constant access to age-mate peers in a "peer-only reared" (PR) condition, and 22 infants were reared with inanimate surrogates and limited peer interactions in a "surrogate/peer-reared" (SPR) condition for the initial 6 months of life (procedure detailed in Champoux et al., 1999). Subjects in each birth-year cohort were socially housed in $7.3 \times 3.4 \times 3.7$-m indoor enclosures equipped with perches, barrels, swings, and wood shavings at the time of study.

Study II. Thirty-eight sexually mature adult female rhesus macaques were selected from three separate birth-year cohorts and had been reared under the same conditions described in Study I. Fifteen subjects were MR, 6 were PR, and 17 were SPR. Of these, 17 subjects were studied at 5 years of age, 13 at 6 years of age, and 8 at 8 years of age. The 5- and 6-year-old females were housed with two adult males and the 8-year-old females were housed with one adult male. Although males were present during data collection, interactions recorded between males and females were not analyzed for the purposes of this study. Subjects from each birth-year cohort were socially housed in indoor ($2.4 \times 2.4 \times 3.05$ m)/outdoor ($2.68 \times 2.74 \times 2.77$ m) enclosures equipped with perches, barrels, swings, and wood shavings. During data collection, subjects were confined to the outdoor portion of their enclosure to ensure visibility.

Early Rearing Conditions

During the first 6 months of life, MR subjects had constant access to the outdoors and remained with their mothers in a stable social group with 10–15 other adults and peers. Both PR and SPR subjects were separated from their mothers 1–3 days postpartum and were subsequently raised for 30 days in a neonatal nursery according to the procedure described by Ruppenthal (1979). At 31 days of age, PR monkeys were moved with their spring-mounted, terrycloth-covered surrogate "mothers" to $71 \times 81 \times 152$ cm cages, where they were constantly housed with 3–4 other age-mate peers. SPR monkeys were housed individually with their surrogates in $64 \times 61 \times 76$ cm cages, equipped with a hanging plastic chain, toys, and blankets for 21–22 h each day, with 2–3 h of daily social interaction in a play group of 4–5 peers. SPR monkeys differed from PR monkeys only in the amount of time that they were allowed to interact with their age-mates each day. This difference lasted only through the first 8–9 months of life.

At approximately 6 months of life, MR and PR infants underwent temporary social separations as part of an ongoing study (Champoux et al., 1999). At approximately 1 year of life, infants from all three rearing conditions born in the same year were placed together into a single large social group without adults as one of two birth-year cohorts. Thereafter, the monkeys from each rearing condition received identical treatment. Within

each of birth-year cohort, there was an average range in age of 6 months between the oldest and youngest member of the group. In Study I, all juvenile subjects were assessed for relative dominance rank within their social group. In Study II, each adult female subject lived in a social group with 1–2 adult males, 7–17 adult female peers from their original birth-year cohort, and their associated offspring during the time of data collection.

Behavioral Data Collection Procedure

For Study I, over 7–10 separate sessions, a total of approximately 1,850 dyadic agonistic interactions were recorded for each cohort when subjects were in their third year of life, with sessions lasting approximately 45 min each. In Study II, over the course of 9–10 sessions, between 550–1,030 dyadic interactions were recorded for each cohort when subjects were in their fifth, sixth, or eighth year of life respectively, with sessions ranging from 30–45 min. Two or three researchers observed and recorded agonistic interactions from a position outside the monkeys' enclosure. In Study I, each pair of investigators reached inter-observer agreement to 95% for approximately 300 specific dyadic interactions recorded during trial sessions for each cohort. In Study II, a videotaped recording of a sample data collection session was used for training to establish inter-rater reliability to a criterion of 95% concordance.

Intragroup conflict was elicited by offering limited quantities of valued food incentives (e.g., peanuts, popcorn, and various fruits), which were selectively thrown or handed to the animal to create dyadic challenges. Aspartame-sweetened water bottles were selectively hung on the side of the cage to elicit further competition. Bouts of spontaneous agonistic behaviors that were observed but not directly elicited by a food treat were also recorded. Because dominance rank does not necessarily predict which of two individuals is more likely to acquire a prized food item (Bernstein, 1969; Strum, 1982), and because it increases the number of interactions, food incentives were used to initiate more frequent interactions between subjects so as to elicit dyadic competition, but the identity of which individuals retained the treats was not recorded.

Relative dominance status was assessed by recording the occurrence of displacements and aggressive interactions during competitive social encounters. Both the initiator and recipient of each observed interaction were noted. Ranks were determined within each cohort by recording the frequency and direction of five principle agonistic behaviors: 1) Displacement: Monkey retreats or abandons its space or an object in the presence of or upon the approach of another monkey from a distance of <2 m; 2) Threat: Bark vocalizations, head bobs, and/or direct stare. May be accompanied by an open mouth; 3) Chase: Monkey pursues another monkey from a distance of >2m (does not include chases in a play context); 4) Contact Aggression: Aggressive physical contact in the form of a bite, slap, shove, pounce, hair or skin pull, and lasting <3 s; and 5) Escalated Contact Aggression: Contact aggression >3 s.

Data Analysis

Dominance Status. We determined relative social status by calculating dominance rank indices based on a matrix table with

row headings that bore the names of initiators and column headings that bore the names of receivers of each target behavior. Each cell, therefore, represented a dyadic relationship. A subject was scored as the "winner" of an interaction if it displaced another subject or initiated an aggressive encounter. It was scored as a "loser" if it was displaced or aggressed by the other animal. Social dominance rankings were obtained by assessing the directionality of wins for each subject when in direct competition with each of the other subjects, a well-established method of assessing dominance ranking in non-human primates (Bramblett, 1981; Higley et al., 1996b). A subject was considered more dominant than another subject when it won more encounters than it lost with that other subject. Tied ranks were considered the same as "no interactions" and were not included in subsequent analyses.

In order to reflect the relative degree to which each subject was dominant over another subject, we generated dominance rank indices by dividing the numerical rank of each subject by the total number of individuals in the group with which each subject could have interacted [X/(N−1)], resulting in the percentage of animals within each cohort to which a given subject was dominant. These rank indices were divided proportionately into high, mid-high, mid-low, and low-low relative dominance categories for the purposes of conducting ANOVAs in which dominance rank was the independent variable. One recognized limitation of our data analysis with the adult groups is that these groups varied in size between 8–17 subjects, while groups size ranged only between 26–27 subjects among the juveniles.

Statistical Analyses. Two juvenile subjects were over 2 *SD* (6 months) older than the average subject in their cohort and were therefore excluded from all analyses. Two subjects were excluded from the adult dataset. Not only were both of these subjects over 2 *SD* older than the average subject in their cohort, one subject was introduced into the cohort several years after the other group members and the other subject was removed from the group repeatedly for veterinary care during the course of the study. Preliminary analyses indicated that weight varied across cohorts in both studies. In order to conduct formal statistical tests in which weight was a variable, raw weight scores (kg) for each subject were transformed into Z-scores, and these cohort-controlled standard scores were used in all subsequent analyses. Pearson correlation, multiple regression, factorial analysis of variance (ANOVA), or analysis of covariance (ANCOVA) with Fisher's PSLD post-hoc comparison were used to test the relationships between various independent variables and dominance status. While it would have been ideal to separately assess dominance status for each sex in juvenile subjects, sample sizes for each rearing condition were not large enough to conduct separate tests. An alpha significance level of .05 was used for all analyses.

RESULTS

Study I

Among the juveniles, dominance rank correlated significantly and positively with within-cohort months of

age, r (51) = .32, $p < .05$. While there was no significant difference found between the weights of male and female subjects at year 3, a positive linear relationship was detected between age and weight, r (51) = .34, $p < .05$. Moreover, while juvenile social dominance status could not be predicted by weight measured just prior to group formation (at approximately 1 year of life), weight measurements taken at the end of the study positively correlated with year 3 social dominance ranks, independent of rearing condition, r (51) = .46, $p < .01$. Year 3 dominance rank was also predictive of weight gain between group formation and year 3, $F(3,49) = 4.59$, $p < .01$ (Figure 1).

Multiple regression analysis indicated that weight, but not age, was a significant predictor of dominance status at year 3, r (51) = .50, $p < .01$. Only weight, therefore, was controlled for in subsequent analyses with dominance status as the dependent variable. With weight controlled, age was not a significant predictor of juvenile dominance status.

One-way ANOVA analyses revealed a significant effect of both rearing condition, $F(2,50) = 4.93$, $p < .05$, and sex, $F(1,51) = 4.94$, $p < .05$, on juvenile dominance indices. When we included weight at year 3 as a covariate in a two-way ANCOVA with rearing condition and sex as the factors and dominance status as the dependent variable, interaction effects on dominance were detected between rearing condition and sex, $F(2,41) = 3.53$, $p < .05$, and between rearing condition and weight, $F(2,41) = 10.28$, $p < .01$. Post hoc tests revealed that PR subjects had attained higher rank than SPR subjects by the third year of life. With weight controlled, only rearing condition showed a significant main effect on dominance, $F(2,41) = 10.57$, $p < .01$. While MR and PR subjects did not differ in dominance status, both MR and PR subjects
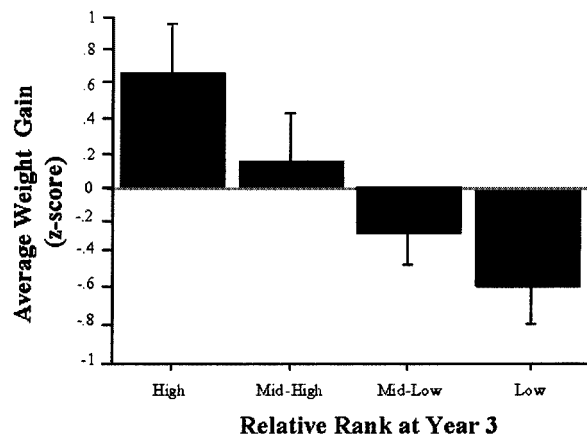

FIGURE 1 Between group formation (approximately 1 year of life) and year 3, more dominant subjects gained more weight than less dominant subjects, $F(3,49) = 4.59$, $p < .01$.
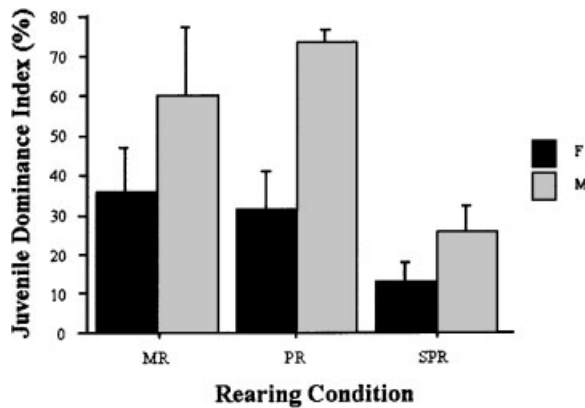
FIGURE 2 With weight controlled, interaction effects on year 3 dominance status occurred between early rearing condition and sex and between rearing condition and weight. Of these three variables, only rearing condition had a significant main effect on dominance status. While no difference was demonstrable between MR and PR subjects, subjects from both rearing conditions outranked their SPR cage-mates, $F(2,41) = 10.57$, $p < .001$.

significantly outranked their SPR cage-mates, $p < .01$ (Figure 2).

Study II

Subjects assessed for dominance as adults did not differ in status according to either within-cohort age or weight. In an attempt to rule out the possibility that pregnancy status (not pregnant with/without infant; pregnant with/without infant) affected dominance status, an ANOVA was performed, revealing no significant relationship between pregnancy status and dominance rank at the time of data collection. There was, however, a significant relationship between early rearing condition and adult dominance status, $F(2,35) = 16.55$, $p < .0001$. Fisher's PSLD post-hoc comparison revealed that adult MR monkeys were more dominant than either PR subjects ($p < .02$) or SPR subjects ($p < .0001$). This test also demonstrated that PR subjects ranked higher than SPR subjects by a nearly-significant trend of $p = 07$ (Figure 3).

DISCUSSION

In accordance with our hypothesis, the results indicate that differences in early rearing experiences have a long-lasting effect on the development of dominance status in rhesus macaques. Consistent with initial predictions, MR monkeys were found to rank significantly higher than their SPR cage-mates when assessed for relative status both as juveniles and as adults. This finding is also consistent with
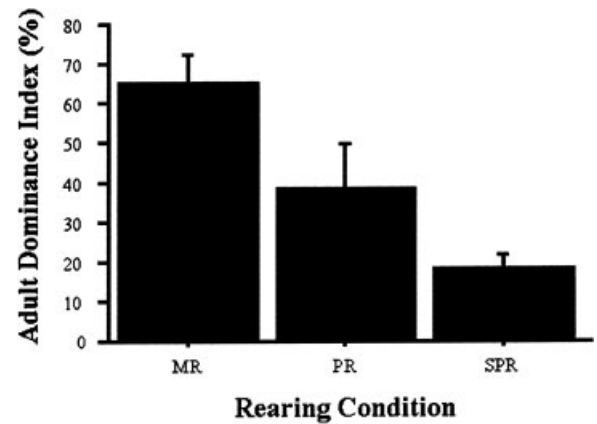

FIGURE 3 Adult MR subjects (ages 5–8) outranked both PR and SPR subjects with PR animals occupying intermediate ranks, $F(2,35) = 16.55$, $p < .0001$.

earlier work that suggested that social deprivation early in life leads to subsequent deficits in normative social functioning (Alexander & Harlow, 1965; Anderson & Mason, 1978; Champoux et al., 1999; Sackett, 1967). The results highlight the importance of adult presence on normative social development and suggest that early parental absence may have long-lasting effects on social development. We were not surprised by our finding that by the third year of life, males rank higher than females, since male macaques typically outrank females by this age in wild populations (Missakian, 1972).

Also consistent with our predictions, juvenile SPR subjects ranked lower than either their MR or PR cage-mates. This finding suggests that infant monkeys reared without a consistently available, stable, responsive attachment source during the initial 6 months of life continue to exhibit social deficits by year 3. Interestingly, no significant difference was detected between the relative dominance ranks of 3-year-old MR and PR subjects, suggesting that the quality of early peer experiences may compensate for parental absence in the acquisition of skills necessary for normal social development. One possible explanation for the equivalent ranks of MR and PR subjects at year 3 is that for young PR monkeys, age-mate peers may serve many of the crucial early attachment roles typically provided by the mother, ameliorating the expected social deficits. Peers form strong bonds with one another. These bonds play a critical role in the formation of alliances against challenge from other subjects during aggressive encounters (Higley et al., 1992). The constant social and physical interaction between peers characteristic of PR subjects within the first months of life may provide a contingent behavioral feedback that simulates certain aspects of adult social interaction, which is lacking in SPR subjects. At least initially, having the constant companionship of 3–4 peers may facilitate defense

against challenge when subjects are placed into larger social groups of other like-aged, but primarily unfamiliar animals (Anderson & Mason, 1974).

Although sex did not interact with weight to affect year 3 social dominance rank, there was a significant interaction between weight and rearing condition on dominance, indicating that with weight controlled, rearing played a significant role in the acquisition of juvenile social dominance rank. Although the monkeys who would become high- and low-ranking monkeys were equal in size at group formation, high-ranking animals gained more weight between group formation at year 1 and year 3. While cause and effect cannot be established from a correlational study, one possible explanation for the higher weight gain observed in high-ranking animals is that high dominance status may result in more rapid growth between the first and third years of life. Evolutionarily, high social dominance may have a long-lasting selective bias towards preferential access to prized or limited resources, which would help to explain the accelerated growth detected in subjects who had acquired high social status by age 3. In the laboratory, however, food is abundantly available at all times and high-ranking animals do not consume all of the food before the lower-ranking animals can eat. Thus it is possible that the increased weight gain reported for high-ranking animals is not simply a result of having access to more food, although food may remain uneaten as a result of a high-ranking animal's intimidation. Alternatively, the stress of low rank may alter other systems and suppress such biochemicals as growth hormone (Schanberg & Field, 1987), insulin-like growth factor (Sapolsky & Spenser, 1997), and testosterone (Sapolsky, 1986).

As predicted, when the adult group was assessed for status, MR subjects outranked their SPR cage-mates and also outranked PR subjects. Unanticipated, however, was our finding that PR subjects did not rank significantly higher than their SPR cage-mates. Comparing results from the juvenile and adult groups reveals a considerable age-related decline in the relative social status of PR subjects. While PR subjects displayed ranks indistinguishable from those of MR animals at year 3, by adulthood they occupied ranks significantly lower than MR subjects, but not significantly different than SPR subjects. Although peer attachment may enable adequate social functioning early in life, the presence of a mother in the initial months of development appears to be necessary for the rhesus monkey to retain social status as it matures. It is necessary to point out, however, that MR subjects are no longer with their mothers at age 3 as they would be under natural conditions. Thus, mothers do not have the same direct effect on the rank attainment of their offspring as they would ordinarily have through matrilineal support. Nevertheless, it would be interesting to examine the pos-

sible effects of adult female rank on the rank attainment of their MR offspring in future studies.

Mothers are more likely than age-mate peers to reward species-appropriate social behavior and to discipline inappropriate behavior (Sameroff & Suomi, 1996). In the absence of maternal care, aggressive tendencies may not be expressed in appropriate settings or intensities (Suomi, 1982). Although our results reveal that overall frequencies of competitive aggression increase proportionately with dominance status in adult female subjects, this aggression is constrained and generally mild, rarely resulting in injury. Previous data suggest that monkeys reared in infant peer groups are more likely than adult female mother-reared monkeys to neglect and abuse their own infants and to initiate episodes of aggression towards infants (Suomi & Ripp, 1983; Higley et al., 1994). Moreover, peer-reared subjects and other monkeys reared without adults are more likely to engage in severe aggression, resulting in trauma that necessitates treatment or removal from the group (Suomi & Ripp, 1983; Higley et al., 1994).

A propensity towards a certain threshold of less restrained aggression may actually benefit young PR monkeys in the short-term, aiding in their attempts to form strong social alliances. Nevertheless, this same aggressive predisposition may prove deleterious as these monkeys mature and begin to have offspring of their own. PR subjects may also benefit from the social bonds they develop as a result of having 24 h access with 3–4 other cage-mates, allowing them to form strong alliances during social challenge, which may explain in part why they initially gain high social dominance.

Owing to disagreement among researchers regarding the best method by which to assess social dominance status in non-human primates, we considered alternative methods. Outcomes of the experimenter-elicited competition method used in the present investigation were compared for all adult subjects ($N = 38$) with dominance indices derived from a second procedure, in which dyadic records of spatial displacements, flees, fear grimaces, and cowers were recorded as they occurred spontaneously over four 15-min focal samples in an undisturbed social context in the absence of food rewards. Dominance scores derived from these two methods were highly and positively correlated (avg. Spearman rho across social groups $=.746, p < .05$).

Taken together, the results of this investigation suggest a difference in the long-term effects of infant rearing condition on individual dominance status in captive rhesus monkeys. They reveal that monkeys reared for the first 6 months of life either by their mothers in mixed-aged social groups or without parents in PR groups attained consistently higher social status than SPR subjects. Alternatively, surrogate/peer-rearing produced consis-

tently low-ranking monkeys. The results of the second study indicate that while the relative dominance ranks attained by juvenile PR monkeys were equivalent to those of MR subjects at year 3 of life, the status of PR animals decreased appreciably by adulthood. Future work in this area would benefit from increasing sample sizes for each rearing condition so that the effects of infant rearing condition might be assessed separately for male and female subjects. The results of this investigation have potential relevance for animal husbandry procedures. They suggest that whenever possible, captive animals ought to remain in groups with conspecifics or be paired with a familiar peer if circumstances require removal of a particular individual from a social group.

Although the findings reported here clearly demonstrate the crucial role of early experience on social development, it is unlikely that rearing condition alone determines dominance status in captive monkeys at any particular stage of an individual's life. It is likely that differences in such critical life experiences as infant rearing condition interact with genetic probabilities for such physiological and cognitive attributes as body weight and temperament to determine dominance status within a social group. Preliminary research indicates that although nursery-reared monkeys are never exposed to their biological fathers for more than the first few days of life, some fathers consistently produce infants who develop high social status, while others consistently produce low status offspring (Scanlan, 1988; Higley, Linnoila, & Suomi, 1989). Whenever possible, future studies should address possible gene-environment interactions to determine both the extent and limits of environmental plasticity within the constraints of heritable predispositions.

NOTES

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