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Longitudinal Stability of Friendships in Rhesus Monkeys (*Macaca mulatta*): Individual- and Relationship-level Effects

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Abstract

The longevity of children's friendships is influenced by a multitude of individual- and relationship-level attributes, but little is known about the factors that impact friendship maintenance in nonhuman primate juveniles. We investigated whether the following predicted the longitudinal stability of friendships in juvenile rhesus monkeys (*Macaca mulatta*): (a) individual characteristics including sex, dominance rank, matriline size, and temperament; and (b) relationship characteristics including kinship, reciprocity, complexity, and similarity between friends in sex, rank, and temperament. We recorded affiliative interactions of 29 two-year-old rhesus monkeys, previously observed as yearlings, at the California National Primate Research Center. Friends were defined as peers with whom subjects spent more time affiliating than expected by chance. Temperament had been assessed at 3–4 months of age. Sex was the only individual characteristic predicting friendship stability: males maintained more friendships from age one to two than did females. Relationship characteristics predicting friendship stability included similarity between individuals in temperament, kinship, and sex. In addition, reciprocated friendships, rather than unidirectional friendships, were significantly more likely to persist over time. Our findings suggest that the factors influencing friendship maintenance in rhesus monkeys are similar to those impacting human friendship longevity.

Keywords

affiliation; friendship; personality; rhesus monkey; temperament

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Many primate species evolved as social beings embedded in a complex network of relationships. This complexity is reflected in the diverse categories of relationships that individuals have (e.g. family relationships, friendships, sexual partnerships), as well as in the qualities that characterize specific relationships within each category. Friendship formation is one of the earliest major tasks in an individual's social development, and has been recognized for its importance in both the human and nonhuman primate literature (Hartup, 1996; Suomi, 2005). Human and nonhuman primate friendships have been defined almost identically: they are characterized by frequent affiliative interactions that show continuity across time and context, and individuals classified as friends exhibit high degrees of tolerance and compatibility (Newcomb & Bagwell, 1995; Silk, 2002; Smuts, 1985).

Numerous benefits have been associated with friendship formation and maintenance in both human and nonhuman primates. For example, research in humans has shown that friendship involvement is related to the development of social skills (Ladd, 1999). In addition, for children and adults alike, friends appear to serve as buffers against the negative behavioral and physiological consequences of acutely stressful circumstances (Bolger & Eckenrode, 1991; Christenfeld et al., 1997; Dubois, Felner, Brand, Adan, & Evans, 1992), and long term social support is associated with decreased mortality rates, better health outcomes, and increased subjective well-being and self-esteem (Helliwell & Putnam, 2004; House, Landis, & Umberson, 1988; Keefe & Berndt, 1996; Uchino, Cacioppo, & Kiecolt-Glaser, 1996). Similar outcomes have been found for nonhuman primates: several studies have demonstrated social buffering against acute stressors (Beehner et al., 2005; Boccia et al., 1997; Crockford, Wittig, Whitten, Seyfarth, and Cheney, 2008; Gust, Gordon, Brodie, & McClure, 1994; Wittig et al., 2008) and the development of chronically elevated basal cortisol levels (Abbott et al., 2003; Brent, Semple, Dubuc, Heistermann, & MacLarnon, 2011; Sapolsky, 2005), as well as reduced mortality (Capitanio, Mendoza, Lerche, & Mason, 1998; Silk et al., 2010). While no study to our knowledge has linked friendship to reproductive success in humans, evidence from nonhuman primate research supports this connection. Adult female savannah baboons (*Papio cynocephalus*) that have stronger friendships with their group-mates are more likely to rear infants successfully, and have offspring who live longer into adulthood, regardless of their dominance rank or of the environmental conditions that they experience (Silk, Alberts, & Altmann, 2003; Silk et al., 2009). Similarly, male Assamese macaques (*Macaca assamensis*) with stronger affiliative relationships sire more offspring than those with weaker relationships (Schulke, Bhagavatula, Vigilant, & Ostner, 2010).

Not all friendships are equal: they vary in terms of stability, quality, reciprocity, and on a number of individual-specific factors. Stable, high-quality friendships, indicated in humans by low levels of conflict, the sharing of intimate thoughts/feelings, and high frequencies of prosocial behavior (Berndt, 2002), appear to confer particularly strong advantages to individuals, and many of the abovementioned positive outcomes only result from involvement in friendships that are both high quality and long-lasting (Hartup & Stevens, 1999; Uno, Uchino, & Smith, 2002). Quality, reciprocity, and stability are interrelated variables, with increasing amounts of the former two predicting the latter (Berndt, 2002; Bukowski, Hoza, & Boivin, 1994; Gershman & Hayes, 1983; Ladd, Kochenderfer, & Coleman, 1996; Schneider, Fonzi, Tani, & Tomada, 1997). Similarity between individuals on a number of demographic factors, including sex, age, socioeconomic status (SES), and race, has also been associated with the formation of stable friendships (Barbu, 2003; Gibbons & Olk, 2003; Kupersmidt, Derosier, & Patterson, 1995; McPherson, Smith-Lovin, & Cook, 2001; Sutor & Keeton, 1997).

Only a few studies have investigated friendship stability in nonhuman primates. As in humans, nonhuman primates generally maintain long-term friendships with individuals

similar in age, sex, and social status, and who share a maternal relationship (Kojima, 1998; Nakamichi, 1996). Even fewer studies of nonhuman primates have examined the role of reciprocity or other measures of relationship quality, in addition to the above factors, in friendship stability. Silk, Alberts, and Altmann (2006) demonstrated, however, that the grooming relationships of adult female savannah baboons that were most reciprocal were the ones most likely to persist over time. Though the evidence is limited, it suggests that the factors predicting friendship stability in nonhuman primates may be similar to those in humans, and warrant further exploration.

The factors described above are general features which, though influential in determining the formation and maintenance of friendships, do not reflect the role played by specific characteristics of the individuals themselves. Friendship quality is likely influenced by the personalities of both individuals (Asendorpf & Wilpers, 1998), yet personality's role in human friendship has received less empirical attention than age, sex, SES, or race, and is consequently less understood, particularly in the case of children (Gleason, Gower, Hohmann, & Gleason, 2005). Personality can influence friendship in several ways. First, it can affect the number and quality of friendships an individual forms (e.g., Gleason et al., 2005). In our previous study of yearling rhesus monkeys (Weinstein & Capitanio, 2008), we found that individuals scoring high on Equability (calm, generally inactive animals) had the fewest friendships with their peers. Second, an individual's personality may interact with that of his or her peers to determine the likelihood of friendship formation. For example, studies have found that children and their friends show significant similarity in temperament (Burlinson, 1994; Dunn & Cutting, 1999; Haselager, Hartup, van Lieshout, & Riksen-Walraven, 1998). We also found significant similarity between yearling rhesus monkeys and their friends on the dimensions of Equability and Adaptability (reflecting how flexibly animals adjust to novel, stressful circumstances; Weinstein & Capitanio, 2008). Finally, personality's role in friendship formation may change throughout development. For instance, Gleason et al. (2005) found evidence that temperament plays a larger role in older children's friendships than those of younger children, though the opposite pattern has also been proposed (Hartup, 1996).

With the exception only of our earlier report (Weinstein & Capitanio, 2008), personality has received no attention in the nonhuman primate friendship literature, though its role in general social behavior has been investigated (e.g. Capitanio, 1999; Capitanio, 2002; Capitanio et al., 2008). In the present paper, we follow up on our previous study of friendship in yearling rhesus monkeys by investigating how both individual- and relationship-level characteristics relate to the persistence of friendships through age two. We examine: (a) whether individual characteristics such as sex, rank, matriline size, and infant temperament predict the number of relationships formed at age one that endure through age two; (b) the role that similarity in demographic and temperamental characteristics play in the persistence of relationships previously formed at age one; and (c) how relationship complexity and reciprocity impact the longitudinal stability of rhesus monkey friendships. We discuss our findings primarily by comparing previous human to nonhuman primate research for a few reasons. First, as already noted, personality has thus far not been examined as a factor influencing friendships of nonhuman primates, or any animal species to our knowledge, but its role has been investigated in a number of studies of humans. Given the similarities between human and nonhuman primate friendships, described above, we feel that it is not only useful to examine whether our results parallel those of human studies, but necessary, as animal personality researchers have recently reproached the fact that animal and human studies of personality rarely reference one another, despite the massive amount of potentially relevant empirical and theoretical human personality literature that exists (Nettle & Penke, 2010). Likewise, friendship quality (i.e. reciprocity and complexity) in relation to stability has received little attention in the nonhuman primate literature, but the

importance of quality in determining friendship longevity has been well documented in humans. Third, rhesus monkeys have long been used as a model for humans with respect to studying biological, emotional, and social processes, and more recently with respect to personality, owing not only to a common evolutionary lineage, but to similarities in cognitive abilities, neuroanatomy, and social and emotional development and complexity (Capitanio & Emborg, 2008; Nelson & Winslow, 2009; Weinstein, Capitanio, & Gosling, 2008; Weiss, Adams, Widdig, & Gerald, 2011). Such a model has obvious limitations; for instance, rhesus macaques are not humans' closest phylogenetic relatives, their social structure is clearly less complex than that of humans, they lack a sophisticated theory of mind and the language skills unique to humans, they do not display adult-adult attachment relationships, and fathers do not directly participate in the care of offspring. Nevertheless, rhesus monkeys share many aspects of social development in common with humans (Suomi, 2005), and they may confer certain advantages over studies of human children since such research almost always relies on the self-reporting of friendships rather than on direct behavioral evidence, and little experimental control is possible. Investigating whether rhesus monkey friendships display similar developmental processes to those of human children may therefore expand our understanding of friendship in both species, and might help us to discern which features of friendship represent possible evolutionary adaptations—either analogous or homologous—to social living in primates.

Method

Subjects and Living Arrangements

Twenty-nine rhesus macaques (16 males) that had participated in our study of yearling friendships approximately seven months earlier were sampled from two outdoor corrals at the California National Primate Research Center (CNPRC; Weinstein & Capitanio, 2008). Each corral measured 30.5 m wide $\times$ 61 m deep $\times$ 9 m high, had chain-link sides and top, and contained 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 was provided twice daily, fruit and vegetable supplements were provided twice weekly, and water was available ad libitum. Each CNPRC corral contained a large multi-male, multi-female group comprising all age/sex classes, and, like wild rhesus monkey groups, was organized around female-headed extended families (matrilines). Each corral contained several separate matrilineal groups, which in turn typically comprised several generations of kin. Group sizes of our two study corrals were 110 and 157 animals at the start of the study. The corrals were demographically similar to one another in composition, and with the exception of new infant births, had not experienced any major changes in group membership since the yearling study. Note that in our original study, we observed 57 animals in four corrals; we excluded two corrals from the present study owing to significant changes in social structure and to time constraints. All of the previously observed subjects from the remaining two corrals participated in the current study. Subjects' ages at the start of the study ranged between 23 and 27 months.

Infant BioBehavioral Assessment

All subjects had previously participated in the CNPRC-wide Infant BioBehavioral Assessment (BBA) program (Capitanio, Mendoza, Mason, & Maninger, 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. This battery of tests is designed to assess infants' behavioral and physiological reactivity, and includes observations of the infant's behavior upon

separation from the mother; interactions with novel objects; recording of responses to video playback of a conspecific displaying both aggressive and nonsocial behaviors, as well as responses to a human intruder; assessment of visual recognition memory; assessment of hypothalamic-pituitary-adrenal regulation; and temperament ratings, which were 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. Due to the temporal spread of infant births, our study subjects participated in the BBA between May and September 2002, and between May and October 2003. One subject, born in 2002, had been assessed at six months of age rather than at three to four months of age.

Behavioral Data Collection in Field Corrals

Thirteen animals from one field corral were observed from late May through mid-July 2004. Sixteen animals from the second field corral were observed from late May through mid-July 2005. All data collection methods were identical to those used previously (Weinstein & Capitanio, 2008). We conducted 15 ten-minute continuous focal observations on each subject using 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 behavior 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. All focal samples were collected by a single trained observer who had demonstrated inter-observer reliability for all behaviors at a level > 80% based on a reliability analysis of six 10-minute focal observations.

Data Analysis

Factor analysis of Infant BBA temperament ratings—At the end of BBA testing, each animal was rated on 16 trait adjectives by a single trained technician who had worked with all of the animals during the entire assessment period using a 7-point Likert scale, with a “1” rating indicating the animal exhibited none of the trait, and a “7” indicating the animal displayed extremely high levels of the trait. Temperament ratings reflected the behavior that the technician observed during testing as well as her interactions with the animals during feeding, handling, blood sampling, and husbandry, and thus represent her overall evaluation of the animals' functioning. Assessment of inter-rater agreement and reliability for the ratings has been described (Weinstein & Capitanio, 2008). Briefly, intraclass correlation coefficients (computed as two-way mixed effects models, Shrout & Fleiss, 1979) were used to estimate inter-rater reliabilities using additional raters, and individual item reliabilities demonstrated an overall mean of .53. Inter-rater agreement, assessed using the chi-square procedure of Lawlis and Lu (1972), was significantly greater than chance for all traits ($p < .000001$), and the mean T index (a kappa-based measure indicating the magnitude of agreement, Tinsley & Weiss, 1975) was .64, when different observers' ratings were allowed to vary from each other by one point. Note that although the use of adjective ratings to assess personality is considered controversial by some animal researchers (e.g. Uher, 2008), numerous studies have demonstrated that such ratings have a strong empirical basis, show high levels of inter-rater agreement, internal consistency, and test-retest reliability, and that they predict individual differences in behavior in a variety of social and nonsocial contexts (Freeman & Gosling, 2010; Weinstein, Capitanio, & Gosling, 2008). Furthermore, research has shown adjective ratings to often be superior to direct measures of behavior in terms of reliability, practicality, and in their ability to quantify a cohesive set of enduring traits that

characterize the whole organism, rather than to simply measure individual behaviors that may be transient and/or context-specific (Vazire, Gosling, Dickey, & Schapiro, 2007; also see reviews by Freeman & Gosling, 2010 and Weinstein, Capitanio, & Gosling, 2008).

We had previously derived three factors using factor analysis (with maximum likelihood estimation) from the temperament ratings of our larger study sample ($N = 70$; see Weinstein & Capitanio, 2008): Adaptability, Confidence, and Equability. Scale reliability (using Cronbach's alpha) coefficients were .93, .84, and .70 for the three factors, respectively. Infants high in Adaptability scored high on the traits flexible and gentle, indicating that they readily adapted to novel situations in an easygoing manner. Highly Confident infants were rated high on the traits aggressive, bold, confident, curious, playful, and vigilant, and scored low on the trait depressed. Infants high in Confidence therefore demonstrated an absence of behavioral inhibition, acted in a bold, assured manner, and were interested in exploring and playing with environmental stimuli. Infants scoring high on Equability were rated high on the traits calm and slow, and low on the trait active, signifying that they were relaxed, not easily agitated, and did not move about very much. Note that we previously found no sex differences in any of our temperament factors, and only one rank-based difference, with middle-ranked animals scoring higher on Adaptability than high-ranked animals, $F(2,54) = 4.91$, $p = 0.01$ (Weinstein & Capitanio, 2008).

Affiliative preference structure—We derived affiliative preferences for each focal animal using only interactions with same-age peers, employing the methods from our previous study (Weinstein & Capitanio, 2008). Each focal animal's data were parceled into five groups of three 10-minute focal observations referred to as "biweeks." Since we had recorded identities of the initiators and recipients of all peer interactions, we recoded our data to reflect only initiations. For example, if subject X received play from subject Y during biweek 1, we transferred the data point to Y's biweek 1 dataset, indicating that Y initiated play with X. For each subject, we converted the total duration of affiliation with each peer during a given biweek into a percentage of total time observed. We entered each of these percentages into a separate table for each subject, with columns representing biweeks ($N = 5$), and rows representing all peer group-mates. Any peer(s) with whom the focal animal did not affiliate during a given biweek received a "0" value in his or her cell. For each biweek, we then calculated the percentage of time the subject would have spent affiliating with each peer if the interactions were distributed equally across all peers during that biweek. To do this, we summed the actual values in each column (i.e. biweek) and divided by the total number of rows (peers) to give us the expected value of that subject's affiliation with each peer if s/he was affiliating at random. For example, if a subject with five peer group-mates spent a total of 10% of her time affiliating with those peers during a given biweek, we would have expected her to spend 2% of her time with each peer if she were interacting randomly. Next, we compared the actual and expected percentages for each individual peer across the five biweeks, using a chi square test ($df = 4$). Subject X was considered to prefer (or have a relationship with) animal Y for behavior Z when X's actual scores were significantly greater than expected ($p < .05$). We calculated preferences for each affiliative behavior separately, in order to classify the behavioral complexity (i.e. uniplex versus multiplex) of each friendship. A uniplex preference was one displayed by the focal animal toward a peer in only one behavioral content area (e.g. proximity). A multiplex preference, in contrast, was one displayed by the focal animal for a fellow peer in more than one content area (e.g. the focal animal preferred the peer for both proximity and play). We also classified relationships according to their quality: a preference displayed by the focal animal for a peer that also preferred the focal animal (regardless of behavioral domain) was categorized as reciprocated, while a preference displayed by the focal animal for a peer who did not prefer that individual was categorized as unidirectional. Finally, we derived a variable, number of stable friends, that measured the number of specific individuals with whom subjects

maintained a stable relationship. To do this, we compared the individual peers that were preferred by the focal animal (irrespective of behavioral domain) at age one to those preferred at age two. The number of stable friends is the number of individuals that were preferred by the focal animal at both time points.

Note that the method we used to calculate affiliative preferences is not the only or necessarily the best way to identify friendships. This procedure has, however, been previously established as a technique that focuses on how a particular individual allocates the time s/he spends affiliating, which we believe is an important indicator of individual preferences (Anderson & Mason 1974; Beehner et al. 2005; Capitanio 1985; Weinstein & Capitanio, 2008).

Following the above analysis, we excluded one female subject (born in 2002) from further analyses because her mother had died shortly before the start of our observations. Examination of her data revealed that she represented an outlier in that she rarely interacted with her peers and did not form or maintain any friendships during the current study. We therefore conducted all subsequent analyses on the remaining 28 animals.

Assessment of dominance ranks—Dominance relations among group members are regularly assessed by colony management staff at the CNPRC by observing the feeding order of animals around temporarily concentrated food sources, and by scoring the direction of displacements and aggression among animals both around and in the absence of the food sources (a commonly used technique in primate facilities). Since each group contained a clear-cut linear dominance hierarchy between the different matriline, such that all members of the highest-ranking matriline were dominant over all members of the second-ranking matriline, who in turn outranked all members of the third-ranking matriline, and so forth, 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 one-third of the hierarchy). Since our subjects had not yet formalized their own ranks in the hierarchy, we classified them according to maternal rank. Of our 28 subjects, four were born to high-ranking matriline, 11 to middle-ranking matriline, and 13 to low-ranking matriline.

Statistical analyses—We report means and 95% confidence intervals (CIs) for our variables, and include effect sizes (Cohen's *d*) where appropriate. We used parametric statistics (*t* tests, ANOVAs, and Pearson correlations) to assess the bivariate relationships between our independent variables (sex, rank, matriline size, and temperament) and the number of stable friends our subjects had. Note that we defined matriline size as the number of maternally related peers in the corral, so that we could specifically examine whether subjects might have had a larger number of stable friends simply as a byproduct of having a greater number of peer kin in their group. When an ANOVA yielded a significant result, we applied a post-hoc Bonferroni adjustment (adjusted $\alpha = .0167$).

We then performed a multivariate analysis to assess the combined and interactive effects of the independent variables on subjects' number of stable friends. Due to our limited sample size, we included only those variables whose bivariate association with the number of stable friends yielded a probability value $< .10$: sex, rank, and Adaptability. We used 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). We coded the dummy variable for sex 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.

Finally, we used logistic regression to determine whether the following independent variables influenced the likelihood that a friendship observed at age one would persist

through age two: similarity in rank, maternal kinship, the sexes of both members of the dyad, relationship reciprocity, relationship complexity, and similarity in temperament.

Results

Number of Stable Friends

Overall, the mean number of peers preferred by our subjects changed very little over time. The mean difference between the number of friends subjects had at age two (4.14; 95% CI = 3.55, 4.73, range = 2-7) versus age one (3.68; 95% CI = 3.13, 4.23, range = 1-6) was 0.46 (95% CI = -0.22, 1.14; range = -3-5), which was not significant, paired $t(27) = 1.34$, $p = .19$. However, animals showed only modest individual consistency in the number of peer friends they had: the correlation between age one and two was $r = .29$, $p = .14$; 95% CI = -.10, .60. In terms of consistency in the specific identities of the peers preferred by our subjects, a mean of 1.46 of subjects' friends at age one continued to be preferred at age two (95% CI = 1.12, 1.81; range = 0-3).

Individual Characteristics Influencing the Stability of Friendships

Bivariate analyses—Sex and temperament both showed a significant, and rank showed a non-significant trend toward, a bivariate association with subjects' total number of stable friends. Males maintained stable friendships with more of their peers ($M = 1.94$; 95% CI = 1.56, 2.32, range 1-3) than did females ($M = 0.83$; 95% CI = .42, 1.24, range 0-2), $t(26) = 3.86$, $p = .0007$, $d = 1.47$. In addition, animals that had scored higher in Adaptability as infants had more stable friends than did animals low on this dimension, $r = .48$, $p = .01$; 95% CI = .13, .72. We found a non-significant trend for middle-ranked animals to have more stable friends ($M = 1.91$; 95% CI = 1.35, 2.47, range 0-3) than high-ranked ($M = 0.75$; 95% CI = 0, 1.69, range 0-2) or low-ranked animals ($M = 1.31$; 95% CI = 0.90, 1.72, range 0-3), $F(2, 25) = 3.08$, $p = .06$. Matriline size did not significantly relate to the number of stable friends, $r = .16$, $p = .42$; 95% CI = -.23, .50.

Multivariate analysis—Because sex, Adaptability, and rank were related to the number of stable friends at a probability level $< .10$, we performed a hierarchical multiple regression analysis to examine the effects of these variables when analyzed together. The regression model for the main effects was significant, $R^2 = .52$, $F(4,23) = 6.16$, $p = .002$. However, sex was the only significant variable in the model (Table 1): males had more stable friends than did females ($\beta = .50$, $p = .004$). Entering all two-way interaction effects as the second set of variables did not significantly improve the model, $\Delta R^2 = 0.07$, $\Delta F(5,18) = 0.65$, $p = .66$.

Relationship-level Variables Influencing Friendship Stability

We categorized each of the friendships exhibited by our subjects at age one into two groups: "yearling-only," meaning we found no evidence for the existence of these friendships at age two, and "stable," indicating that these friendships were again detected at age two. Of the 86 friendships that our subjects were involved in at age one, 33 persisted through age two. We used a logistic regression to determine how our classification was related to the following variables: similarity between friends in the three temperament factors (using the absolute values of the differences between subjects' and friends' temperament scores as the measures of similarity); whether subjects and friends were maternally related; whether they shared the same rank; whether they were both males, both females, or opposite-sexed; and two measures of friendship quality: reciprocity and behavioral complexity. The likelihood ratio test of model fit showed that entering the above independent variables into the regression equation was a significant improvement over the null model, $\chi^2(9, N = 86) = 46.55$, $p < .0001$, and as a result the percentage of correct classifications increased from 61.6% in the null model to 81.4%. Examination of the odds ratio of each model coefficient (Table 2)

revealed that the greater the degree of similarity between subjects and their friends in Equability (as indicated by smaller difference scores), the more likely they were to stay friends through age two. Specifically, for every increase of one standard deviation in the difference between two friends' Equability scores, their likelihood of remaining friends through age two decreased by 86.7% when holding all other independent variables constant. Friendships that were reciprocated, friendships among maternal kin, or friendships between two males also had a significantly higher probability of persisting over time. In particular, 53.8% of reciprocated relationships remained stable through age two, compared to only 14.7% of unidirectional relationships; 81.0% of friendships among maternal kin persisted, versus 24.6% of non-kin friendships; and 48.8% of friendships between two males remained stable, compared to 23.1% of opposite-sex friendships. Finally, we found two near-significant trends: friendships that were multiplex or those between two females tended to be more likely to remain stable through age two (61.1% of multiplex versus 22.0% of uniplex friendships; 35.3% of female-female friendships versus 23.1% of opposite-sex friendships).

Discussion

Our findings demonstrate that sex, kinship, temperament, and relationship quality influence whether friendships formed at age one persist through age two. We discuss our findings in the same order in which they were presented above.

Individual Factors Influencing Number of Stable Friendships

Subjects maintained stable relationships with a mean of approximately 1.5 peers—about 40% of their original yearling friends—indicating that most animals had one or two close friends with whom they continued to affiliate. Sex was an important factor influencing friendship maintenance, such that males had a greater number of stable friends than did females. This difference likely represents the well-documented divergence in the social behavior of male versus female macaques as they mature: females begin to spend less time with non-kin peers and more time with close female kin (sisters, mothers, grandmothers, etc.), while males continue to affiliate with similarly-aged group-mates, particularly other males (Bernstein, Judge, & Ruehlmann, 1993; Eaton, Johnson, Glick, & Worlein, 1986; Ehardt & Bernstein, 1987; Nakamichi, 1989). In the wild, this divergence precedes males' emigration from their natal troop during adolescence, after which males often form temporary gangs before immigrating into a new troop (Lindburg, 1971). Males may emigrate together; thus juvenile friendships may eventually become alliances during emigration. Females, in contrast, remain in their natal troop for their entire lives, and may benefit from strengthening their relationships with close maternal female kin rather than with peers, since the matriline is the unit to which they will be tied for the rest of their lives. Across multiple cultures, male children, like male rhesus monkeys, are overall less tied to the family and consequently have more non-kin and peer friends than females (Benenson, Morganstein, & Roy, 1998; de Guzman, Carlo, Ontai, Koller, & Knight, 2004; Kon & Losenkov, 1978; Tietjen, 1982). The sex differences we found in friendship longevity have been documented in human children as well, with males having longer-lasting friendships than females (Benenson & Alavi, 2004; Benenson & Christakos, 2003; Hardy, Bukowski, & Sippola, 2002; Kon & Losenkov, 1978). Researchers have postulated that throughout development, human males generally maintain larger, more extensive social networks than females, whose relationships are smaller in number but more intimate in quality, as a result of the greater importance to males of forming broader alliances in order to achieve higher social status (Vigil, 2007). This hypothesis certainly merits further investigation by researchers studying humans, and, if supported, would suggest the presence of a common motivational factor (whether due to convergent evolution or to common ancestry) underlying the sex differences in both human and rhesus monkey friendships.

Though we did not find any significant differences in number of stable friends according to rank, we caution against drawing any firm conclusions from our current results due to the relatively small number of high-ranked animals and to the unequal sex ratios in each rank category. Only one of our four high-ranked subjects was male, compared to seven of 11 middle-ranked and eight of 13 low-ranked monkeys. In our larger study of yearlings, we had found that animals born into high-ranking matriline had the most friendships (Weinstein & Capitanio, 2008); perhaps we would have found a similar difference in number of stable friends had we been able to follow up on all of the animals in our previous study. The fact that we did not find rank differences in number of stable friends, however, suggests the possibility that being high-ranking may not necessarily predispose individuals to form more long-lasting relationships with members of their troop, at least with respect to peers. We also did not find a significant association between matriline size and number of stable friends, suggesting that forming multiple long-term peer friendships does not simply result from having a greater number of peer kin in one's group.

Infant temperament did not predict the number of stable friends that our subjects had, a result that was somewhat unexpected in light of our earlier findings. We had previously demonstrated that yearlings higher in Equability (those that were calmer, more easygoing, and less active) had fewer friends than animals low on this factor (Weinstein & Capitanio, 2008). Temperament may not play as influential a role in determining the number of friends individuals maintain over time because other factors, such as sex, become more important as the animals mature. Our results are consistent with Hartup's (1996) notion that temperament plays a larger role in younger children's friendships than those of older children. It is important to note, however, that temperament may have interacted with other variables like sex and rank in complex ways which we did not have the power to test, since we were only able to follow up on half of the animals in our original study. Finally, although temperament may not influence the overall number of stable friends, it may still play a role in determining which specific peers subjects continue to prefer. Our results with respect to the similarity in temperament between friends, discussed below, suggest that this is indeed the case.

Relationship Factors Influencing Friendship Stability

Relationship-level factors played a substantial role in determining the longitudinal stability of friendships. The degree of similarity between friends in a few areas predicted the longevity of their relationship. First, animals were more likely to maintain friendships with maternal kin than with non-kin. It is well-established that maternal relatedness governs many of the relationships formed by both juvenile and adult nonhuman primates (de Waal, 1996; de Waal & Luttrell, 1986; Ehhardt & Bernstein, 1987; Nakamichi, 1996; Silk et al., 2006). The role of kinship in human friendship formation and maintenance is less understood, particularly for children (Ackerman, Kenrick, & Schaller, 2007), but research suggests that throughout the lifespan, people retain stronger ties with close kin: older adults are more likely to maintain relationships with close kin over distant kin, friends, and neighbors (Ikkin & van Tilburg, 1999); individuals devote more social investment toward full-siblings than half-siblings (Pollet, 2007); monozygotic twins express greater social closeness towards their nieces/nephews than do dizygotic twins (Segal, Seghers, Marelich, Mechanic, & Castillo, 2007); and genetic relatedness has generally been found to predict subjective closeness among adult friends (Neyer & Lang, 2003). Though kinship may be of lesser importance in humans than in the highly nepotistic rhesus monkey societies, members of both species may enhance their inclusive fitness by investing more time with kin than with unrelated individuals.

In comparison to friendships between opposite-sexed individuals, friendships that were between two males were significantly more likely, and friendships between two females were marginally more likely, to persist through age two. This finding is consistent with

previous research in juvenile macaques (Kojima, 1998; Nakamichi, 1996) and human children (Barbu, 2003; Feiring & Lewis, 1987), and demonstrates that segregation between the sexes becomes more marked as individuals mature. As discussed above, such segregation may serve important functions related to status-seeking for males, and investment in kin for females. Interestingly, the increased likelihood of same-sex friendships to persist over time reached statistical significance only for males, while the likelihood for females was marginally above the significance threshold ($p = .053$). This could be due to limitations in sample size: our data contained only 17 female-female friendships, compared to 43 male-male friendships. Another possibility is that friendships among female peers are indeed more fragile than those among males, a finding that has been demonstrated in human children (Benenson & Alavi, 2004), and is suggested by data in juvenile and adolescent macaques showing that females interact with a wider range of group-mates than males, who are more likely to consistently limit their interactions to same-age, same-sex peers (Bernstein, Judge, & Ruehlmann, 1993; Nakamichi, 1989). Future studies should aim to gather a large enough sample of peer friendships to sufficiently address these possibilities.

Previous studies of macaques and humans alike have found similarity in social status to increase the likelihood that a friendship will persist over time (macaques: de Waal & Luttrell, 1986; Nakamichi, 1996; humans: see review by McPherson, Smith-Lovin, & Cook, 2001). However, despite the fact that we previously had found yearling rhesus macaques to show a significant preference for similarly-ranked peers (Weinstein & Capitanio, 2008), our current results suggest that similarity in rank is not as important as other relationship-level factors in determining friendship stability. One explanation for the apparent discrepancy between our present results and those of other nonhuman primate studies is that, in contrast to our analysis, almost none of these studies has examined whether the effects of shared rank persist after taking reciprocity and behavioral complexity into account (but see Silk et al., 2006), and none have tested the effects of shared rank after accounting for similarity in temperament. Future studies of nonhuman primate friendships should therefore investigate the role of rank similarity in combination with the abovementioned variables, in order to determine whether our lack of significant results with respect to rank generalizes to other primate populations.

Similarity in temperament played a significant role in determining friendship stability: members of longitudinally stable friendships were more similar to one another in Equability than members of terminated friendships. At age one, monkeys preferentially affiliated with peers similar to themselves in Equability and Adaptability (Weinstein & Capitanio, 2008). To our knowledge, ours are the first nonhuman primate studies to demonstrate the importance of temperament not only in friendship formation, but in friendship stability as well. During the Infant BBA, animals that scored high on Equability were easygoing, calm, and behaved more slowly and in a more relaxed manner, while low-scoring animals were more active, fast-moving, and easily agitated. The persistent attraction between animals similar in Equability therefore suggests that animals with similar activity levels are more likely to become and remain friends. Human friendship research shows that children and adolescents prefer peers who engage in similar types of activities and styles of play (Kandel, 1978; Rubin, Lynch, Coplan, Rosekrasnor, & Booth, 1994; Urberg, Degirmencioglu, & Tolson, 1998). Children typically cite common activities as the most important characteristic of a friendship (Furman & Bierman, 1983), and children who share similar activity preferences are less likely to terminate their relationships than friends who do not share these traits (Kandel, 1978; Urberg et al., 1998; Werner, & Parmelee, 1979). For our subjects, similarity in Equability—not in Adaptability or Confidence—was most important for friendship stability, suggesting that young rhesus monkeys, like children, may value common activity patterns over other behavioral characteristics. Further supporting the notion that coordination of general activity levels can have long-lasting social consequences is

evidence implicating sex differences in activity levels as one of the key factors underlying sex segregation not only in children (Bohn-Gettler et al., 2010; Pellegrini, Long, Roseth, Bohn, & Van Ryzin, 2007), but in a wide range of ungulate species (Ruckstuhl & Neuhaus, 2002). Although Equability does not explicitly measure the kinds of activities that monkeys prefer, activity level is likely related to specific activity choices (Chess & Thomas, 1996). The near-significant trend for multiplex friendships (i.e. those comprising multiple behaviors, such as proximity and play) to show greater longevity than uniplex friendships is consistent with the idea that the more activities two individuals share in common, the more likely they are to stay friends. Note, however, that because this trend did not reach statistical significance, additional studies are needed to further examine the role of specific activity choices in friendship persistence.

Affiliating with peers based on activity level is almost certainly not a rational or conscious decision, it may simply be based on the fact that individuals with similar activity levels are more likely to spend time together, presumably experience less conflict in interests, and therefore develop a closer, more stable relationship (Hartup, 1996). It can be difficult, however, to infer whether such similarities precede friendship formation, or whether individuals simply become more similar to their friends over time. In humans, studies have found that behavioral similarities precede (and presumably contribute to) children's friendship formation, rather than that friends converge over time (Kandel, 1978; Rubin et al., 1994; Urberg et al., 1998). Temperament ratings of our subjects were conducted at 3-4 months of age, a time during which infants still spend the majority of their time with their mothers, and for the most part have not formed any peer relationships (Hinde & Spencer-Booth, 1967). Since our assessments of friendship took place over a year after the Infant BBA, we can reasonably conclude that monkeys indeed actively chose to affiliate with peers that are similar to themselves, and not that similarity (e.g., in Equability) results from friends' influence on one another.

In terms of the potential fitness consequences of forming friendships with temperamentally similar peers, we previously speculated whether such assortative friendship pairings could precede assortative mating according to personality (Weinstein & Capitanio, 2008), a strategy that has been shown to increase reproductive success in great tits (*Parus major*; Both, Dingemanse, Drent, & Tinbergen, 2005). Studies of human mate choice have demonstrated that people generally choose mates with similar personalities, and that this strategy is associated with increased marital satisfaction and subjective well-being (Caspi, & Herbener, 1990; Gaunt, 2006). Unlike great tits and humans, rhesus monkeys clearly do not practice monogamy, and the question of whether this (or any) polygamous species mates assortatively according to personality, and the fitness consequences, is one that certainly warrants investigation, and could help provide an evolutionary explanation for the assortative friendship pairings that we have observed.

Finally, friendship quality impacted longevity, in that reciprocated friendships were more likely to persist over time than were unidirectional friendships. Few studies of nonhuman primates have examined the influence of reciprocity on relationship stability (and none, to our knowledge, have done so for juvenile friendships), but those that have investigated reciprocity demonstrate consistency with our results: Silk et al. (2006) found that the grooming relationships of adult female baboons that were most reciprocal were the most stable over time, and Mitani (2009) demonstrated the same phenomenon in adult male chimpanzees (*Pan troglodytes*). Many studies of human children's friendships have established the importance of reciprocity in determining longevity (Drewry & Clark, 1985; Gershman & Hayes, 1983; Newcomb & Bagwell, 1995). Mutual friendships are higher in quality in terms of companionship, conflict, aid, security, and closeness than are non-mutual friendships (Bukowski et al., 1994). That individuals cease investing time in relationships in

which they give more than they receive therefore makes sense. Hartup (1996) noted that the status of children's unidirectional friendships is unclear—in some ways the interactions between unidirectional friends are very similar to those between non-friends, and in other ways they are similar to reciprocated friendships. Our data suggest that unidirectional friendships may better resemble the mere passing affiliative interactions between our subjects and other peers in their group ("acquaintances") than reciprocated friendships. Unidirectional friendships may also represent a "try-out" phase between two individuals, in which one animal spends time with another to see whether a friendship would be worth the time and effort. The lack of stability of such friendships may indicate that individuals are not benefitting from these unreciprocated interactions, and have instead chosen to invest their time in another activity or individual.

To conclude, we demonstrated that one individual-level factor—sex—impacted friendship longevity, with males maintaining stable friendships with more of their peers than females. In comparison, several relationship-level factors predicted friendship persistence—including the similarity between individuals in kinship, sex, and temperament, as well as friendship quality as measured by reciprocity and complexity. Specifically, friendships that were between same-sex animals, maternal kin, or individuals with similar Equability scores, and friendships that were of higher quality, were more likely to persist from age one to two. Malloy, Barcelos, Arruda, DeRosa, and Fonseca (2005) postulated that among animals whose behavior is relatively plastic and likely to be influenced by environmental factors, relationship-level effects play a larger role in determining stability than individual-level effects, which play a larger role in animals whose behavior is primarily determined by genetics. Our current findings support this hypothesis, and illustrate important similarities between the relationships of rhesus monkeys and those of humans. Together, our results along with those of human friendship studies suggest that scientists attempting to gain a better understanding of the variables influencing the formation and stability of primate social relationships should analyze the personality characteristics of both members of a relationship, as well as continue to explore the importance of reciprocity and relationship complexity. In recent years, researchers interested in nonhuman primate social relationships have begun to adopt social network analysis, a technique whose origins are rooted in studies of human relationships, as a methodological tool to better quantify the structure of social groups (Brent et al., 2011; Kasper & Voelkl, 2009; Krause, Lusseau, & James, 2009; McCowan, Anderson, Heagarty, & Cameron, 2008). With only one exception (McCowan et al, 2011), nonhuman primate researchers applying social network analysis to their data have not yet incorporated measures of personality. We strongly recommend doing so, however, a suggestion that has already been advocated by non-primate personality researchers (Krause, James, & Croft, 2010; Sih, Hanser, & McHugh, 2009). Just as the human friendship and personality literature has already informed conceptual and methodological approaches taken by animal researchers, studies of nonhuman primates may likewise broaden the examination and understanding of human relationships. While rhesus monkey friendships are certainly not a perfect model of human friendships, studying individual differences in the affiliative relations of rhesus monkeys can provide a vital behavioral complement to the survey-based research that is typically conducted in humans, and may inform us about the evolutionary roots of human social complexity.

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Table 1

Sex, Rank, and Temperament Regressed on Total Number of Stable Friendships

Variable		β	p
Sex ^a		.50	.004
Rank ^b	Dummy1	-.03	.893
	Dummy2	.30	.230
Adaptability		.22	.194

^aThe dummy variable for sex was coded such that Female = 0 and Male = 1.

^bFor rank, Dummy1 = 1 for high rank, Dummy2 = 1 for middle rank, and both dummy variables = 0 for low rank.

Table 2

Logistic Regression Analysis of Friendship Stability

Variable	B	Wald χ^2	df	Odds Ratio	95% CI	p
Equability Difference	-2.02	4.81	1	0.13	[0.02, 0.81]	.028
Confidence Difference	-1.01	2.47	1	0.37	[0.10, 1.28]	.116
Adaptability Difference	0.32	0.30	1	1.37	[0.44, 4.22]	.584
Maternal Kinship	3.20	9.07	1	24.62	[3.06, 197.97]	.003
Same Rank	0.45	0.41	1	1.572	[0.39, 6.29]	.522
Sex						
Same Sex: Males	1.73	4.27	1	5.64	[1.09, 29.06]	.039
Same Sex: Females	2.05	3.73	1	7.74	[0.97, 61.75]	.053
Reciprocity	1.76	6.80	1	5.78	[1.55, 21.62]	.009
Multiplex Friendship	1.16	3.27	1	3.18	[0.91, 11.14]	.070

Note. The reference groups for each of the above categorical variables, in order, are: non-kin friendships, friendships between differently-ranked animals, opposite-sexed friendships, unidirectional friendships, and uniplex friendships. The interpretation of the partial regression coefficient *B* in logistic regression is identical to its interpretation in ordinary least squares regression, and controls for the effects of the other independent variables in the model. The odds ratio is the exponentiation of *B*, and is the amount by which the odds of staying friends are multiplied for a one unit increase in each predictor variable. 95% CI indicates the 95% confidence interval of the odds ratio.