American Journal of Primatology 62:243–259 (2004)

RESEARCH ARTICLE

Response to Social Challenge in Young Bonnet (*Macaca radiata*) and Pigtail (*Macaca nemestrina*) Macaques Is Related to Early Maternal Experiences

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Previous experience affects how young primates respond to challenging social situations. The present retrospective study looked at one aspect of early experience, the quality of the mother-infant relationship, to determine its relationship to young bonnet and pigtail macaques' responses to two social challenges: temporary maternal separation at 5-6 months and permanent transfer to an unfamiliar peer group at 16–17 months. Relationship quality was measured quantitatively on 30 macaque mother-infant pairs with the Relationship Quality Index (RQI), the ratio of relative affiliation to relative agonism as previously applied to capuchin monkeys. Infants with high RQI values had amicable mother-infant relationships and infants with low RQI values had agonistic mother-infant relationships. Young monkeys with amicable and agonistic relationships showed consistent differences in behavior before, during, and after each social challenge, supporting the hypothesis that juveniles from amicable mother-infant relationships based on the RQI coped more effectively with social challenges than did juveniles from agonistic mother-infant relationships. Results suggest 1) characteristic amicability or agonism in early mother-offspring macaque relationships has the potential to influence offspring behavior in tense social contexts and 2) the RQI is useful as one of a coordinated suite of methods for studying the development of social skills. Am. J. Primatol. 62:243–259, 2004.

Contract grant sponsor: National Institutes of Mental Health; Contract grant number: MH37373; Contract grant sponsor: University of Colorado Developmental Psychobiologist Endowment Fund of the Developmental Psychobiology Research Group, Department of Psychiatry, UCHSC; Contract grant sponsor: NIMH; Contract grant number: T32 MH15442.

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Revision accepted 7 January 2004

DOI 10.1002/ajp.20019
Published online in Wiley InterScience (www.interscience.wiley.com).

Key words: social development; affiliation; agonism; mother; infant; juvenile; capuchins; macaques; coping

The nature of the mother–infant relationship affects the behavior of offspring in many ways [Andrews & Rosenblum, 1992, 1993, 1994a, b; Fairbanks & McGuire, 1987, 1993; Harlow & Harlow, 1969; Harlow & Zimmerman, 1958; Weaver, 1997]. The impact of maternal availability and style on offspring behavior becomes particularly evident when offspring are stressed [Andrews & Rosenblum, 1992, 1994b; Kraemer et al., 1991; Reite & Field, 1985]. Studies of young macaques reared in the absence of maternal care (that is, with surrogates or peers, or in isolation) represent an extreme deprivation for the development of socially complex organisms. It is not surprising that the later consequences of these early rearing experiences can be quite dramatic when these monkeys are challenged [Mitchell, 1968; Sackett, 1967; Suomi et al., 1983]. However, the extent to which differences in maternal care (ranging from low to high quality) will affect behavioral patterns in the offspring has only recently been explored. Indeed, the mother's interactions with her offspring will affect the developmental trajectory that an infant follows. This trajectory influences adult behavior in fundamental ways, and a number of factors may affect maternal care.

Across primate species and settings, the mother's rank in the social group is highly correlated with the mother's behavior directed toward her infant [Altmann, 1980]. A ''laissez-faire'' mothering style (e.g., restraining their infants less, discontinuing restraint at a younger age, rarely following the infant, making fewer contacts with the infants, and increasing distance between themselves and their infants more often) is found in high-ranking baboon mothers. Low-ranking baboon mothers are more restrictive, exhibiting a pattern opposite to that of ''laissez-faire'' mothers. Infants of low-ranking mothers spend more time in contact with their mothers during the first 6 months of life. Low maternal rank is also correlated with greater tension in the mother–infant relationship. In low-ranking mothers, a high proportion of attempts to contact the nipple are rejected, and infants play a greater role in maintaining proximity to their mothers [Hinde & McGinnis, 1977]. Rank operates through complex interactions with other factors. Regardless of its source, tension in the mother–infant relationship is predictive of greater infant behavioral reactions during social challenge.

In previous studies [Fairbanks, 1993; Fairbanks & McGuire, 1993], vervet monkey infants that experienced high levels of maternal protectiveness and control during infancy were more cautious in response to novelty compared to adolescents that experienced less control by their mothers. The presence of a new male in the social group led to increased maternal protectiveness and control over infants. Infants present during the introduction of a new male were more cautious and had significantly longer latencies to approach a novel stimulus when compared to infants born in the presence of a long-standing male [Fairbanks & McGuire, 1993]. These studies suggest that some specific aspects of the mother–infant relationship affect later behavioral patterns in the offspring.

Indeed, these relationships are quite similar across both human and nonhuman primates. Children with controlling mothers make a poorer behavioral adjustment to entry into school [Barth & Parke, 1993], and children with poor early attachment relationships with their mother are more likely to show aggressive behavior patterns when they are of school age [Lyons-Ruth, 1996]. Mothers exhibiting excessive control of their infants has also been correlated with

anxious-avoidant attachment in their children [Belsky et al., 1984; Lewis & Feiring, 1989].

Multiple orthogonal dimensions by which a mother can be characterized with regard to her relationship to her offspring have been described. These dimensions include rejecting, protecting, demanding, and responsive [Maestripieri, 1999]. These patterns differ across species and are thought to be affected by the nature of social interactions the infant experiences with other members of the social group [Maestripieri, 1994a]. In social groups in which the handling of the infant by other members of the group may endanger the well-being of the infant, maternal care is far more restrictive. However, other views regarding the source of restrictive mothering styles have been expressed.

Simpson [1985] noted that in rhesus mother–infant pairs, mothers that were more restrictive at 4 weeks of age were more likely to have offspring that explored the environment at 52 weeks. This appears to be in direct contrast to the observations of Fairbanks [1993] regarding restrictive vervet mothers and their offspring's response to novelty. Simpson concluded that the more ''enterprising'' infants (i.e., infants that are more likely to attempt to investigate the environment at 4 weeks of age) were restricted by mothers more because of their more enterprising nature. This trait was still reflected in their behavior at 1 year. This interpretation argues that appreciating the behavior of the infant is critical in order to gain an accurate understanding of the long-term effects of the behavior of the mother.

Many of the preceding conceptualizations focused primarily on the mother or the characteristics of the social group, and rarely on the characteristics of the infant (other than its gender). A characterization of a social group includes the extent to which dominance status affects mother–infant relationships [Altmann, 1980] and how species-typical behaviors affect infant-handling by other members of the group [Maestripieri, 1994b]. However, the mother–infant relationship represents a dyad that includes both partners. The response of the infant affects subsequent responses by the mother, and so on. This aspect has been largely overlooked in studies of nonhuman primates, but has influenced child psychology since the 1970s [Appelbaum & McCall, 1983; Brazelton et al., 1974; Sameroff, 1983; Sander, 1977]. Some approaches applied in nonhuman primates have included using the actions of both partners to characterize dyadic relationships. For example, the Hinde Proximity Index (HPI) [Hinde & Atkinson, 1970] characterizes the extent to which both members of the dyad are responsible for maintaining proximity. Berman [1980] applied similar measures reflecting the role of the mother *and* the infant in maintaining ventral contact in the dyad, and the shift in control toward the infant with development. Although they include both members of the dyad in computations, these indices do not characterize the quality of the relationship.

Following a similar path of including both maternal and infant behaviors, Weaver and de Waal [2000, 2002, 2003] characterized the quality of the mother–offspring relationship based on relative rates of affiliative and agonistic interactions within the mother–infant dyad, i.e., the Relationship Quality Index (RQI). The RQI is based on the ratio of relative affiliative events that occur between a mother and offspring divided by the relative rate of agonistic events that occur between that mother and offspring. The relative rate of agonism or affiliation refers to whether a pair was more or less agonistic or affiliative than the norm for the subjects under investigation. Thus, when relative affiliation exceeds relative agonism in this index, the mother–infant relationship is considered to be of high quality.

In previous studies [Weaver & de Waal, 2000, 2002, 2003], capuchin (*Cebus apella*) offspring that experienced a high-quality relationship with their mother, based on the RQI, showed higher-level skills in conflict resolution with other members of their social group. Rates of reconciliation (affiliative interactions between two monkeys that were previously engaged in an agonistic interaction) were higher. Reconciliation is a vital social skill, and the exchange of friendly behavior between opponents after they have fought often mitigates the tension of conflict [Aureli & de Waal, 2000]. The nature of the mother–infant relationship has been associated with the development of social skills and emotional functioning by the infant. This early relationship serves as a template upon which young monkeys can draw in the development of their conciliatory styles.

In the present work, we report on a retrospective analysis of a convenience sample from behavioral data collected as part of a separate research study. That study investigated the impact of a temporary 2-week maternal separation on behavioral, immunological, and endocrinological responses in 6-month-old bonnet (*Macaca radiata*) and pigtail (*M. nemestrina*) macaques [Laudenslager et al., 1990, 1995, 1996; Laudenslager & Boccia, 1996; Worlein & Laudenslager, 2001]. These monkeys were subsequently transferred to peer groups at approximately 16–17 months of age, at which time behavioral, immunological, and endocrinological responses were assessed as well. In the current study we examine the relationship between the behaviors of these young macaques during the two social challenges and the RQI determined from observations collected prior to the 6-month separation experience. It is important to emphasize that these data were collected for purposes other than the determination of the RQI, but there was adequate information in these data to provide an estimate of the RQI as described below.

The aim of the present analysis was to determine whether a simple global measure of the early mother–infant relationship (i.e., the RQI) was a useful predictor of behavioral and physiological response to social challenge. We hypothesized that offspring from high-quality relationships would be less affected by temporary removal of the mother from the social group. We further predicted that offspring from high-quality mother–infant relationships would show more affiliative social behavior than offspring with low-quality mother–infant relationships when introduced to a new peer group. We consider the present results to reflect only preliminary investigations using retrospective data analysis. However, we were encouraged by the fact that this approach was informative and is likely to be useful in accounting for some individual differences in macaques' responses to social challenges.

MATERIALS AND METHODS

Subjects

The subjects represented a convenience sample for the present retrospective analysis. The subset of subjects that was included in this analysis was selected because their behavior had been sampled by means of a common behavioral taxonomy that included sufficient behaviors to calculate the RQI (see below). Some subjects were eliminated from the analysis because of incomplete data or because of zero-frequency behaviors (particularly agonistic events) associated with the limited sampling interval (5 min per sampling epoch) used in the parent study. The final group (from an initial group of 42 subjects) included 30 infants (17 bonnet macaques (*Macaca radiata*) and 13 pigtail macaques (*M. nemestrina*)). The focal mothers that contributed to the overall analysis were 11 pigtail mothers (two of which contributed with two offspring) and nine bonnet mothers (four of

which contributed with two or three offspring). We recognize that this was not ideal, but reemphasize the exploratory nature of this retrospective analysis. The final sample group consisted of 10 males and 20 females with a mean age of 191 ± 32 days at the time the mother–infant observations were collected. These 30 infants participated in the study of behavior in response to the first social challenge, which was temporary mother–infant separation. Fourteen infants experienced the separation (SEP). Each separated monkey was paired with an age-matched control monkey from the same social group (thus a half sibling) that did not experience separation (CONT). Both SEP and CONT animals were included in the retrospective analysis. For the second social challenge, which was a permanent transfer to a new social group, data were available on 22 monkeys (11 bonnet and 11 pigtail monkeys). The mean age was 492 ± 42 days at the time of introduction to the new group. Due to the retrospective nature of this analysis, eight macaques (six bonnets and two pigtails) of the original 30 infants were excluded from behavioral analysis during the second social challenge because their behavior had been sampled with a different behavioral taxonomy. All observations were collected between June 1994 and October 2000 at the University of Colorado Health Sciences Center Primate Research Center. This project was approved by the University of Colorado Health Sciences Center Institutional Animal Care and Use Committee.

The subjects were socially housed with their natal groups (an adult male, five or six adult females, and offspring of various ages) in $2.1 \times 2.5 \times 4$ m pens with glazed cinderblock walls, wire mesh ceilings, and PVC piping for sitting and climbing. Lighting (700 lux) was timer-controlled on a 14 hr/10 hr light/dark cycle (lights on at 0700 hr). Commercial monkey biscuits were fed at 0900 hr, and food and water were available ad libitum. Fresh supplemental forage and manipulable items (i.e., cardboard boxes) were provided from 1230–1430 hr for enrichment.

Data Collection and Experimental Procedure

Focal animal observations were collected in real time with The Observer software (DOS Version 2.0, Noldus, Inc.) mid-morning and mid-afternoon to avoid feeding or enrichment practices. Trained observers (R.R. and J.W.) demonstrated 90% interobserver reliability (across all behavioral categories) during concurrent observations of the same focal animal in the group. Discrepancies were discussed until agreement was established. This procedure was repeated every 6–8 months. Observations were made through one-way mirrors and the animals were unaware they were being observed. Data were collected as frequencies (occurrence per 5 min) and durations (total seconds per 5 min) of all-occurrences of social and self-maintenance behaviors during 5-min focal animal samples [Altmann, 1974], with the offspring as the focal animals. Modifiers included the mothers and ''other'' (any other member of the social group).

Data for social challenges were collected in phases. Data were collected twice daily (morning and afternoon) during the 2-week phases before (baseline week 1, baseline week 2), during (separation day 1, separation week 1, and separation week 2), and after (reunion day 1, reunion week 1, and reunion week 2) mother–offspring separation (see below). On separation day (see below) and reunion day (applicable to the first social challenge only), three focal animal samples (instead of two) were collected for each subject in the morning and afternoon, for a total of 30 min of observation time on these transition days. A total of 60 min of observation for the baseline period, and 80 min each for the separation and reunion phases, were analyzed.

First Social Challenge: Temporary Maternal Separation

Macaques born within 1–2 months of each other in the same natal group were paired, with one randomly assigned to the separation condition (SEP) and the other assigned to the matched control (CONT) condition. At 5–6 months of age, SEP infants remained in their natal group while their mothers were removed to another location out of sight and sound of the infant for 2 weeks (mean $\pm$ standard deviation (SD) of the age of separation $= 185 \pm 18$ days for the bonnets and 169 ± 25 days for the pigtails). CONT infants did not experience separation.

Second Social Challenge: Permanent Maternal Separation.

When the subjects reached 15–17 months of age (492+42 days), the juveniles were removed from their natal groups and introduced together as SEP-CONT pairs into a follow-up group of older (21–42 months old), unfamiliar peers that had previously undergone a similar SEP-CONT procedure. Since the developmental study spanned 6 years, the size and composition of the peer group varied at the time each SEP-CONT pair was introduced. The same observers (R.R. and J.W.) used the sampling protocol described above for the juveniles.

Mother–Infant RQI

Indices were calculated for each species separately from the baseline behavioral data collected before maternal separation. The RQI formula is the ratio of relative affiliation to relative agonism. Table I defines the baseline

TABLE I. Macaque Ethogram Used to Calculate Mother-Infant Relationship Quality Index (RQI) Values*

Behavior	Definition
Initiate touch mother	Infant makes affiliative physical contact with or grooms its mother's body, including tail-to-tail contact, excluding nipple contact.
Receive touch mother	Infant is the recipient of affiliative physical contact or grooming from its mother or its mother's body.
Initiate cradle mother	Infant makes affiliative physical contact with its mother's ventral surface without nipple contact and is frequently embraced by her.
Receive cradle mother	Mother gathers and/or embraces infant against her ventral surface.
Initiate aggression to mother	Infant directs physical and/or non-contact aggressive behaviors including threaten, bite, hit, etc. to mother.
Receive aggression from mother	Mother directs physical and/or non-contact aggressive behaviors including threaten, bite, hit, etc. to her infant.
Submit	Infant grimaces, flees, crouches, screams, and/or lipsmacks to mother.
Receive submit	Infant receives grimaces, flight, crouched posture, screams, and/or lipsmacking from mother.
Wean	Infant is denied the nipple with agonistic or aggressive gestures.

*Behaviors were recorded during baseline focal animal samples with offspring as focal animals and recorded as bi-directional, i.e., either given or received by the focal animal.

behaviors from the ethogram [Laudenslager et al., 1995] that were used to calculate the RQI. The categories included dyadic interactions of the mothers and their infants only. Affiliation was measured using two mutually exclusive behaviors: 1) initiates and 2) receives touching and cradling. In the present ethogram, touch was not mutually exclusive to grooming (in contrast to Weaver and de Waal's [2002] study, in which grooming was used as the measure of affiliation). To calculate mother–infant affiliation, all episodes of mother–infant touching and cradling were combined (i.e., infant touches mother, infant is touched by mother, infant cradles with mother, and infant is cradled by mother). Agonism was measured from three mutually exclusive behaviors: aggression, submission, and weaning. As with affiliation, all mother–infant episodes (both initiates and receives) of these behaviors were combined to calculate mother–infant agonism. A Pearson's product moment correlation of these two categories was nonsignificant ($r = 0.18$, ns, $n = 30$). Correlated measures would have been redundant and cannot be used to calculate an index that compares distinctly different behaviors (e.g., affiliation and agonism). The RQI numerator and denominator values are relative rates. Thus, relative affiliation and agonism are calculated for each mother–infant pair by dividing their rates of affiliation and agonism by the mean rate of affiliation and agonism, respectively, determined from the mother–infant pairs included in this study of the same species. Thus these relative rates quantify each pair relative to the norm for the species in the same housing and social conditions, that is, above or below the average. Final RQI values were obtained by dividing each pair's relative affiliation rate by their relative agonism rate. Using the RQI values, the subjects were divided by median split into high and low groups [Weaver & de Waal, 2002]. On the basis of this split, their behavior during separation, reunion, and introduction to new peers was compared. The RQI value represents the proportion of relative affiliation to agonism in the mother–infant relationship, rather than either affiliation or agonism alone. Importantly, the behavior of *both* the mother and infant is included in its calculation. Also, mother–infant RQI values were not affected by the separation challenge because the infants underwent separation after the behavioral measures used to calculate the RQI were collected.

Analysis

Observations were analyzed by independent *t*-tests and 2×2 analyses of variance (ANOVAs) when appropriate. Independent variables included the RQI (high vs. low) and rearing experience (separated vs. control). For observations made during and following separation, a total of 30 subjects were available. Species was not included as an independent measure because 1) the RQI is a standardized measure that obscures species differences, and 2) bonnet and pigtail observations were limited to subjects with sufficient data for analysis, which thus limited the statistical power. For observations made after introduction to a new social group, a total of 22 subjects were available. Species was collapsed as before, and the independent variable included RQI (high vs. low) and rearing experience (separated vs. control). Since separation effects have been reported elsewhere [Laudenslager et al., 1990, 1995, 1996; Laudenslager & Boccia, 1996; Worlein & Laudenslager, 2001], we focused on the RQI and its relationship to the social challenges. Maternal rank information, admittedly an important factor, was not available for all mothers due to changes in data that were collected during the project, and was therefore not included in the analysis. Study-subject attrition over the course of this 6-year study was due to several causes, including a change

in the ethograms, removal of study subjects for health reasons, and loss of the mother of control subjects before the subjects were transferred to the peer groups.

RESULTS

Mother–Infant RQI Values

Macaque mother–infant RQI values ranged from 0.24 to 5.35 with a mean ± SD of 1.19 ± 1.01 (Tables II and III). Mother–infant pairs with values above the median for their species (bonnet = 0.85; pigtail = 1.27) were considered high-quality mother–infant relationships and are referred to as ''high'' in the text (mean ± SD = 1.83 RQI ± 1.09, n = 15). Mother–infant pairs with RQIs below the median were considered to be low-quality mother–infant relationships and are called ''low'' in the text (mean ± SD = 0.55 RQI ± 0.19, n = 15). Mean high and low mother–infant RQI values were significantly different ($t = 4.52$, $P = 0.00$, $df = 28$). Mother–infant RQI values did not differ by gender ($t = 0.47$, ns, $df = 28$, mean ± SD: males 1.34 ± 1.44, n = 10; females 1.08 ± 0.70, n = 20) or by species ($t = 0.14$, ns, $df = 28$, mean ± SD: bonnets 1.16 ± 1.16, n = 17; pigtails 1.23 ± 0.81, n = 13). Gender and species were collapsed for subsequent analysis because there were too few subjects in the species/rearing/RQI cells to analyze. Tables II and III show that of the 30 monkeys that began the study, 15 were high RQI, 15 were low RQI, 14 were SEP, and 16 were CONT. Of the 22 monkeys that finished the study, 10 were high RQI, 12 were low RQI, 11 were SEP, and 11 were CONT.

TABLE II. Rearing Condition and Data Used to Calculate RQI Values for 17 Bonnet Macaque Infants

Animal ID	Rearing condition	Absolute affiliation rates[a]	Relative affiliation rates	Absolute agonistic rates[b]	Relative agonistic rates	RQI values	High (H) or low (L) RQI	Retained
2765	SEP	4.40	1.54	0.20	1.23	1.25	H	Yes
2766	SEP	2.25	0.79	0.10	0.62	1.28	H	Yes
2767	CONT	4.25	1.49	0.19	1.14	1.30	H	No
2768	CONT	2.50	0.87	0.17	1.03	0.85	L	No
2925	SEP	2.95	1.03	0.25	1.54	0.67	L	Yes
2928	SEP	2.30	0.80	0.10	0.62	1.31	H	No
22176	CONT	2.65	0.93	0.20	1.23	0.77	L	Yes
34155	CONT	2.20	0.77	0.39	2.37	0.32	L	Yes
34157	CONT	2.15	0.75	0.34	2.06	0.36	L	Yes
34158	CONT	2.10	0.73	0.10	0.62	1.18	H	Yes
34159	SEP	4.65	1.63	0.15	0.92	1.77	H	No
34816	SEP	1.50	0.52	0.35	2.16	0.24	L	Yes
38513	CONT	2.95	1.03	0.30	1.85	0.56	L	Yes
38514	CONT	2.80	0.98	0.20	1.23	0.79	L	Yes
62537	CONT	4.75	1.66	0.05	0.31	5.35	H	No
231213	SEP	3.05	1.07	0.25	1.54	0.69	L	Yes
341552	CONT	4.55	1.59	0.25	1.54	1.03	H	No

[a]Combined rates of initiated and received touch/5 min and cradle/5 min.; bonnet mean = 2.86 affiliative exchanges/5 min.
[b] Combined rates of initiated and received aggression/5 min, submit/5 min, and wean/5 min.; bonnet mean = 0.16 agonistic exchanges/5 min.
Retained, Retained in analysis at 16–17 mo of age.

TABLE III. Rearing Condition and Data Used to Calculate RQI Values for 13 Pigtail Macaque Infants

Animal ID	Rearing condition	Absolute affiliation rates[a]	Relative affiliation rates	Absolute agonistic rates[b]	Relative agonistic rates	RQI values	High (H) or low (L) RQI	Retained
1012	CONT	2.60	1.25	0.28	2.30	0.54	L	No
17274	SEP	2.50	1.20	0.05	0.41	2.96	H	Yes
17275	SEP	1.40	0.67	0.05	0.41	1.66	H	Yes
17313	CONT	1.95	0.94	0.23	1.89	0.49	L	Yes
17386	CONT	2.05	0.98	0.25	2.03	0.48	L	No
26156	SEP	1.55	0.74	0.05	0.41	1.83	H	Yes
36634	CONT	4.30	2.06	0.20	1.62	1.27	H	Yes
49117	SEP	3.65	1.75	0.10	0.81	2.16	H	Yes
49710	SEP	2.30	1.10	0.30	2.43	0.45	L	Yes
50744	CONT	3.10	1.49	0.65	5.27	0.28	L	Yes
261411	SEP	3.90	1.87	0.15	1.22	1.54	H	Yes
831313	SEP	2.65	1.27	0.10	0.81	1.57	H	Yes
831314	CONT	0.60	0.29	0.05	0.41	0.71	L	Yes

[a]Combined rates of initiated and received touch/5 min and cradle/5 min.; pigtail mean = 2.08 affiliative exchanges/5 min.
[b]Combined rates of initiated and received aggression/5 min, submit/5 min, and wean/5 min.; pigtail mean = 0.12 agonistic exchanges/5 min.
Retained, retained in analysis at 16–17 mo of age.

Behavioral Differences Between High and Low Infants

Baseline behavior

Infant macaques with high and low RQI values showed several behavioral differences in addition to those used to compute the RQIs. High-RQI infants approached their mother more ($t = -2.19$, $P = 0.03$; $df = 28$, mean $\pm$ SD high 2.65 approaches/5 min $\pm$ 1.02 > low 2.09 $\pm$ 0.81), touched their mother more ($t = -2.29$, $P = 0.03$, $df = 28$, mean $\pm$ SD high 0.68 $\pm$ 0.45 touches/5 min > low 0.36 $\pm$ 0.23), and had shorter durations of passive bouts ($t = 2.49$, $P = 0.02$, $df = 28$, mean $\pm$ SD low 30.21 s $\pm$ 27.8 > high 10.51 s $\pm$ 9.61) compared to low-RQI infants. As illustrated in Fig. 1, high-RQI infants followed their mother more (baseline week 1: $t = -2.42$, $P = 0.02$; $df = 28$, baseline week 2: $t = -2.42$, $P = 0.02$, $df = 28$), received more maternal approaches ($t = -2.64$, $P = 0.01$, $df = 28$), and were less passive (e.g., staring and unresponsive exclusive of napping or dozing, $t = 2.51$, $P = 0.01$, $df = 28$) compared to low-RQI infants.

Separation behavior

On the first day of temporary mother–infant separation, SEP infants with a low RQI spent the most time in passive states (rearing condition $\times$ RQI interaction $F(1,26) = 13.69$, $P = 0.00$). During the 2 weeks of separation, there were several significant main effects of RQI on infant passivity (ignoring social interactions of others), vocalizations, and the duration in seconds of time spent in an alert-inactive state.

Figure 2 shows that high-RQI infants were more alert than low-RQI infants ($F(1,26) = 4.89$, $P = 0.04$). Low-RQI infants were more passive than high-RQI infants during week 1 (passivity 1, $F(1,26) = 10.99$, $P = 0.00$) and week 2 (passivity 2, $F(1,26) = 8.06$, $P = 0.01$). Low-RQI infants vocalized more frequently than high-

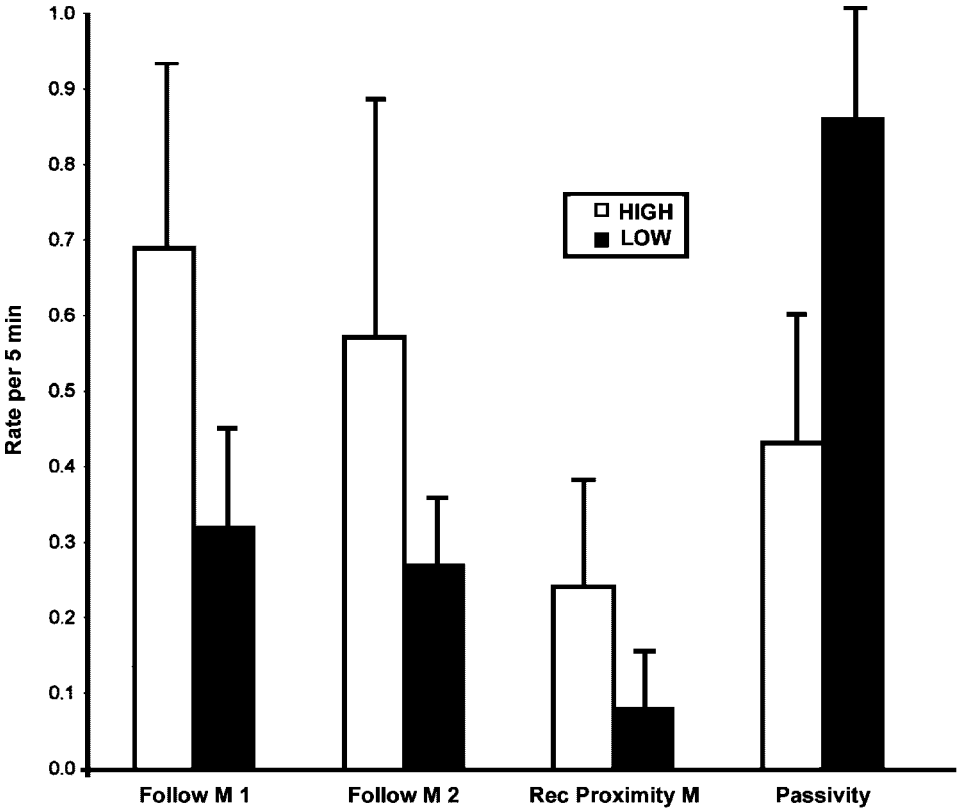


Fig. 1. Baseline infant behavior of 5–6-month-old macaques with high- and low-quality mother–offspring relationships ($N_{HIGH} = 15$, $N_{LOW} = 15$). Mean $\pm$ SD rates per 5 min of observation. Follow M = infant follows its mother. Rec Proximity M = mother moves within arm's length of her infant. Passive rates = occurrence of infant withdrawal per 5 min. All differences are significant at $P < 0.05$ or better.

RQI infants ($F(1,26) = 5.10$, $P = 0.04$, mean $\pm$ SD low: 0.55 vocalizations/5 min $\pm$ 0.43 > high: 0.16 $\pm$ 0.48). The low-RQI monkeys were less responsive to social overtures from other social group members, tended to sit alone, and vocalized more compared to the high-RQI animals.

Reunion behavior

On the day the mothers were returned to the social group, there were significant main effects of RQI on infant scratching (considered an indication of anxiousness), passivity, and self-grooming. Low-RQI infants scratched more (scratch, $F(1,26) = 4.47$, $P = 0.04$), showed greater passivity ($F(1,26) = 9.05$, $P = 0.01$), and self-groomed more ($F(1,26) = 4.34$, $P = 0.04$) (Fig. 3).

Behavioral Differences Between Juveniles From High- and Low-Quality Relationships

Baseline behavior

Before the juveniles were transferred to the new group at 16–17 months of age, there were several effects of RQI on social behavior of the subjects housed in their natal groups. High-RQI juveniles were in proximity to and touched their

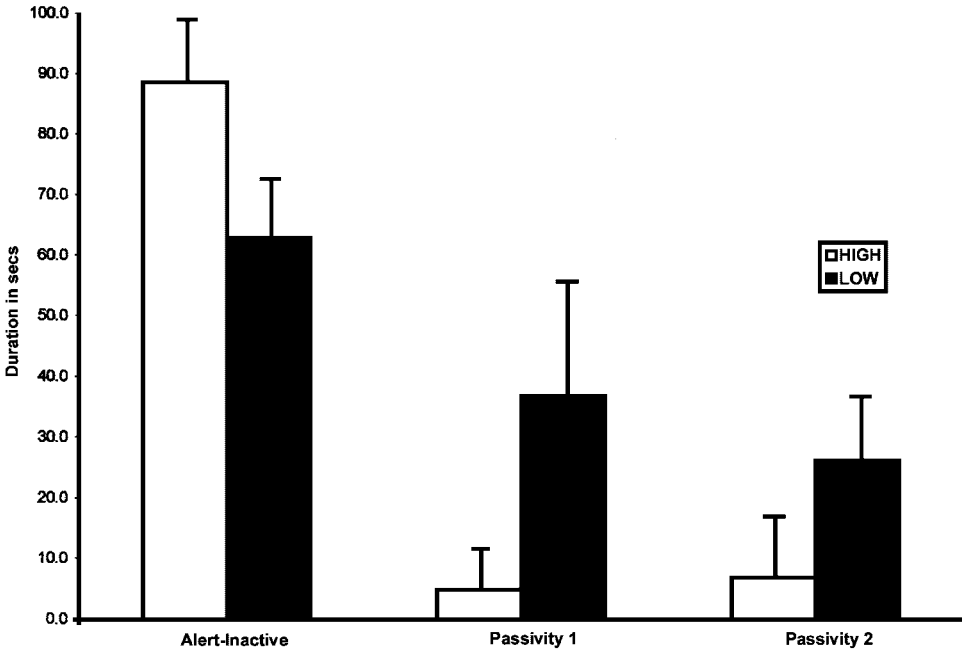


Fig. 2. Infant behavior during temporary maternal separation of 5–6-month-old macaques with high- and low-quality mother–offspring relationships (mean durations ± SD in seconds per 5 min of observation, $N_{HIGH} = 15$, $N_{LOW} = 15$). The infant remained in the natal group while the mother was temporarily housed elsewhere. All differences are significant at $P < 0.05$ or better.

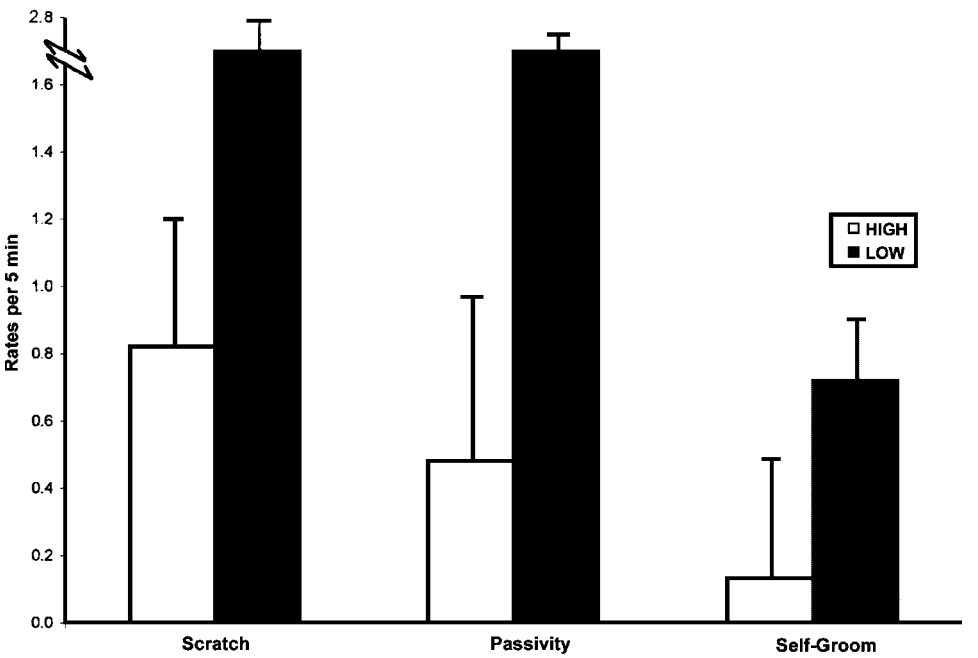


Fig. 3. Infant behavior during reunion with mother after temporary separation (mean ± SD) of 5–6-month-old macaques with high- and low-quality relationships ($N_{HIGH} = 15$, $N_{LOW} = 15$). All differences are significant at $P < 0.05$ or better.

TABLE IV. Differences in the Baseline Behavior (M ± SD) of 16-Month-Old Macaque Juveniles With High- and Low-Quality Mother–Infant Relationships

	F(1,18)	High RQI	Direction	Low RQI
Proximity to mother rates	8.76**	2.79 ± 1.19	>	1.61 ± 0.95
Touch mother rates	5.16**	1.19 ± 0.83	>	0.64 ± 0.45
Initiate proximity to others	6.84*	1.77 ± 0.75	>	1.04 ± 0.66
Remain in proximity to others	9.53**	8.01 ± 3.03	>	5.94 ± 2.20
Receive proximity from others	7.75**	0.43 ± 0.32	>	0.15 ± 0.16
Touch others rates	10.11**	3.36 ± 1.80	>	2.20 ± 1.34
Explore environment	6.91*	7.31 ± 1.56	>	5.38 ± 1.65

Data are rates per 5 minutes. Other, non-mother conspecifics.
*$P < 0.05$. **$P < 0.01$.

mothers more than low-RQI juveniles ($P < 0.01$). Similar relationships were noted in interactions with other members of the natal group (i.e., high-RQI juveniles were in proximity to and touched other group members more than low-RQI juveniles ($P < 0.01$). Thus, high-RQI juveniles socialized more with their mothers and other conspecifics than low-RQI juveniles. The differences between high- and low-RQI juveniles are illustrated in Table IV.

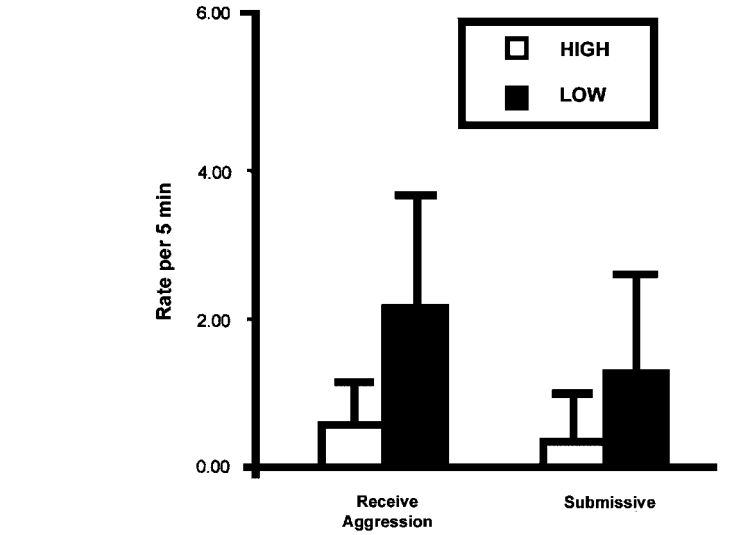
Introduction behavior

Juvenile macaques were permanently separated from their natal groups and introduced to the unfamiliar peer group in SEP-CONT pairs at approximately 16 months of age. Although there were occasionally half or full siblings in the new peer group, these monkeys had not been previously housed together and were thus considered unfamiliar. On the first day following introduction, high-RQI juveniles approached unfamiliar peers more frequently ($F(1,18) = 14.38$, $P = 0.00$, mean ± SD: high 14.18 approaches/5 min ± 5.53 > low 8.51 ± 2.47). Low-RQI juveniles spent more time in passive states ($F(1,18) = 3.84$, $0.05 < P < 0.10$; mean ± SD: low 36.10 sec of passivity ± 54.32 > high 0.73 sec ± 1.43).

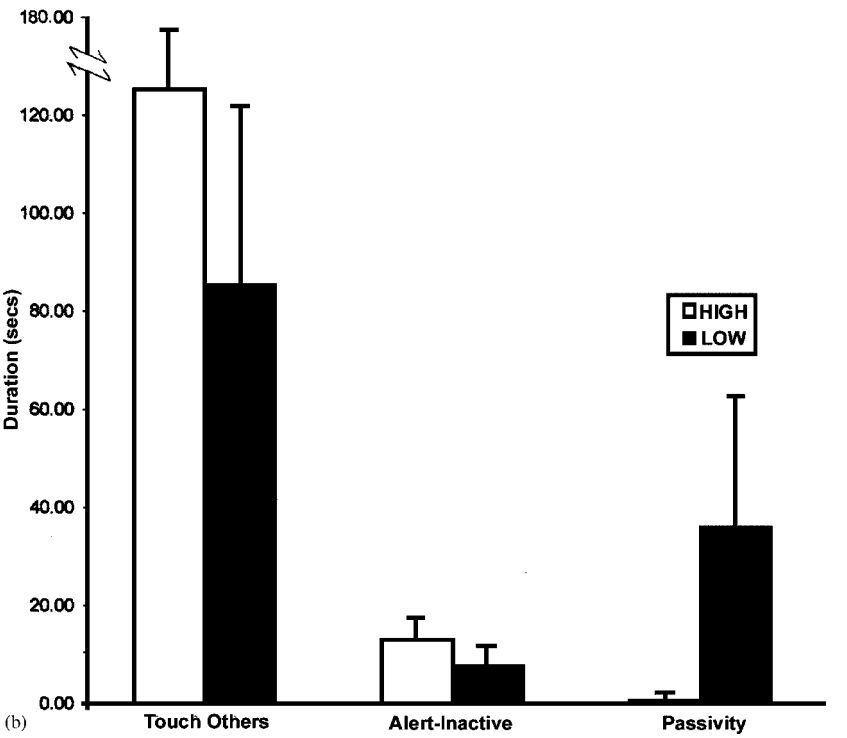
Figure 4 illustrates several effects of RQI during the subsequent 2 weeks in the new peer group. Low-RQI juveniles received more aggression from unfamiliar peers ($F(1,18) = 5.82$, $P = 0.04$; Fig. 4a) and gave significantly more submissive signals compared to high-RQI juveniles (submissive, $F(1,18) = 5.67$, $P = 0.04$; Fig. 4a). Figure 4b shows that high-RQI juveniles spent significantly more time touching conspecifics ($F(1,18) = 5.36$, $P = 0.04$; Fig. 4b) and in a alert-inactive state (visually monitoring the environment independently of social interactions) when alone ($F(1,18) = 13.26$, $P = 0.00$; Fig. 4b). In contrast, low-RQI juveniles spent more time in a passive state ($F(1,18) = 6.58$, $P = 0.01$; Fig. 4b) and groomed unfamiliar peers significantly less often than high-RQI juveniles ($F(1,18) = 6.38$, $P = 0.00$; mean ± SD: low 0.18 groom/5 min ± 0.27 < high 0.43 ± 0.47).

DISCUSSION

The present retrospective analysis of a convenience sample indicates that the RQI developed for a New World monkey species [Weaver & de Waal, 2002, 2003] can be applied to Old World macaque species. The available data set had several limitations, including the total amount of sampling time for which there were behavioral observations. In addition, calculation of the RQI was based on a brief window of development for young macaques between 5 and 6 months.



(a)



(b)

Fig. 4. Juvenile social behavior toward unfamiliar peers of 16–17-month-old macaques with high- and low-quality maternal relationships. **a:** Mean $\pm$ SD rates per 5 min of observation. **b:** Mean $\pm$ SD durations in seconds per 5 min of observation. All differences are significant at $P < 0.05$ or better.

Nonetheless, the RQI derived from these data differentiated the responses of young macaques in a predictable manner. For example, young macaques above the median RQI evidenced less anxiety (vocalization, scratching/shaking, etc.) during the challenge of temporary maternal separation at 6 months than did young macaques with low RQI values. Longer-term influences of the early high- and low-quality relationships were noted as the juveniles were integrated into a new social group. Thus, adolescents with a high RQI showed more affiliative behavior with members of an unfamiliar social group.

The RQI quantified common aspects in each mother–infant macaque relationship by calculating the proportion of species-typical bidirectional affiliative behaviors to species-typical agonistic behaviors exchanged between mothers and their infants. The index is an assessment that reflects dyadic relationships rather than the behavior of individual members (more often the mother) of the dyad or single behaviors. The HPI [Hinde & Atkinson, 1970] characterizes the extent to which both members of the dyad are responsible for maintaining proximity. Berman [1980] applied similar measures that reflected the efforts of both the mother and the infant in maintaining ventral contact in the dyad. Although they include both members of the dyad in computation, these indices do not characterize the quality of the relationship. Dyadic interactions have been explored to some extent in nonhuman primate research, and more so in human developmental studies [Appelbaum & McCall, 1983; Brazelton et al., 1977; Sameroff, 1983; Sander, 1977].

Some caveats are in order. For example, the RQI collapses considerable information into a single number. High-intensity (i.e., high frequency and duration) dyadic relationships that are balanced between affiliation and agonism are probably different from similarly balanced low-intensity (low frequency and short duration) dyadic relationships, yet the same value for the RQI would result. Further studies are needed to determine the consequences of differences in the intensity of the relationship when the resultant RQI is equivalent.

However, when infant macaques were divided into two groups based on their characteristic RQI, a number of significant differences in behavior emerged. Not surprisingly, at 5–6 months of age (prior to temporary separation), both bonnet and pigtail infants with a high RQI actively sought social interactions with their mothers, that is, they approached their mother more frequently. Low-quality relationships were associated with the infants that spent more time in the passive state and thus interacted less with conspecifics in the social group, including their mother. These infants were ''wall flowers'' that ignored nearby social activities and potential interactions. This behavior may imply a basic reluctance to engage the social environment.

During the period in which infants were temporarily separated from their mothers but remained in their familiar natal group, infants from low-quality relationships vocalized more and showed a dramatic rise from baseline in total time spent in passive behaviors. In contrast, infants from high-quality relationships showed less overall change in their behavior. They spent more time during separation engaged in object exploration and in an alert behavioral state compared to the low-quality infants. This might suggest greater vigilance during separation in the infants from the high-quality relationships. Human children with secure attachments cope with social challenges with less behavioral disorganization compared to insecure children [Belsky & Nezworski, 1988; Main & Weston, 1981]. Secure offspring that have good working relationships with their mothers have a greater internal basis for the relationship and are thus not as threatened by a separation. In contrast, insecure relationships, which are not

good working relationships, are considerably threatened by a separation–hence, the apparent contradiction in the behavior of the young.

High-quality relationships in macaques may also be related to better emotional regulation. These differences have implications for physiological homeostasis as well. One might predict reduced physiological disruption [Laudenslager et al., 1990] in offspring of high-quality relationships. We have certainly noted differences in autonomic regulation as predictive of subsequent behavioral responses to separation in the macaque [Laudenslager et al., 1990, 1995, 1996ab; Worlein & Laudenslager, 2001]. Infants with high baseline heart rates were more likely to evidence greater vocalization and postural collapse when the mother was removed from the social group [Boccia et al., 1994]. One might conjecture that the monkeys with higher heart rates might have had a low-quality relationship with their mother. These are important questions in need of further investigation.

When reunited with their mothers (Fig. 3), infants from low-quality relationships showed significantly elevated levels of scratching and self-grooming. Scratching corresponds to arousal and anxiety, and serves as a visible behavioral indicator of these conditions [Maestripieri et al., 1992]. The elevated rates of scratching by infants in low-quality relationships suggested that they were anxious during the reunion. Furthermore, they were also more passive, as observed during the earlier maternal separation experience. Avoidant-attached human children are characteristically passive at reunion; they behave as if they had not experienced a separation, and often ignore the mother [Ainsworth et al., 1978]. Thus, macaques with low RQIs might represent a similar pattern, further reinforcing the utility of this index for discriminating between high- and low-quality mother–infant relationships.

Juvenile pigtail and bonnet macaques from high- and low-quality relationships continued to show differences in behavior similar to what they had shown as infants (Table IV). Most of the differences had to do with sociability toward natal group members. Juveniles from high-quality mother–infant relationships continued to show more frequent affiliation toward their mothers, and they were significantly more sociable with other conspecifics than were juveniles from low-quality maternal relationships. Juveniles from high-quality maternal relationships initiated more interactions with natal group conspecifics, spent more time near them, and touched them more often.

When the juveniles were transferred to an established social group of unfamiliar peers, they faced a significant social challenge even though they had been introduced together as pairs from the same natal social group. The two monkeys that were introduced to the new group were related as half siblings (each had the same father). The challenge for these juveniles was to integrate into a well-established network of older macaques with which they were unfamiliar. Juveniles from high-quality mother–infant relationships showed greater sociality toward unfamiliar peers than juveniles from low-quality relationships. This was reflective of their sociability in the natal group prior to introduction to the new social group (Fig. 4). Offspring of high-quality relationships were in the proximity of unfamiliar peers more often. They touched unfamiliar conspecifics more often and for longer periods. Juveniles from high-quality maternal relationships also groomed unfamiliar peers more, although this was a low-frequency behavior. The ability to initiate and promote interactions (via reciprocal grooming) in this challenging situation led to more successful integration into the new social group. In striking contrast, juveniles from low-quality maternal relationships were passive and readily submissive, and were attacked four times

more often by unfamiliar peers compared to juveniles from high-quality relationships.

These data reveal an association between the nature of early mother–infant relationships and young monkeys' subsequent behavioral patterns during social challenges. Continued research is required to determine whether the association was causative with the quality of a mother–infant relationship functioning as a template of social interactions upon which developing macaques draw when dealing with socially challenging situations. A second alternative is that these relationships are only correlational, and may be related to maternal rank or other variables that represent a complex interaction between heritability and environment on the development of behavior. Future detailed studies will test predictions about whether this classification scheme predicts distinct trajectories in the development of social behavior and physiologic measures during times of social challenge.

ACKNOWLEDGMENTS

The authors are grateful to S. Ekard, D. Fragaszy, M.H. Gouwens, H. Gouzoules, and M.D. Weaver for challenging and inspiring discussions. Ann Weaver received an NIMH postdoctoral traineeship (T32 MH15442). The University of Colorado Health Sciences Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care.

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