Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques

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Kin selection promotes the evolution of social behavior that increases the survival and reproductive success of close relatives. Among primates, maternal kinship frequently coincides with a higher frequency of grooming and agonistic aiding, but the extent to which paternal kinship influences adult female social relationships has not yet been investigated. Here, we examine the effect of both maternal and paternal kinship, as well as age proximity, on affiliative interactions among semifree-ranging adult female rhesus macaques, *Macaca mulatta*. Kinship was assessed by using both microsatellites and DNA-fingerprinting. Our study confirms that the closest affiliative relationships characterize maternal half-sisters. We provide evidence that adult females are significantly more affiliative with paternal half-sisters than with nonkin. Furthermore, paternal kin discrimination was more pronounced among peers than among nonpeers, indicating that age proximity has an additional regulatory effect on affiliative interactions. We propose that kin discrimination among cercopithecine primates emerges from ontogenetic processes that involve phenotype matching based on shared behavioral traits, such as inherited personality profiles, rather than physiological or physical characteristics.

Kin selection promotes the evolution of social behavior that increases the survival and reproductive success of close relatives (1, 2). Hamilton (ref. 1, p. 22) proposed that one possible mechanism mediating kin selection could be "familiarity of appearance. . . being [that] relatives must tend to look alike. . . ". Kin discrimination can arise if individuals classify relatives on the basis of shared family traits (3, 4), i.e., phenotype matching, or if individuals identify relatives on the basis of frequent association patterns (5, 6), i.e., familiarity, but whether these two mechanisms are mutually exclusive or overlapping is unclear (7).

Evidence of kin discrimination has been reported for a variety of vertebrate species, e.g., Cascades frog tadpoles, *Rana cascadae* (8), long-tailed tits, *Aegithalos caudatus* (9), house mice, *Mus musculus* (10), white-footed mice, *Peromyscus leucopus* (11), spiny mice, *Acomys cahirinus* (12), Belding's ground squirrels, *Spermophilus beldingi* (3, 13), beavers, *Castor canadensis* (14), golden hamsters, *Mesocricetus auratus* (15), and chimpanzees, *Pan troglodytes* (16). Although most studies of kin recognition have focused on the discrimination of kin versus nonkin, only a few have been able to distinguish paternal half-siblings from nonkin, e.g., Belding's ground squirrels (17), peacocks, *Pavo cristatus* (18), and savanna baboons, *Papio cynocephalus* (19). Although Wu *et al.* (20) concluded that pigtailed macaques, *Macaca nemestrina*, exhibit kin recognition in the absence of familiarity, based on their finding that unfamiliar juvenile peers prefer to sit closer to their paternal half-siblings than to nonkin, all subsequent studies of cercopithecine primates have failed to replicate the original findings (21–24), which are therefore likely to represent a type I error. Whether kin discrimination charac-

terizes primates is uncertain. On the one hand, the failure to substantiate the original study suggests that kin discrimination is absent, but recent evidence to the contrary has been reported (16, 19). We examined the potential for paternal kin discrimination by combining the study of social relationships among semifree-ranging adult female primates with genetic analyses.

Rhesus macaques, *Macaca mulatta*, live in multimale, multifemale groups characterized by female philopatry and male dispersal (25). Females mate with an average of three males per conception cycle (26), resulting in a situation where paternal relationships are unknown in the absence of genetic data. Close mother–infant bonds produce a social system in which maternal kinship and familiarity are tightly associated. Maternal kinship frequently coincides with spatial proximity patterns and a higher frequency of grooming and agonistic aiding (27–29), making it difficult to distinguish the effects of kinship from those of familiarity on structuring social relationships. In addition, dominance ranks usually track matrilineal relatedness (30), but high ranking females are often preferred social partners (31), implying that relative social status also guides affiliation patterns. If relatedness *per se* were regulating social relationships relevant to kin selection, then one would expect adult females to associate as often with maternal as with paternal kin.

When sirehood is restricted to a limited number of males each year (32), peers are likely to be paternal half-siblings (33). Female rhesus macaques bear only a single offspring in more than 99% of cases (34) and tend to conceive from different males in consecutive years (unpublished data). Therefore, full siblings are extremely rare and infants born to the same mother are maternal half-siblings of different ages (i.e., nonpeers). Offspring born to different mothers, but sired by the same male, are paternal half-siblings of the same age (i.e., peers) or often in close age proximity. In addition, rhesus macaques of similar age play more often with each other and spend more time together than do individuals of different ages (35). If familiarity *per se* were regulating social relationships relevant to kin selection, then one would expect adult females to associate more frequently with (often paternally related) peers than with nonpeers.

Both age proximity and paternal kinship influence mating behavior in savanna baboons. Alberts (19) found that paternal half-siblings engaged in lower levels of affiliative and sexual behavior than do nonkin. She also found that individuals from

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Table 1. Affiliative interaction as a function of kinship and age proximity

Kinship/age	n	Interactions per h			
		Proximity	Grooming	Approach	Affiliation index
MS/NP	34	2.117 ± 0.186	0.372 ± 0.052	1.581 ± 0.129	10.771 ± 1.039
PS/P	15	0.588 ± 0.108	0.088 ± 0.031	0.521 ± 0.085	1.745 ± 0.739
PS/NP	19	0.450 ± 0.069	0.012 ± 0.006	0.308 ± 0.037	0.063 ± 0.199
NK/P	34	0.360 ± 0.028	0.024 ± 0.005	0.327 ± 0.023	0.041 ± 0.160
NK/NP	34	0.350 ± 0.019	0.011 ± 0.001	0.232 ± 0.009	−0.403 ± 0.069

Values of proximity, grooming, and approach are given as mean frequency per h (±SE), the affiliation index is a composite score (see *Methods*); MS, maternal half-sisters; PS, paternal half-sisters; NK, nonkin; P, peers; NP, nonpeers; *n*, number of focal females.

the same cohort tended to avoid mating with each other, but a limited sample size precluded simultaneous examination of age proximity and kinship. In this paper, we significantly expand Alberts' hypothesis by scrutinizing the influence of maternal and paternal kinship, as well as age proximity, on affiliative relationships among adult female rhesus macaques.

Methods

Study Population. We studied one troop (group R) of rhesus macaques residing on Cayo Santiago, a 14-hectare island offshore from Puerto Rico that has been inhabited by rhesus macaques since 1938 (ref. 34). All monkeys are recognized on an individual basis, and demographic records are available for tracing matrilineal relationships back to 1956. During the behavioral observations, group R had a total of 141 members (excluding adult males) but the analysis of dyadic interactions was restricted to 91 individuals (adult females and their female descendants). We limited our analysis to females, who, in contrast to males, remain in their natal group throughout their lives and interact with both kin and nonkin.

Subjects and Behavioral Data. Focal samples (36) from 34 adult females were collected between May and December 1997. In total, we obtained 645 h of focal data, by using a 20-min focal sample. During focal sampling, all behavioral interactions between the subject and all other females in the troop (*n* = 91) were noted. All 91 females in the study troop were assigned dominance ranks based on the outcome of dyadic agonistic interactions. Analyses were confined to the three friendly dyadic interactions of spatial proximity, grooming, and approach because cooperative interactions with kin have been proposed to exert a greater impact on primate female lifetime reproductive success than noncooperative, or antagonistic, interactions directed against nonkin (37). Spatial proximity was based on point samples (36) taken every 4 min during each sampling period and involving all neighbors within a 5-m radius. For every pair consisting of focal animal and potential social partner, the observed frequency of spatial proximity was divided by the observation time. Grooming and approaches involving the focal animal were also analyzed as rates per hour, calculated from the continuous focal samples. Dyadic scores for social partners who were related to the focal animal, but who were neither maternal nor paternal half-siblings of the focal animal, were excluded from further analysis. In our study, the crucial comparison was between nonkin on the one hand, and close kin of identical genetic relatedness (*r* = 0.25), but different coparental gender, on the other. Data for each type of behavior were next standardized by using the overall mean and SD for that behavior, taken over all pairs of focal subject and social partner as specified above (i.e., including maternal and paternal half-siblings and nonkin). Standardized scores were then summed over all three behavioral categories to generate an affiliation index per focal animal per potential social partner. In cases where one or more of the original dyadic scores were below the overall mean,

negative affiliation indices could result. Affiliation indices below zero do therefore not imply that the respective relationship was necessarily aversive.

Paternity Analysis. Paternal kinship was assessed by genotyping all group members and all males resident on the island by using 15 microsatellites (38). For 76 of 91 females studied (84%), paternity could be discerned. We regarded sirehood as established when a male reached a log-likelihood ratio in favor of paternity that was (*i*) larger than 2 (corresponding to a standardized paternity probability of 99%) and (*ii*) at least one unit larger than the log-likelihood ratio of any other male. The 15 cases that were unresolvable by using microsatellites were further analyzed by DNA fingerprinting (39), and the presence of any paternal siblings in group R during behavioral observation in 1997 could be ruled out for each of them.

Age Proximity and Kinship. From the longitudinal database of the Caribbean Primate Research Center, we obtained both age and maternal kinship for all subjects. Females were regarded as maternally related when they belonged to the same family. A family consisted of the oldest surviving daughter (or granddaughter, if the daughter was deceased) of a matrilineal founder and her offspring (*n* ≥ 3 offspring). Paternal half-siblings and their descendants were considered as paternally related. To control for the actual degree of relatedness among kin, however, we restricted the analysis to maternal half-sisters (same mother, paternally unrelated, coefficient of relatedness *r* = 0.25), paternal half-sisters (same father, different family, *r* ≈ 0.25), and nonkin (different family and different father, *r* ≈ 0). Pair-wise relatedness of all monkeys who were not parent–offspring, full-, or half-siblings was assessed by using the regression approach by Lynch and Ritland (40), and indicated that 75% of all dyads have a coefficient of relatedness of less than 0.0625. These results suggest that the island population is not closely inbred.

Statistical Analyses. Affiliation indices of each focal animal were averaged over social partners for specific kin and age categories. These mean affiliation indices were then compared between kin and age categories by using paired *t* tests, with the sequential Dunn–Šidák method (41) adopted to correct for multiple testing. The Wilcoxon test was used when data were not normally distributed. A two-way ANOVA was incorporated to simultaneously examine the influence of both kinship and age proximity on the affiliation index. All statistical analyses were performed with the SPSS 10.0 package.

Results

We first compared affiliation indices between peers and nonpeers to test for effects of age proximity on affiliation. Possible kinship effects were eliminated by restricting this comparison to nonkin. A significantly higher affiliation index was observed among nonkin peers than among nonkin nonpeers (paired *t* test = 2.898, 33 df, *P* = 0.007, Dunn–Šidák correction for
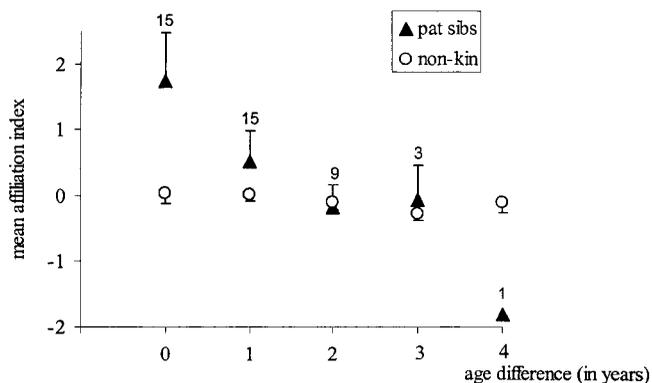
Fig. 1. Relationship between mean affiliation index and exact age difference for the 34 focal females and their paternal half-sisters (▲) and their nonkin (○). The graph displays mean affiliation indices (±SE). Observations on interactions with unrelated females were available for all focal females, so each open circle represents 34 data points. For interactions with paternal half-sisters, the actual number of data points is given above the SE bars. Given the small sample size for age differences of 3 and 4 years, we calculated Spearman's rank correlation coefficients only for age differences of 0 to 2 years. A significant negative correlation emerged for paternal half-sisters ($r_s = -0.316$, $n = 39$, $P = 0.050$) but not for unrelated females ($r_s = -0.085$, $n = 102$, $P = 0.397$).

multiple testing $P' = 0.017$, Table 1). Therefore, we differentiated between peers and nonpeers in all subsequent analyses.

As expected, maternal half-sisters scored highest on all three measures of affiliation. Nonkin scored lowest and paternal half-sisters were between the two (Table 1). Maternal half-sisters, who can only be nonpeers, exhibited a significantly higher mean affiliation index than paternal half-sisters who were nonpeers (paired $t = 7.382$, 18 df, $P < 0.001$, $P' = 0.013$), and than nonkin nonpeers (paired $t = 10.837$, 33 df, $P < 0.001$, $P' = 0.010$). Intriguingly, the affiliation index of paternal half-sisters was significantly higher than that of nonkin, both among peers (paired $t = 2.945$, 14 df, $P = 0.011$, $P' = 0.025$) and among nonpeers (paired $t = 2.358$, 18 df, $P = 0.030$, $P' = 0.050$, Table 1). A comparison of the two latter results suggested that paternal kin discrimination worked more efficiently among peers than among nonpeers. Indeed, when tested by means of two-way ANOVA, treating mean affiliation indices of the same focal animal with social partners of different levels of relatedness as independent, the interaction between paternal kinship and peerage was found to be statistically significant ($F_{1,98} = 5.20$, $P = 0.025$).

We refined our analysis of age proximity and kinship by considering the exact age difference between interacting social partners. A significant negative correlation was observed between the affiliation index and the age difference of paternal half-sisters, but not of unrelated females (Fig. 1). This observation implies that the level of affiliation between paternal half-sisters, but not between nonkin, increases gradually with decreasing age difference.

Discussion

Our study confirms that the closest social bonds among adult female rhesus macaques follow maternal relatedness. We also provide evidence that both paternal relatedness and age proximity exert a significant impact on affiliation patterns among adult female primates. Adult female rhesus macaques are capable of discriminating between paternal kin and nonkin, with kin discrimination (*i*) more pronounced among peers than among nonpeers and (*ii*) inversely related to age proximity.

Our data suggest that cooperation between female rhesus macaques is promoted by paternal kinship, but the mechanisms underlying paternal kin discrimination are unknown. Proximate mechanisms mediating kin discrimination are likely to differ across taxa as a function of both key sensory modalities used in communication and the structure of the social system. One possible explanation for our findings could be that females nurture cooperation among their patrilineally related offspring by encouraging infants to play with offspring of females who have mated with the same male. Maternal affiliation patterns partly drive the development of infant affiliation patterns among peers (42) so that if mothers who have conceived infants from the same male were closely associated, their offspring could develop affiliations with same-age paternal relatives. We tested this explanation by comparing mothers who were nonkin, nonpeers, but whose infants were either same-age paternal half siblings or same-age nonkin. We found no significant difference in the affiliation indices of these two sets of mothers [mean affiliation index (±SE) between mothers of same-age paternal half-siblings 0.367 ± 0.301 vs. mothers of nonkin peers 0.509 ± 0.123; paired $t = -0.446$, 15 df, $P = 0.662$]. Therefore, mothers do not appear to mediate affiliation between their infants as a function of shared paternity. Instead, adult females tend to associate with their own kin and/or peers regardless of the identity of the sire of their offspring.

A second possible explanation for paternal kin discrimination could be that dominance rank influences affiliation patterns. In rhesus macaques, as in other cercopithecine primates, maternal half-sisters not only affiliate with each other at high rates, but tend to occupy adjacent dominance ranks within a troop (30). To test whether dominance rank was a confounder in the analysis, we compared directly the mean rank difference between focal subjects and their paternal half-siblings with the mean rank difference between focal subjects and their nonkin, controlling for age proximity. No significant differences in mean rank difference were observed, neither for peers [mean rank difference (±SE) between paternal half-siblings $= 33 \pm 5$ vs. nonkin $= 32 \pm 3$; Wilcoxon test, $z = -0.031$, 14 df, $P = 0.975$] nor for nonpeers (paternal half-siblings $= 35 \pm 3$ vs. nonkin $= 32 \pm 1$; Wilcoxon test, $z = -0.322$, 18 df, $P = 0.748$). However, including all females in the analysis could bias results if younger females were dependent in rank on their mothers. To control for this potential bias, we repeated the analysis excluding younger females for which the social rank could still be dependent on their mothers' rank ($n = 42$). Of the 19 focal subjects with paternal half-sibling, nonpeers (PS/NP; see Table 1) present in the cohort, three of them were removed from the analysis because all of their paternal siblings were immature animals. Results remained consistent with no significant differences noted, neither among peers [mean rank difference (±SE) between focal and paternal half-siblings $= 18 \pm 3$ vs. 17 ± 1 for nonkin; Wilcoxon test, $z = -0.114$, 14 df, $P = 0.910$] nor among nonpeers (paternal half-siblings $= 20 \pm 2$ vs. nonkin $= 18 \pm 1$; Wilcoxon test, $z = -0.724$, 15 df, $P = 0.469$). Therefore, though paternal half-siblings and nonkin had a similar rank in relation to the focal females, the latter still affiliated more with paternal kin than nonkin, implying that differences in affiliation are unlikely to be caused by differences in relative dominance rank.

A third explanation for paternal kin discrimination could be phenotype matching, by using shared characteristics within lineages, such as appearance, odor, or vocalizations, against a reference template (3, 4, 6, 43, 44). Our data are compatible with the phenotype matching hypothesis because paternal kin discrimination was found to occur both within and across birth cohorts. However, phenotype matching cannot account for the peer effect, and the observed interaction between kinship and age proximity suggests that familiarity (among age mates) also contributes to paternal kin discrimination.

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Given the crucial importance of vision among cercopithecine primates, the most likely sensory mechanism presenting cues for phenotype matching is visual recognition, as suggested for chimpanzees by Parr and de Waal (16). However, in contrast to chimpanzees, Old World monkeys have consistently failed mirror self-recognition tests (45, 46) and long-tailed macaques, *Macaca fascicularis*, do not seem to perceive physical resemblance between relatives (47). Furthermore, for the age proximity effect to be regulated by visual cues, adult females would need to be able to distinguish same-age peers from those who are a couple of years older or younger than themselves. Therefore, we suggest that paternal kin discrimination in rhesus macaques is not visually mediated.

Among rodents, olfactory cues have been implicated in kin discrimination (e.g., refs. 15 and 48). New World monkeys scent mark and discriminate both sex and reproductive state of conspecifics (e.g., refs. 49–51), but Old World monkeys do not scent mark and have a poorly developed olfactory sense (52). Most olfactory inspection among rhesus macaques occurs when males sniff the anogenital region of females (F.B.B., unpublished observation). Olfactory cues among mice are used to detect dissimilarity in the major histocompatibility complex (MHC) region as a means of mate choice (53) and humans prefer the odor of MHC-dissimilar individuals (54, 55). However, unlike the situation with house mice, no reproductive advantage was found in our study population when comparing dissimilar to similar mates in terms of MHC type i.e., Mamu-DQB locus (56). It is unlikely that females adjust social behavior with female conspecifics according to MHC type when their reproductive success is not dependent on adjusting mating behavior according to MHC type. Therefore, we suggest that paternal kin discrimination in rhesus macaques is not scent-mediated.

Auditory cues provide signals indicating maternal relatedness in both rhesus macaques (57, 58) and savanna baboons (59). However, in these species matrilineal relatedness corresponds with familiarity (60) and these studies have not distinguished paternal kin from nonkin. For vocal cues to mediate kin discrimination among adult females, they would need to match paternal half-sibling utterances to self utterances, and distinguish them from nonkin calls, but auditory matching to self is difficult because the sounds emitted by an individual are perceived differently by the sender than they are by the receiver. Therefore, we suggest that paternal kin discrimination in rhesus macaques is not mediated by means of auditory channels.

We hypothesize a previously undescribed mechanism of phenotype matching in primates. We suggest that phenotype matching in rhesus macaques, and other cercopithecine primates, is guided by behavioral traits, such as personality and temperament rather than by morphological or physiological attributes. Nonhuman primates develop and display distinct personality profiles (61-63). In rhesus macaques, some personality traits, such as increased impulsivity and aggressiveness, are closely associated with diminished concentrations of cerebrospinal fluid monoamine metabolites, which have a significant paternal genetic component (64, 65) and are fairly stable throughout life (66, 67). About 30–50% of the variance in personality traits among people is thought to be due to genetic factors (68, 69). Hence, shared paternally inherited personality attributes could be modulating social relationships and provide a mechanism fostering behavioral phenotype matching. One prediction of our hypothesis is that if individuals choose social partners on the basis of age and personality traits, and if these traits are partly determined by paternal genes, then preferred social partners will share paternity and age proximity more often than expected by chance alone. Comparing the relatedness and personalities of playmates within and between cohorts should be the next step in testing this hypothesis.

In summary, paternal kin discrimination influences the structure of social relationships in rhesus macaques as a function of both age proximity and shared sirehood. We propose that paternal relatedness and age proximity regulate the development of social relationships through an ontogenetic process of phenotype matching by using behavioral cues modulated by inherited personality traits.

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