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Individual Differences in Infant Temperament Predict Social Relationships of Yearling Rhesus Monkeys (*Macaca mulatta*)

Tamara A.R. Weinstein and John P. Capitanio

Department of Psychology, University of California, Davis California National Primate Research Center

Abstract

Affiliative relationship formation in nonhuman primates is known to be influenced by kinship, rank, and sex, but such factors do not fully explain observed variation in primate social relations. Individual differences in temperament have a number of important behavioural and physiological correlates that might influence relationship formation. We observed 57 yearling rhesus macaques at the California National Primate Research Center for 10 weeks to determine whether individual differences in temperament relate to the number and quality of affiliative relationships formed with peers. Subjects' temperament characteristics had previously been quantified during a colony-wide biobehavioural assessment at 90–120 days of age. Yearlings that had scored high on Equability (demonstrating calmness and low levels of physical activity) as infants had fewer peer relationships compared to animals low on this dimension. Additionally, yearlings preferentially affiliated with peers that were similar to themselves in Equability as well as in Adaptability (reflecting the degree of behavioural flexibility that subjects displayed during the biobehavioural assessment). Although kinship, rank, and sex influenced relationship formation as expected, temperament remained a significant predictor of affiliative preferences even after controlling for these variables. Our findings suggest that temperament is a proximate determinant of variation in affiliative relationship formation in group-living primates.

Keywords

affiliation; juveniles; *Macaca mulatta*; relationships; rhesus macaque; personality; social behaviour; temperament

In nonhuman primates, affiliation, typically defined by such behaviours as proximity, contact, grooming, and play, constitutes a central component of social living. Frequent affiliative interactions between specific individuals over a period of time give rise to affiliative relationships or “friendships” (Hinde 1976), which may benefit individuals in a variety of ways. For example, male friends may protect females and their infants (Manson 1994; Palombit et al. 1997), males may gain increased opportunities to mate with their female friends (Hill 1990), and in the presence of friends, individuals exhibit an attenuated behavioural and physiological response to an acute stressor (Higley et al. 1992; Gust et al.

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Correspondence: T.A.R. Weinstein, Department of Psychology, University of California, One Shields Avenue, Davis, CA 95616 (email: tweinstein@ucdavis.edu). J.P. Capitanio is at the California National Primate Research Center, University of California, One Shields Avenue, Davis, CA 95616.

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1994; Boccia et al. 1997; Beehner et al. 2005). Even outside the context of friendship, affiliative interactions are associated with important fitness-related consequences; grooming, for example, can be exchanged for agonistic support (Silk 1992; Hemelrijk 1994), food (de Waal 1989), protection against harassment (Silk 1982), and access to infants (Muroyama 1994; Henzi & Barrett 2002). Post-conflict affiliation prevents further aggression from developing and reduces distress and uncertainty (Silk 2002). The tension-reducing effects of affiliation, particularly grooming, are evident even in the absence of prior agonistic encounters (Schino et al. 1988; Aureli et al. 1999). In fact, grooming bouts that occur neither following aggression nor in exchange for commodities are quite frequent, and likely function to establish and maintain cohesion amongst group members (Rowell et al. 1991; Borries et al. 1994; Cooper & Bernstein 2000).

Nonhuman primates begin forming affiliative relationships with their group-mates during juvenility, and such friendships can persist through adulthood. For juveniles, formation of peer relationships reflects a transition from affiliating primarily with the mother to becoming a fully integrated member of the group (Hinde & Spencer-Booth 1967). Crucial to the success of this integration is the mastery of myriad complex social skills, which arises out of juveniles' social interactions (Joffe 1997). For example, social play, a behaviour seen primarily in the juvenile period, has long been considered important in this regard (Poirier & Smith 1974). Relationships formed during juvenility have been suggested to play a vital role in facilitating the acquisition and formalisation of dominance rank during adolescence (de Waal & Luttrell 1985; Datta 1988). Moreover, relationship formation during juvenility may have long-term fitness consequences, as the degree of social integration during adulthood has been shown to impact reproductive success independently of dominance rank or environmental condition (Silk et al. 2003).

Individuals display specific affiliative preferences in that they only establish relationships with certain group-mates; the number and qualities of such preferences vary from individual to individual. Studies investigating the proximate basis of this variation have found that animals often form relationships based upon kinship, sex, and rank (Seyfarth 1977). For example, animals generally prefer to affiliate with kin over non-kin, with same-sex group-mates over those of the opposite sex, and with similarly-ranked animals over distantly-ranked animals (de Waal & Luttrell 1986; Ehardt & Bernstein 1987; Nakamichi 1996). The extent to which affiliative relationship formation fits these general patterns, however, often depends upon the specific behaviour in question (e.g. grooming relationships are often more kin-biased than play relationships), and many exceptions to these patterns exist (de Waal 1996; Janus 1989; Nakamichi & Shizawa 2003). Studies typically overlook this "unexplained" variation in affiliative preferences, however, in favor of stressing the abovementioned general patterns (although see Nakamichi & Shizawa 2003).

Unexplained variation in affiliative preferences likely arises from individual-specific characteristics that have yet to be examined in this context. Research in humans has suggested that personality may be an influential factor. For example, the human trait Extraversion has been shown to relate to the size and quality of an individual's social network (e.g. Asendorpf & Wilpers 1998). The study of personality has recently attracted increasing interest from animal behaviour researchers (Weinstein et al. in press). The term "personality" refers to individual differences in behaviour that persist over time and across situations, and many consider it interchangeable with terms such as "temperament," "behavioural syndrome," or "style" (Clarke & Boinski 1995; Gosling 2001; Sih et al. 2004). Individual variation in personality reflects stable differences in underlying affective, motivational, physiological, and cognitive processes, which are influenced by both genetic and environmental factors (Champoux et al. 2002; van Oers et al. 2005). Personality is often assessed by measuring individuals' responses to novel or stressful stimuli, and studies of

non-primates typically classify these responses along a Shy-Bold continuum (Wilson et al. 1993; Verbeek et al. 1994). Individual variation along this continuum has been related to variation in aggressiveness, exploratory behaviour, response to predators, foraging behaviour, social learning, and risk taking in birds, fish, and insects (Sih et al. 2004). In addition to direct measures of behaviour, personality is often assessed using researchers' ratings on behaviourally-defined trait adjectives (e.g. Aggressive, Curious, Playful), which are conducted after having observed the animals either in a natural social setting or in a variety of experimenter-designed situations (Capitanio 2004; Weinstein et al. in press). These trait ratings are broad, qualitative descriptors of the individual's overall style of responses, and are usually investigated using factor- or principal component-analysis to identify higher-order factors reflecting underlying latent traits (Itoh 2002). The resulting factors are strongly rooted in empirical data, show high reliability and longitudinal stability, are replicable with different samples, and relate to behavioural variation in both social and nonsocial situations (Weinstein et al. in press).

Although individual variation in personality in nonhuman primates has been associated with a number of important behavioural and physiological correlates, such as early rearing experience, dominance status, aggressive and affiliative behaviour, immune function, and personality characteristics of offspring (Weinstein et al. in press), few studies have examined the relationship between personality assessed at one time point and social outcomes at later time points. Exceptions include studies by Capitanio (1999), who demonstrated correlations between personality factors in adult male rhesus monkeys and behaviour recorded in several different social situations up to four years following the original personality assessments; and by Fairbanks et al. (2004), who found that individual differences in Impulsivity during adolescence predicted adult dominance status in male vervet monkeys (*Cercopithecus aethiops*).

We are aware of no studies, however, that have examined the role of personality in affiliative relationship formation. Given that much variation in relationship formation remains unexplained, we investigated whether measures of infant temperament predict the quantity and quality of relationships that an individual forms during juvenility. We examined relationships of different behavioural content (e.g. proximity versus play relationships), complexity (relationships in one versus multiple content areas), and quality (i.e. reciprocated relationships). We were also interested in whether individuals may be attracted to group-mates with similar temperament characteristics.

METHODS

Subjects and Living Arrangements

Fifty-seven yearling rhesus macaques (29 males) were sampled across four half-acre outdoor corrals at the California National Primate Research Center (CNPRC). These corrals consist of large multi-male, multi-female groups comprising all age/sex classes, and group sizes of the corrals in our study ranged from 96 to 146 animals at the start of the study. The four corrals were demographically similar to one another in composition (Table 1), and fell within the observed range of wild rhesus monkey group size and composition (Seth & Seth 1983). Only corrals comprising socially stable groups with well-established matriline were included in our study. Each CNPRC corral measures 30.5 metres wide × 61 metres deep × 9 metres high, has chain-link sides and top, and contains a natural substrate, several wooden A-frame structures, PVC-coated perches along the four inside corners and on the poles supporting the cage top, a variety of climbing devices, and several food hoppers. Primate laboratory chow is provided twice daily, fruit and vegetable supplements are provided twice weekly, and water is available ad libitum from several Lixit devices located along the periphery.

Only yearlings that had participated in the CNPRC-wide Infant Biobehavioural Assessment program (see below), and whose mothers were living with them in the corral at the start of the study, were included as subjects. Subjects were selected such that no more than 30 animals were observed each year. Because these corrals are part of the breeding colony at the CNPRC, infants can be removed from mothers at birth for experimental and colony management purposes. Such removals typically occur in alternate years for any given female, leaving many yearlings with no younger siblings. We sampled all yearlings without younger siblings in the four corrals ($N = 48$), but included nine yearlings that did have younger siblings for comparison purposes. Subjects' ages ranged from 13 to 19 months at the start of the study. Paternity was known for all subjects based upon a panel of 24 autosomal microsatellite loci using one-parent paternity exclusion analysis (Garber & Morris 1983). Genetic analyses were performed by the Veterinary Genetics Laboratory (VGL), University of California at Davis according to procedures developed by the laboratory for primate DNA testing.

Infant Biobehavioural Assessment

The methods of the Infant Biobehavioural Assessment (BBA) have been described elsewhere (Capitanio et al. 2005). Briefly, at 90–120 days of age, infants were removed from their home cages and separated from their mothers for a 25-hour period of testing. All testing occurred in cohorts of five to eight monkeys at a time, drawn from multiple field corrals. During testing, subjects were housed individually, and each infant was individually assessed in several test situations according to a predetermined random order. The battery of tests is designed to assess infants' behavioural and physiological reactivity, and includes focal observations of the infant's behaviour upon separation from the mother; interactions with novel stimuli; responses to video playback of a conspecific displaying both aggressive and nonsocial behaviours; response to a human intruder; a preferential looking task to assess visual recognition memory; measures of plasma cortisol; and temperament ratings conducted at the end of testing. Temperament ratings were designed to provide an overall evaluation of each animal's style of responsiveness during testing, and constitute the principal measures used in the present analyses. Immediately following the end of testing, infants were reunited with their mothers and returned to their home cages. It is important to note that due to the temporal spread of infant births, our study subjects participated the BBA between May and September 2002, and between May and October 2003. One subject, born in 2002, was assessed at six months of age rather than at three to four months of age.

Yearling Behavioural Data Collection

We collected 15 ten-minute continuous focal samples on each subject during a 10-week period. Twenty-nine subjects in two field corrals (born in 2002) were observed from mid-September through mid-November 2003, and 28 subjects from two different field corrals (born in 2003) were observed from mid-August through mid-October 2004. Observations were conducted between 0800 and 1200 hr four to five days per week, no more than 12 animals were observed on any given day, and the order of animals to be observed at a given cage on a given day was determined randomly. We used a Psion Workabout handheld computer equipped with The Observer Mobile 3.0 (Noldus Information Technology) to record frequencies and durations of **proximity** (within arm's reach of another animal); **play** (shoving, grabbing, slapping, chasing, pushing, wrestling, and/or mouthing behaviour accompanied by a play face (wide eyes, open mouth without bared teeth) or a loose, exaggerated posture and gait); non-aggressive physical **contact**; and **grooming** (picking through and examining the fur of another monkey, parting the fur with the hands or mouth). We recorded the identity of each interactant, and indicated which animal initiated and terminated each interaction. Inter-observer reliability was > 80% for all behaviours. Note

that the person conducting the yearling observations (TARW) was blind to all of the BBA data, which were collected by a different individual.

Data Analysis

Factor Analysis of Infant BBA Temperament Ratings—At the end of the 25-hr BBA, each animal was rated on 16 trait adjectives using a 7-point Likert-type scale, with a “1” rating indicating the animal exhibited none of the trait, and a “7” indicating the animal displayed extremely high amounts of the trait. A single rater, who had conducted the Biobehavioural Assessments on all animals, rated each monkey. Intraclass correlation coefficients (computed as two-way mixed effects models: Shrout & Fleiss 1979) were used to estimate inter-rater reliabilities using additional raters. With the exception of Nervous (0.129), individual item reliabilities ranged from 0.355 (Slow) to 0.683 (Gentle), with an overall mean of 0.529. Inter-rater agreement, assessed using the Chi-Square procedure of Lawlis & Lu (1972), was significantly greater than chance ($p < 0.000001$) for all traits, and the T-index (a kappa-based measure indicating the magnitude of agreement: Tinsley & Weiss 1975) ranged from 0.397 (Confident) to 0.849 (Aggressive), with a mean of 0.636, when different observers’ ratings were allowed to vary from each other by one point. In the present sample, two traits, Nervous and Tense, demonstrated extremely abnormal skew and kurtosis, inasmuch as more than 75% of the subjects were rated “1” or “2”, and were excluded from further analysis. Z-scores were computed for the remaining 14 traits for the subject animals and all of their peer (same-aged) cage-mates that had participated in the Infant BBA but were not selected for the yearling affiliation study ($N = 70$ total). Exploratory factor analysis (using maximum likelihood estimation) was then performed, and the solution was given a promax rotation. Scales were constructed based on the factor analysis; one trait was dropped from each factor because inclusion decreased scale reliability by more than 10% (two traits) or in order to facilitate interpretation (one trait). Three scales resulted: **Adaptable** (Flexible, Gentle), **Confident** (Aggressive, Bold, Confident, Curious, Playful, Vigilant, *Not Depressed*), and **Equable** (Calm, Slow, *Not Active*); see Table 2. Scale reliability (using Cronbach alpha) coefficients were 0.93, 0.84, and 0.70 for the three factors, respectively. Note that Confidence and Equability resemble the two same-named factors derived by Capitanio and Widaman’s (2005) confirmatory factor analysis of personality in adult male rhesus monkeys, despite substantial differences in ages and assessment procedures.

Affiliative Preference Structure—We derived affiliative preference networks for each focal animal using only interactions with same-age peers, employing previously established methods (Anderson & Mason 1974; Capitanio 1985; Beehner et al. 2005). Each focal animal’s observations were parcelled into five two-week periods referred to as “bi-weeks,” with each bi-week containing three 10-minute focal observations. Total durations of affiliative interactions were calculated across each bi-week as a percentage of total time observed. As the identities of the initiators and recipients were available for all peer interactions, we recoded our data to reflect only initiations. For example, for a particular bi-week, if subject X received proximity from subject Y, we recoded it as Y initiating proximity to X, and the datum was transferred to Y’s dataset. The peer interactions initiated by each focal animal were then arranged in a two-dimensional matrix, with columns representing bi-weeks ($N = 5$), and rows representing all peer group-mates. We computed an expected value for the focal animal for each bi-week by assuming that for a given bi-week, the subject could have distributed her interactions equally among all peers. Thus, the percentages in each column (i.e. bi-week) were summed and divided by the total number of peers, with the result being the expected value of that subject’s affiliative behaviour for that bi-week. The actual and expected percentages were then compared for each peer across the five bi-weeks, using a Chi Square test. Subject X was considered to prefer (or have a

relationship with) Y for behaviour Z when X's actual scores were significantly greater than expected ($P < 0.05$). Preferences were calculated for each affiliative behaviour separately, resulting in each focal animal having a separate list (or network) of preferred peers for proximity, play, grooming, and contact. Preferences were subsequently classified according to their quality (Table 3). Low frequencies of grooming and contact (detailed below) resulted in most yearlings displaying zero peer preferences in these behavioural domains. We therefore conducted our analyses on the following four preference measures: proximity preferences initiated, play preferences initiated, multiplex preferences, and reciprocated relationships. Note that in deriving multiplex preferences and reciprocated relationships, we did include the few preferences that existed for grooming and contact.

We note that the above procedure reflects one way of identifying an animal's social network; we do not claim that this is either the best or the only way to look at affiliative relationships. This method does, however, emphasise how a particular animal allocates the time she spends affiliating. An animal that spends a lot of time affiliating with her peers, for example, may only display one or two preferences if she distributes her time fairly equally across all peers. Alternatively, an animal that spends relatively little time affiliating can display three or four preferences if she affiliates almost exclusively with those three or four animals, and spends little or no time with the rest of her peers.

Assessment of Dominance Ranks—Dominance relations are regularly assessed by colony management staff at the CNPRC by observing the feeding order of animals around temporary concentrated food sources, and scoring the direction of displacements and aggression among animals both around and in the absence of the food sources. We used the numerical dominance ranks derived by the staff for each adult female to classify matriline as high-, middle-, or low-ranking (i.e. top, middle, or bottom 1/3 of the hierarchy). Since yearlings had not yet formalized their rank in the hierarchy, we classified our subjects according to maternal rank. Of the 57 yearlings sampled, 14 were born to high-ranking matriline, 18 to middle-ranking matriline, and 25 to low-ranking matriline.

Statistical Analysis—Kolmogorov-Smirnov tests for normality revealed only one significant deviation from normality (see below); consequently, we employed parametric statistics, and report means and standard errors for our variables. We assessed the bivariate relationships between our independent variables and affiliative behaviour and preference measures using Unpaired *t* tests (sex differences), ANOVAs (rank differences), and Pearson correlations (matriline size and temperament). When an ANOVA yielded a significant result, post-hoc comparisons employed a Bonferroni adjustment (adjusted $\alpha = 0.0167$).

Following the bivariate analyses, we performed a multivariate analysis to assess the combined and interactive effects of the independent variables on our affiliative preference measures. Since Confidence failed to show a significant bivariate relationship with any preference measure, it was excluded from the multivariate analysis. Before conducting the multivariate analysis, we assessed the relationships among our independent variables, and found three results: 1) temperament differed according to rank (ANOVA: $F_{2,54} = 4.908$, $P = 0.0110$), with middle-ranked yearlings scoring significantly higher in Adaptability than high-ranked yearlings; 2) matriline size tended to correlate negatively with Adaptability ($r = -0.249$, $P = 0.0617$); and 3) Equability correlated positively with Adaptability ($r = 0.570$, $P < 0.0001$). Note that we did not find any sex differences in temperament (Unpaired *t* test: all $P > 0.19$). For the multivariate analysis of each preference measure, we employed hierarchical regression to test main effects (entered together as the first set of variables) as well as two-way interaction effects (entered as the second set). Because addition of the interaction terms did not explain significant variance in any of the models (*F* test for sets of variables: all $P > 0.21$), we only consider main effects for the remainder of the paper. The

dummy variable for sex was coded such that Female = 0 and Male = 1. For rank, we created two dummy variables: Dummy1 = 1 for high rank, Dummy2 = 1 for middle rank, and both dummy variables = 0 for low rank.

We examined yearlings' attraction to each other in terms of similarity in rank, kinship, and temperament. We used Paired *t* tests to compare, for each subject, the observed versus expected proportions of preferences directed toward peers of similar rank and toward kin. For temperament, we used Spearman rank correlations to calculate the similarity between subjects and their preferred peers' temperament scores, because the distributions differed significantly from normal.

We performed all analyses on our entire sample of animals, $N = 57$, as we did not find significant differences between yearlings with and without younger siblings for measures of temperament or affiliation (Unpaired *t* test: all $P > 0.21$). One subject had been tested in the BBA at six months of age instead of the usual three to four, but as she was not an outlier on any of our measures, we included her data in all analyses as well.

RESULTS

We present our results in the following order: first, we describe the data on affiliative behaviour and preference structure, and examine the bivariate relationships between these measures and our independent variables (sex, rank, kinship, and infant temperament). We next present the multivariate analysis of the combined effects our independent variables on each preference measure. Finally, we analyse the similarity between subjects and their preferred peers in terms of rank, kinship, and temperament.

Affiliative Behaviour and Network Structure

Bivariate Analyses

Behaviour Durations: The mean percentage of time across the entire study that subjects spent affiliating with peers was $7.696\% \pm 0.660$. In comparison, the mean percentage of time spent affiliating with mother was $17.983\% \pm 1.368$. Most affiliation consisted of proximity $4.171\% \pm 0.369$ and play $(2.110\% \pm 0.287)$. Yearlings spent little time grooming $(0.837\% \pm 0.186)$ or in contact $(0.578\% \pm 0.106)$ with peers. As a result, we excluded grooming and contact interactions from all subsequent analyses, except where noted. We then examined whether any of our independent variables (sex, rank, matriline size, and temperament) related to variation in total time spent in proximity or playing with peers. We found that males spent more time playing with peers than females (Unpaired *t* test, $t_{55} = 5.239$, $P < 0.0001$), and that time spent in proximity with peers differed according to rank (ANOVA: $F_{2,54} = 3.214$, $P = 0.0480$): high-ranking yearlings spent more time in proximity with their peers than did low-ranking animals. We did not find matriline size, Adaptability, or Equability to correlate significantly with durations of proximity or play with peers (all $P > 0.12$). We did find a marginally significant association, however, between Confidence and total time spent playing with peers ($r = 0.255$, $P = 0.0554$).

Social Network Size: Subjects preferred a mean of 2.772 ± 0.206 peers for proximity range 0–6) and 1.965 ± 0.175 peers for play (range 0–5), and displayed a mean of 1.333 ± 0.131 multiplex preferences (range 0–5). In addition, subjects had a mean of 1.965 ± 0.179 reciprocated peer relationships (range 0–6). All four preference measures were positively correlated with one another, with *r*s ranging from 0.360 to 0.650 (Table 4). We note that subjects with a large number preferred peers did not necessarily interact with a large number of animals. For example, the correlation between number of peers preferred for proximity and total number of peers with whom subjects initiated any proximity interaction (but did

not statistically prefer) was modest, $r = 0.254$. This suggests that our preference measures indeed reflected the way subjects preferentially allocated affiliative interactions, and did not simply reflect the number of peers with whom subjects interacted.

Sex: We found only one sex difference in social network size: males displayed play preferences toward a significantly greater number of peers than females (Unpaired t test: $t_{55} = -1.195$, $P = 0.0004$).

Rank: Yearlings from high-ranking matriline had significantly more peer relationships than middle- or low-ranking yearlings for two of our preference measures: proximity preferences initiated (ANOVA: $F_{2,54} = 4.628$, $P = 0.0140$), and reciprocated relationships (ANOVA: $F_{2,54} = 7.895$, $P = 0.0010$). We did not find rank-based differences in number of play preferences initiated or multiplex preferences ($P > 0.49$).

Kinship: The size of an individual's matriline was modestly associated with the number of relationships formed with peers. Most yearlings (43 out of 57) had at least one peer group-mate from the same matriline, and the mean number of related peers for all subjects was 2.228 ± 0.255 . Matriline size (measured by the number of peers in an individual's matriline) was positively correlated with the number of proximity preferences initiated ($r = 0.261$, $P = 0.0493$).

Temperament: Infant temperament was significantly correlated with social network size in our yearling subjects. Specifically, Equability was negatively correlated with each of the four preference measures (proximity preferences initiated: $r = -0.260$, $P = 0.0504$; play preferences initiated: $r = -0.289$, $P = 0.0288$; multiplex preferences: $r = -0.405$, $P = 0.0016$; reciprocated relationships: $r = -0.373$, $P = 0.0040$). In addition, Adaptability demonstrated a significant negative correlation with the number of proximity preferences initiated ($r = -0.270$, $P = 0.0416$). Confidence did not correlate with any network measure (all $P > 0.55$).

Multivariate Analysis—The regression models of the independent variables' main effects on each of the four preference measures were all statistically or marginally significant (Table 5), and for three of our four social network measures, temperament explained significant variation beyond that explained by sex, rank, and kinship. Specifically, Equability continued to demonstrate a significant negative correlation with the number of play preferences initiated, multiplex preferences, and reciprocated relationships, but not with proximity preferences initiated. Rank was also a significant predictor in three of the four models: high rank predicted a larger number of proximity preferences initiated and reciprocated relationships, and tended to predict more play preferences initiated. As in the bivariate analyses, sex demonstrated a significant association only with play preferences initiated, with males having more than females. Finally, matriline size tended to predict proximity preferences initiated, with yearlings born to larger matrilines displaying the greatest number.

Similarity between Friends

Yearlings were significantly more likely than expected by chance to form relationships with similarly-ranked peers. A mean of $56.182\% \pm 4.967$ of yearlings' proximity preferences and $53.404\% \pm 5.598$ of their play preferences were directed toward peers of similar rank. The proportion of preferences that we expected each subject to direct toward similarly-ranked peers merely by chance was determined by the proportion of peers in the corral with whom each subject shared a similar rank. We compared, for each subject, the expected proportions with observed proportions of preferences initiated toward similarly-ranked peers for

proximity and play, and found that observed proportions were significantly greater than chance (Paired t test: $t_{54} = 4.935$, $P < 0.0001$ and $t_{46} = 3.682$, $P = 0.0006$, respectively).

Yearlings were significantly more likely to form peer relationships with maternal kin than with non-kin. Yearlings that had at least one peer in their matriline initiated a mean of $38.537\% \pm 5.564$ of their proximity preferences and $34.518\% \pm 5.841$ of their play preferences toward peers from the same matriline. Using the same analysis as we used for rank to compare expected with observed values, we found that these proportions were greater than expected by chance (Paired t test: $t_{40} = 4.838$, $P < 0.0001$ and $t_{37} = 3.876$, $P = 0.0004$, respectively). We found no evidence that yearlings preferentially affiliated with peers sharing the same sire (both $P > 0.16$).

We calculated the Spearman rank correlation between members of all dyads for each temperament dimension, and found significant similarity between subjects and their preferred partners for the traits Adaptability and Equability. Because a single individual could appear in multiple dyads (e.g. animal X prefers animal W, and is preferred by both animals Y and Z), we created three models to address the relative non-independence of our data. Model A consists of all combinations of subjects and their preferred partners, i.e. if a given subject had three preferred peers, we included all three of those dyads in the dataset. In Model B, each subject and only her most preferred peer (i.e. the animal with which the subject spent the most time) was included in the dataset. Model C takes into account genetic factors that may influence temperament similarity between dyad members by excluding dyads that shared a genetic relationship (whether through the matriline or due to sharing the same sire); all remaining dyads were included. For proximity preferences, models A, B, and C all yielded essentially the same result: the correlations between subjects' and their preferred partners' temperament were positive and significant, equalling approximately 0.5 for both Adaptability and Equability (Table 6). For play preferences, we calculated the correlations in each model first for all dyads, and then, because of the sex differences in play, separately for male and female subjects' preferences (Table 7). Males showed significant positive correlations, ranging from 0.339 to 0.686, with their preferred partners for both Adaptability and Equability in all models. The number of dyads for female subjects was smaller than for male subjects, and we found that the correlations between females and their preferred partners were also positive for both Adaptability and Equability in all models, but did not always reach significance, with r_s ranging from 0.248 to 0.629. We found no significant correlations between subjects and their preferred partners for Confidence (all $P > 0.14$).

DISCUSSION

Our study demonstrates a clear association between infant temperament and affiliative preferences during the second year of life, supporting our hypothesis that temperament plays a significant role in nonhuman primate relationships. We will discuss our findings in the same order in which they were presented above.

Affiliative Behaviour and Network Size

Although subjects spent an average of only 7.7% of their time affiliating with peers over the course of the study—while 18.0% was spent with mother—clear peer preferences emerged for each individual. Most preferences were in the proximity and play domains, and subjects spent little time grooming or in contact with their peers. We found no significant associations between temperament and affiliative behaviour durations (except for the marginally significant result for Confidence, discussed below). We did, however, find substantial individual variation in both the number and identity of subjects' preferred peers.

Our findings suggest that individuals differed in the criteria they used to select friends, with temperament being an especially important factor.

Sex, Rank, and Kinship

In accordance with previous research, we found that sex, rank, and kinship influenced affiliative relationship formation in our subjects. Males displayed more play preferences than females, yearlings with high maternal rank had the largest social networks, and yearlings from larger matriline displayed a greater number of proximity preferences. These patterns are consistent with results of previous studies of social behaviour of both wild and captive macaques (de Waal & Luttrell 1986; Ehhardt & Bernstein 1987; Nakamichi 1996). Nonetheless, as in previous studies, sex, rank, and kinship failed to fully explain observed variation in the social relations of our animals.

Temperament

Temperament played an important role in determining both the number and identity of peers with whom yearlings formed relationships, explaining significant variation in preferences even after taking into account the significant effects of sex, rank, and kinship. Equability correlated negatively with all four of our preference measures, and remained a significant predictor for three of these measures in the multivariate analysis. During the Infant BBA, animals that scored high on Equability were easygoing, calm, and behaved more slowly and in a more relaxed manner. Conversely, animals that scored low on this dimension were more active and easily agitated. The finding that highly Equable animals initiated fewer play preferences seems reasonable, as play is a behaviour characterised by high levels of activity involving intense bursts of running, wrestling, climbing, and jumping. However, highly Equable individuals, who seemed to adjust best to the stressful conditions of BBA testing, also formed fewer multiplex and reciprocated relationships with peers, which did not always involve social play. This finding seems counterintuitive, since such easygoing animals might be expected to be skilled at forming friendly non-play relationships with their peers. However, the smaller number of relationships formed by these individuals may not reflect a low level of social skill, but a low level of social motivation. Calm, slow, and easygoing animals may be less motivated to form friendships because they may not reap one of the primary benefits of such relationships: the calming effects that friends have on each other during stressful situations (Higley et al. 1992; Uchino et al. 1996; Boccia et al. 1997; Sachser et al. 1998). Equable individuals may not gain this benefit precisely because they are already calm and easygoing. Specifically, if these animals are able to cope with the day-to-day stressors of their lives (e.g. being rejected and/or ignored by their mothers, receiving reprimands from adults in response to social transgressions) as well as they did with the stressful BBA conditions, they may be less motivated to seek out relationships with peers. We are following up on this possibility by examining whether our subjects do in fact seek out preferred peers during acutely stressful conditions.

Alternatively, highly Equable individuals may in fact be quite skilled at forming strong relationships with their peers, but such skill may be reflected more in the quality, not the quantity, of their relationships. For example, highly Equable animals may be more likely to form relationships that exhibit longitudinal stability, a quality that may help juveniles become integrated into their group's social network. We are in the process of following up on our subjects to examine the long-term stability of yearling relationships.

We cannot discount the possibility, however, that individuals that remain calm in response to novel, stressful circumstances may simply not be skilled at establishing relationships with peers. In fact, research on humans suggests that it is high activity level (i.e. being low on Equability) that is associated with greater social skill. Activity is one of the facets that make

up the Extraversion dimension (McCrae & Costa 1987), and infant/childhood activity level has been shown to be a developmental precursor to Extraversion, being positively correlated with later scores on this factor (e.g. Hagekull & Bohlin 1998). Since humans low on Extraversion have smaller social networks (Asendorpf & Wilpers 1998), we would indeed expect our highly Equable (i.e. less active) subjects to likewise form fewer peer relationships. Such a lack of friendships may hinder these animals' integration into their group's social network. Silk et al. (2003) found that increased social integration was associated with increased reproductive success in adult female savannah baboons (*Papio cynocephalus*), suggesting that the decreased involvement in relationships exhibited by our highly Equable subjects could result in decreased reproductive success later on. The possibility that low involvement in relationships as a juvenile could negatively impact fitness is intriguing, as it suggests that the advantages associated with being highly Equable in one situation (that of acute stress) do not carry over into another (that of social living), and vice versa. Such trade-offs have been demonstrated in several studies of animal personality (Sih et al. 2004), and reflect the fact that the suites of correlated behaviours that define personality evolved as a package (Price & Langen 1992). The notion that individuals do well in some contexts and poorly in others helps explain how individual differences in behaviour were maintained during the course of evolution.

Adaptability demonstrated a significant bivariate correlation with the number of proximity preferences initiated by our subjects, but did not remain a significant predictor in the multivariate analysis. This is most likely due to the fact that rank and matriline size, which were both related to Adaptability, were stronger predictors of this preference measure. Animals that had scored high on Adaptability as infants demonstrated flexibility and adaptability in their responses to the novel stimuli that they encountered during the BBA, while low-scoring animals were emotionally reactive and aggressive toward the technician. Adaptability related to maternal rank in an interesting way, in that middle-ranking animals scored the highest. A great degree of behavioural flexibility appears to be required of middle-ranked monkeys in their daily lives: they occupy a unique social position due to being dominant over and subordinate to approximately equal numbers of their group-mates, and must be skilled at frequently switching between these two roles. Therefore, it is not surprising that infants born into middle-ranked matrilineages showed the most flexible style of responses during BBA testing. Middle-ranked macaques have previously been shown to be especially good at responding to their partners' cues in a cooperative conditioning situation (Miller 1975), and to display heightened visual attentiveness toward partners during experimentally created pairings (Haude et al. 1976) and toward videotapes of conspecifics displaying social behaviour (Capitanio et al. 1985). Though several studies of nonhuman primate personality have examined differences between high- and low-ranking animals (e.g. Sapolsky & Ray 1989), surprisingly few have specifically targeted middle-ranking animals. Our findings suggest that such an examination may be warranted.

Confidence, the third temperament factor, did not correlate with any of our preference measures, although it did show a modest positive association with the duration of play with peers. The Confidence dimension reflects the level of interest, curiosity, and (lack of) inhibition that infants displayed when interacting with novel stimuli during the BBA. Confidence may reflect a style of responsiveness specific to the inanimate—as opposed to social—environment, which could explain its modest association with durations of social play: the CNPRC corrals contain various toys and structures around which juveniles frequently play. If highly Confident animals spend more time playing with such objects, by virtue of association these individuals may end up playing with their peers. Alternatively, Confidence may show a stronger relationship to social differences seen later in development, for example in relation to rank attainment or to aspects of adult personality. The question of the extent to which early measures of temperament (assessed in response to novel situations)

relate to personality in adulthood (as assessed in a more naturalistic, social setting) is a critical one for which there is very little data. Our follow-up studies on these animals will address some of these issues.

Similarity Between Preferred Partners

Yearlings formed relationships with peers that were similar to themselves in terms of rank, maternal kinship, and temperament. Attraction to kin and to similarly-ranked conspecifics has been demonstrated numerous times by nonhuman primate researchers (de Waal & Luttrell 1986; Ehardt & Bernstein 1987; Nakamichi 1996). We note that for our subjects, attraction to similarly-ranked peers was not simply a result of attraction to kin. In fact, only a mean of $54\% \pm 6.242$ of yearlings' same-ranked proximity preferences were kin, indicating that both rank and kinship were important criteria in yearlings' selection of friends. Temperament was no less important a criterion, though attraction to group-mates similar in temperament has never been demonstrated to our knowledge. Our subjects specifically preferred peers that had scores similar to their own on Adaptability and Equability. This finding could not be explained by shared genetic factors: excluding kin dyads from our analysis did not attenuate the strong positive correlations. One possible reason for attraction to similar temperament characteristics is that individuals simply "get along" better with animals that are like themselves. Since aggression was extremely rare amongst our subjects, we do not have sufficient data to determine whether individuals engaged in fewer agonistic interactions with animals that were temperamentally similar to themselves. A second possibility is that assortative pairing during juvenility is a developmental precursor to assortative mating during adulthood. Though we are aware of no studies that have examined the possibility that rhesus monkeys mate assortatively (or disassortatively) according to temperament, evidence for this phenomenon does exist in birds (Dingemanse et al. 2004), fish (Budaev et al. 1999), and humans (Caspi & Herbener 1990). In great tits (*Parus major*), assortatively mated pairs at both ends of the Shy-Bold continuum produced fledglings in better condition than disassortatively mated pairs (Both et al. 2005). It is thus possible that rhesus monkeys are attracted to individuals similar to themselves throughout the lifespan as an evolutionary byproduct of selection for assortative mating.

In summary, we found that individual differences in infant temperament amongst rhesus monkeys related to later variation in the animals' social networks. Temperament predicted affiliative preferences even after accounting for sex, rank, and kinship. As complex interactions between these variables may exist that we did not have the power to detect, future studies should aim to gather a large enough sample size in order to test for possible higher order interactions. Although our study demonstrated cross-contextual and longitudinal consistency of individual differences, many studies of animal personality have been unable to substantiate such stability, and have thus concluded that individual differences in personality are context-specific (e.g. Coleman & Wilson 1998). Many of these studies have assessed personality using direct measures of behaviour, often scoring only a few behaviours displayed by the individual in just a single situation to serve as an index of the individual's overall, more general response tendencies (but see Wemelsfelder et al. 2001). A ratings approach such as the one we used, in contrast, assesses behavioural style at the level of the whole organism, rather than focusing on discrete behaviours, and may be more useful in predicting responses in diverse contexts and at other time-points.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Table 1

Demographic data of the four field corrals

	NC5	NC7	NC11	NC13
Total Animals	96	134	141	146
Adult Females	38	48	48	45
Adult Males	9	9	14	10
Older Juveniles	18	33	28	30
Yearlings Males	9	9	9	11
Females	7	19	10	12
Number of Matrilines	11	9	16	9
Mean Number of Adult Females/Matrine	3.45	5.33	3.00	5.00

Table 2

Infant Biobehavioural Assessment temperament ratings

Active, energetic	Moves about a lot, distance traveled by walking, running, climbing, or jumping. Not lethargic.
Aggressive	High frequency of displays, threats.
Bold	Fearless; is daring, not restrained or tentative. Not timid, shy, or coy.
Calm, equable	Reacts in an even, calm way; is not easily disturbed. Not agitated. Restful, peaceful.
Confident	Behaves in a positive, assured manner, not restrained or tentative.
Curious, exploratory, inquisitive	Readily explores new situations, seeking out or investigating novel situation.
Depressed	Subject appears isolated, withdrawn, sullen, brooding, and has reduced activity.
Flexible, not rigid	Adapts to situations. Is able to accommodate new ways of doing things.
Gentle	Subject responds to technicians in an easy-going, kind, and considerate manner. Subject is not rough or threatening.
Playful	Engages in self-play (hanging, swinging, jumping), or object play.
Slow	Moves and sits in a relaxed manner; moves slowly and deliberately, not easily hurried.
Vigilant, alert	Ready, attentive, watchful, notices with special attention. Not oblivious to surroundings.

Table 3

Preference measures and definitions

Preference Initiated	A preference displayed by the focal animal for another peer
Multiplex Preference	A preference displayed by the focal animal for another peer in more than one behavioural domain (e.g. the focal animal prefers the peer for both proximity and play)
Reciprocated Relationship	Any preference displayed by the focal animal for a peer that also prefers the focal animal, regardless of behavioural domain

Table 4

Pearson correlations between preference measures

	Proximity Preferences	Play Preferences	Multiplex Preferences	Reciprocated Relationships
Proximity Preferences	1.000	---	---	---
Play Preferences	0.360	1.000	---	---
Multiplex Preferences	0.468	0.542	1.000	---
Reciprocated Relationships	0.625	0.650	0.451	1.000

Table 5

Standardized regression coefficients of sex, rank, matriline size, and temperament in each model

	Proximity Preferences	Play Preferences	Multiplex Preferences	Reciprocated Relationships
Sex [†]	0.124	0.462 ^{***}	0.154	0.111
Rank [†] Dummy1	0.341 [*]	0.230 ^a	0.079	0.465 ^{***}
Dummy2	−0.054	0.093	0.036	−0.079
# Peer kin	0.244 ^a	0.089	0.097	0.173
Adaptability	−0.017	0.170	0.142	0.197
Equability	−0.189	−0.372 [*]	−0.474 ^{**}	−0.419 ^{**}
Multiple R²	0.264	0.354	0.211	0.391
ANOVA F_{6,50}	2.997	4.569	2.233	5.339
P value	0.0140	0.0009	0.0550	0.0003

[†]The dummy variable for sex was coded such that Female = 0 and Male = 1. For rank, Dummy1 = 1 for high rank, Dummy2 = 1 for middle rank, and both dummy variables = 0 for low rank.

^a0.05 < *P* < 0.1

^{*}*P* < 0.05

^{**}*P* < 0.01

^{***}*P* < 0.001

Table 6

Models of temperament similarity between preferred partner dyads for proximity (Spearman rank correlations)

	Adaptable	Equable	Confident
Model A: all dyads (<i>N</i> = 140 dyads)	0.454 **	0.483 **	0.080
Model B: most preferred partner (<i>N</i> = 54 dyads)	0.536 **	0.486 *	0.056
Model C: unrelated dyads only (<i>N</i> = 76 dyads)	0.507 **	0.531 **	0.171

*
P < 0.01**
P = 0.0001.

Table 7

Models of temperament similarity between preferred partner dyads for play (Spearman rank correlations)

		Adaptable	Equable	Confident
Model A	All ($N = 97$ dyads)	0.392 ***	0.390 ***	0.062
	Males ($N = 64$ dyads)	0.486 ***	0.339 **	0.117
	Females ($N = 33$ dyads)	0.293 [†]	0.248	−0.042
Model B	All ($N = 46$ dyads)	0.586 ***	0.605 ***	0.200
	Males ($N = 28$ dyads)	0.601 **	0.686 **	0.454 *
	Females ($N = 18$ dyads)	0.554 *	0.323	−0.231
Model C	All ($N = 55$ dyads)	0.462 **	0.569 ***	−0.003
	Males ($N = 37$ dyads)	0.555 **	0.445 **	0.094
	Females ($N = 18$ dyads)	0.262	0.629 **	−0.123

[†] $P < 0.1$ * $P < 0.05$ ** $P < 0.01$ *** $P < 0.0001$.