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Determinants of Affiliative Interactions between Adult Males and Lactating Females in Pigtail Macaques (*Macaca nemestrina nemestrina*)

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Abstract

In some species of Cercopithecine primates, unrelated adult males and females maintain affiliative relationships ('friendships') that are apparently unrelated to mating or parental care. This study investigated the occurrence of friendships in a captive group of pigtail macaques, and some of their possible determinants. Study subjects were six adult males and 15 adult females with their newborn infants. Females were focally observed for 2 h every week during the first 12 wk of lactation. With the exception of the fourth-ranking male, adult males showed little interest in initiating affiliative interactions with lactating females and their infants. Most episodes of contact and grooming were initiated by high-ranking females and directed to the alpha male. Because female grooming was not generally reciprocated by the alpha male, it is likely that females benefited from associating with him in terms of agonistic support or protection. Genetic data on paternity determination indicated that the fourth-ranking male, who displayed high levels of affiliation towards mother–infant dyads, sired most of the infants born in the group in the year prior to this study. Thus, whereas females may be interested in associating with males to obtain their support, some males may affiliate with females as a consequence of their previous mating relationships with them or to increase the chances of future mating success. Taken together, however, the findings of this study provide little evidence that adult males and lactating females maintain strong reciprocal bonds that may qualify as friendships.

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Introduction

In all animal societies, affiliative behavior between unrelated individuals is often associated with activities that require some degree of cooperation and coor-

dination such as mating, parental care, play, or alliance formation. Affiliative interactions that are not apparently associated with any cooperative activity are rare and, when they occur, they raise a number of interesting questions at all four levels of behavioral analysis: ontogeny, causation, function, and evolution.

In macaques, baboons, and other female-bonded primate species (Wrangham 1980), individuals live in social groups typically composed of clusters of genetically related females and a few unrelated adult males. In such groups, most affiliative behavior is concentrated between mothers and offspring and between adult females that are close in dominance rank (Seyfarth 1977). Affiliative interactions between unrelated adult females and males are most frequent during periods of female estrus, when repeated copulation between male and female is associated with long periods of proximity, contact and grooming (e.g. Bernstein 1963). Intensification of female affiliation with males during the mating period is accompanied by reduced affiliation and increased aggression between females (Wallen & Tannenbaum 1997). When infants are born, females are mainly involved in care-giving activities and re-establishing affiliative relationships with other females (Dunbar & Dunbar 1988; Maestripieri 1994). The increase in female–female affiliation during the lactation period is significantly affected by the presence of infants, as non-lactating females groom new mothers at high rates in order to gain access to their infants (Maestripieri 1994).

Although interactions between adult females and males are typically less frequent during the birth than during the mating period, some females maintain affiliative relationships with unrelated adult males also during lactation (in baboons and some macaque species: Kaufmann 1967; Ransom & Ransom 1971; Judge & Rodman 1976; Takahata 1982; Chapais 1983, 1986; Hornshaw 1984, 1985; Furuichi 1985; Hill 1986, 1990; Manson 1994). Such affiliative relationships, often referred to as ‘friendships’, are characterized by frequent exchange of approaches, contact and grooming between male and female. Some relationships persist for several years, but in some cases new pairs are formed in different years (Grewal 1980; Chapais 1983).

Friendships appear to be a more common phenomenon in baboons than in macaques. Recent evidence from chacma baboons (*Papio ursinus*) suggests that the primary function of friendships may be protection against the risk of infanticide from immigrating males (Palombit et al. 1997). In macaques, there is little evidence that infants are at risk of infanticide from unrelated males and this perhaps explains why friendships appear to be less common than in baboons. In the genus *Macaca*, friendships have been documented in Japanese (*M. fuscata*) and rhesus macaques (*M. mulatta*), but their occurrence has not been unequivocally demonstrated in other macaque species. For example, in the Sulawesi crested black macaque (*M. nigra*), lactating females groomed males less than females in other reproductive conditions, and adult males groomed lactating females the least (Hadidian 1979). In stump-tail macaques (*M. arctoides*), Bruce et al. (1988) reported that new mothers spent less time in proximity to adult males and received more aggression from them during lactation than prior to it. Moreover, even in Japanese macaques, some studies failed to report evidence of male–female friendships (e.g. Tsukahara 1990).

Thus, more research is needed to characterize the friendship phenomenon in the genus *Macaca*.

More research is also needed to understand the costs and benefits of friendships to the individuals involved. In fact, since Cercopithecine adult males typically do not participate in parental care (Maestriperi 1998), the reason why friendships occur is not immediately apparent. In some macaque species in which adult males use infants as buffers during interactions with other males (e.g. in *M. sylvanus*, *M. radiata* and closely related species; Maestriperi 1998), adult males may be interested in affiliating with lactating females to gain access to their infants. The ‘baby-buffering’ phenomenon, however, does not occur in *M. mulatta* and *M. fuscata* (Maestriperi 1998), in which friendships have been reported.

Studies of Japanese and rhesus macaques have not unequivocally clarified whether friendships are mostly initiated and maintained by the females, the males, or both. One study reported that during the birth season proximity was mostly maintained by females (Hill 1986), whereas another reported that males groomed lactating females more than vice versa (Furuichi 1985). Other authors reported that, although females generally groomed males more than vice versa, both males and females played a role in maintaining proximity and in grooming, their involvement being greater the higher the rank of their partner (Takahata 1982; Chapais 1983, 1986; Manson 1994).

The possible benefits of friendships to the individuals involved have mostly been discussed in the context of agonistic support and mating, but many issues still remain unresolved. In Japanese macaques, males and females have been shown to support their friends in conflicts against other females or males (Oki & Maeda 1973; Takahata 1982; Huffman 1991). In rhesus macaques, Chapais (1983, 1986) reported that high-ranking males supported their female friends against low-ranking males but not against other females. Adult females supported high-ranking males against other males but not against females. In another study, rhesus males supported their female friends against lower-ranking males or other females, but females never supported male friends (Manson 1994). Males never supported unrelated females against higher-ranking males. These findings support only in part Chapais’s (1986) suggestion that both females and males benefit from their friendship in the context of agonistic interactions with lower-ranking males.

Males may benefit from friendships with lactating females if they gain preferential mating access when their friends return to estrus (Smuts 1985). Early studies of rhesus macaques suggested that females chose their mating partners on the basis of previous long-term affiliative bonds (Lindburg 1971; Rowell 1972). Other studies, however, have suggested that, although sexual activity between male and female associates may precede the formation of social bonds, neither males nor females subsequently mate with their friends (Baxter & Fedigan 1979; Takahata 1982; Chapais 1983, 1986; Furuichi 1985; Manson 1994). For example, Takahata (1982) reported that, during the mating season, male and female friends maintained frequent proximity only when the female was not in estrus.

In the present study, I investigated the social interactions between adult males and lactating females in a macaque species, the pigtail macaque (*M. nemestrina*

nemestrina), in which evidence of friendships has not yet been reported. The aims of this study were: (1) to assess the occurrence of male–female affiliative relationships that could be characterized as friendships; (2) to investigate the role played by males and females in initiating and maintaining these relationships; (3) to investigate whether the presence of infants plays any role in male–female friendships; (4) to test indirectly the hypothesis that agonistic support plays a role in male–female friendships by investigating male and female behavior in relation to dominance rank, and (5) to test indirectly the hypothesis that adult males gain a mating advantage from friendships by investigating the relation between male affiliative behavior and their mating success in the previous year.

Methods

Subjects and Housing

Study subjects were pigtail macaques living in a captive social group at the Field Station of the Yerkes Regional Primate Research Center in Lawrenceville, GA (USA). The group was housed in a 30 × 30 m outdoor compound with attached indoor areas. At the beginning of the study, the group consisted of five adult males, one subadult male, and 32 adult females (see Table 1 for demographic characteristics). Sixteen females had one offspring older than 6 mo. The five adult males and the subadult male were born into another social group at the Yerkes Field Station. Two adult males, Qe and Oh, were brothers. All adult females were wild-caught when reproductively immature and their genetic relationships were unknown. Since all animals were captured in the same location, however, it cannot be ruled out that some of them were genetically related to each other. The group was formed 2 yr before the onset of this study.

Procedure

Fifteen adult females and their newborn infants were focally observed in four weekly 30-min observation sessions, from the day after parturition until the end of the 12th week of lactation. The first 12 wk of lactation is the period when infants spend most of their time with their mothers. Lactation obviously continues beyond this period, but the mother's social behavior becomes progressively less affected by the infant's presence.

Each mother–infant pair was observed for 24 h for a total of 360 h of observations. Observation sessions were randomly distributed between 08:00 and 19:00 h. All data were collected by the same observer using a portable computer programmed to allow the collection of frequencies, durations and sequences of behavior. The frequency of occurrence of the following behavioral interactions between adult females and adult males was recorded (duration was recorded only for grooming bouts): Approach = movements that brought one individual within about 60 cm of another individual without making contact for at least 5 s. Contact = movements that resulted in any body contact between two individuals except brief hits. Grooming = picking through and/or slowly brushing aside the fur of

Table 1: Socio-demographic characteristics of subjects

ID	Rank ¹	Age (yr)	Parity (P, M ²)	Infant sex (M, F ³)
Adult females				
Ar	5	5	P	F
Dt	7	6	M	M
Gn	11	7	P	F
Gs	12	5	P	M
Hn	31	7	M	F
Ko	15	7	M	M
Ks	3	5	P	F
Mo	18	7	P	M
Qr	26	6	M	F
So	27	7	P	F
Sr	25	7	M	F
Vo	17	7	M	F
Vs	2	7	P	M
Zq	13	7	M	M
Zs	4	5	P	M
Adult and subadult males				
Bl	6	7		
Ii	5	11		
Ji	3	11		
Oh	2	12		
Qe	4	17		
Te	1	17		

¹Rank refers to the individual's position in the female or male hierarchy. ²P = primiparous; M = multiparous. ³M = male; F = female.

another individual with one or both hands. A pause of 10 s in grooming was used as the criterion for the end of a bout. Aggression = aggressive acts, including threats, bites, and chases. Submission = bared-teeth displays and hindquarter presentations. Avoidance = withdrawal in response to an approach from another individual. In addition to male–female interactions, the number of male infant handling episodes was also recorded. Infant handling was recorded when an adult male briefly touched, held, or groomed an infant. Infant handling did not include play, i.e. mouthing, wrestling, and chasing interactions during which the infant clearly displayed the ‘open mouth play face’.

Dominance relationships among all adult individuals were established on the basis of data on unidirectional aggression and bared-teeth displays collected in conjunction with other behavioral studies. Data on unidirectional aggression and bared-teeth displays were ordered in a matrix to minimize the number of scores falling below the diagonal when winners of agonistic encounters were listed in the columns and losers in the rows. The dominance ranks of the males are listed in

Table 1. The subadult male (BI) was lower-ranking than all the adult males, although during the course of the study he repeatedly challenged and eventually outranked the fifth-ranking adult male (Ii). All 32 adult females could be ranked along a linear dominance hierarchy, which remained stable throughout the study period. All adult males were dominant over all females during individual agonistic encounters. The subadult male was dominant over most middle- and lower-ranking females but was outranked by a few high-ranking females.

Data were analysed with parametric statistics, i.e. analysis of variance (followed by Bonferroni-Dunn post-hoc tests), Student's t-test, and Pearson's correlation test. Whenever the data failed to meet the assumptions necessary for the use of parametric tests, they were transformed by using square-root transformations. All tests were two-tailed. Probabilities ≤ 0.05 were considered statistically significant.

Results

Differences in Male- and Female-Initiated Interactions

A two-factor repeated-measures ANOVA was used to investigate changes in male-female interactions over the first 12 wk of lactation and to compare the frequencies of male- and female-initiated interactions. The only significant change in behavior over the 12 wk concerned female avoidance ($F_{11,179} = 1.80$, $p = 0.05$). Females avoided adult males less frequently as lactation progressed (Fig. 1). None of the other male- or female-initiated behaviors showed significant changes over the 12 wk of lactation, although there was a tendency for male infant handling to

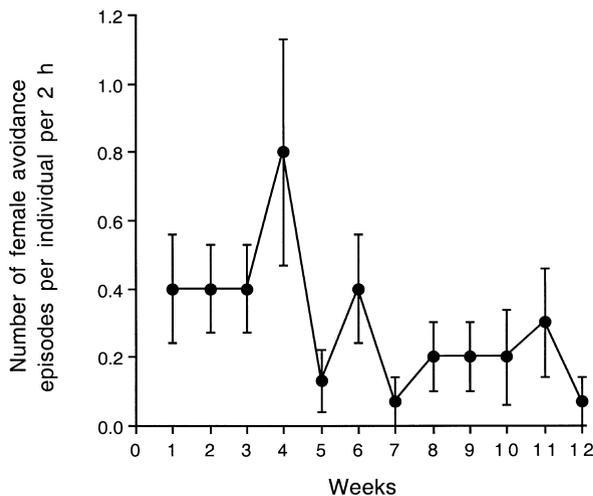


Fig. 1. Number of episodes ($\bar{x} \pm SE$) of female avoidance of males over the 12 wk of lactation

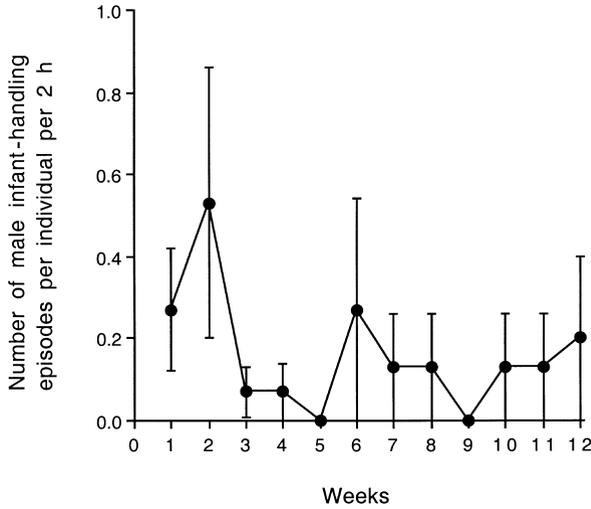


Fig. 2: Number of episodes ($\bar{x} \pm SE$) of male infant handling over the 12 wk of lactation

be more frequent in the first 2 wk (Fig. 2). Males approached females more than vice versa ($F_{1,28} = 65.79$, $p < 0.001$; Fig. 3a). Females, however, made contact with males ($F_{1,28} = 5.59$, $p < 0.05$; Fig. 3b) and groomed them more often ($F_{1,28} = 7.45$, $p = 0.01$; Fig. 4a) and for longer ($F_{1,28} = 6.52$, $p = 0.01$; Fig. 4b) than males. There were no significant differences between male and female aggression ($F_{1,28} = 2.26$, ns). Females, however, showed more avoidance ($F_{1,28} = 20.91$, $p < 0.001$) and submissive behavior ($F_{1,28} = 24.67$, $p < 0.001$) than males. In fact, only the sub-adult male avoided females on a few occasions, and none of the males ever showed submissive behavior towards females.

Male–Female Interactions in Relation to Female and Infant Characteristics

There was a significant correlation between female dominance rank and the number of contacts made by females (Pearson's correlation, $r = -0.66$, $n = 15$, $p < 0.01$), and both the frequency ($r = -0.65$, $n = 15$, $p < 0.01$) and the duration ($r = -0.59$, $n = 15$, $p < 0.05$) of grooming performed. Thus, the higher the female's rank the greater her involvement in seeking contact and grooming with adult males. Female approaches and avoidance were not correlated with dominance rank. However, mothers with sons approached the adult males significantly more often than mothers with daughters (t-test for unpaired samples, $t = 3.00$, $df = 13$, $p = 0.01$). Female dominance rank did not predict variability in any male behavior directed toward females, including approach, contact, grooming, aggression, avoidance, and infant handling. The frequency of infant handling was positively correlated with the frequency of contacts ($r = 0.84$, $n = 15$, $p < 0.001$) and grooming ($r = 0.72$, $n = 15$, $p < 0.01$) received by females. These correlations, however, were

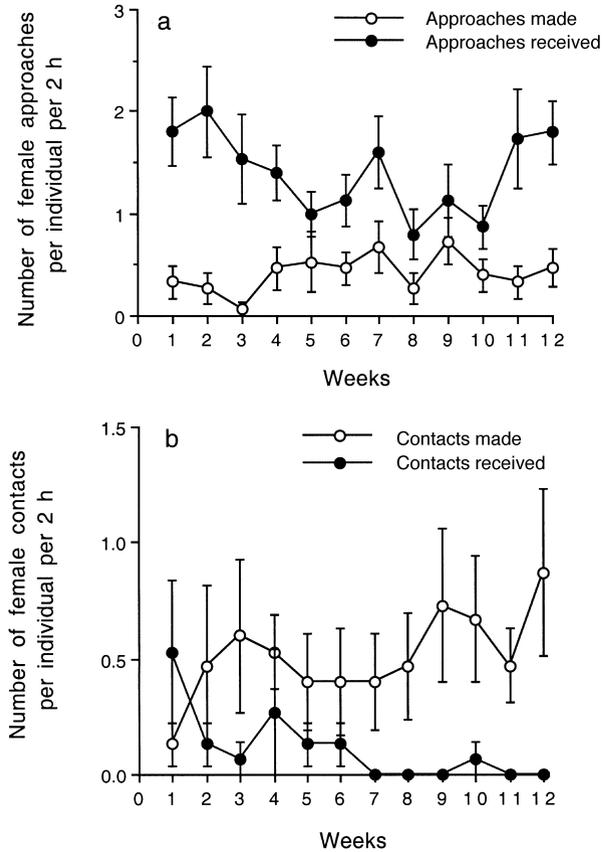


Fig. 3. a. Number of approaches ($\bar{x} \pm SE$) made and received by females over the 12 wk of lactation. b. Number of contacts ($\bar{x} \pm SE$) made and received by females over the 12 wk of lactation. Data refer only to male–female interactions

mostly due to the high frequency of interactions between one adult male (Qe) and one adult female (Gs) and her infant.

Aggressive interactions between females and males were not significantly affected by female dominance rank or infant sex. There was a significant positive correlation between aggression performed and aggression received by females ($r = 0.63$, $p = 0.01$), so that the most aggressive females were also attacked most often by males. There was also a significant positive correlation between aggression received and female involvement in making contact with males ($r = 0.68$, $p < 0.01$) and grooming them (frequency, $r = 0.74$, $p = 0.001$; duration, $r = 0.80$, $p < 0.001$), so that the females who were most active in making contact and grooming the males were also attacked most often by them. These correlations, however, were mostly due to the behavior of one female (Dt), who had frequent interactions, both affiliative and agonistic, with adult males.

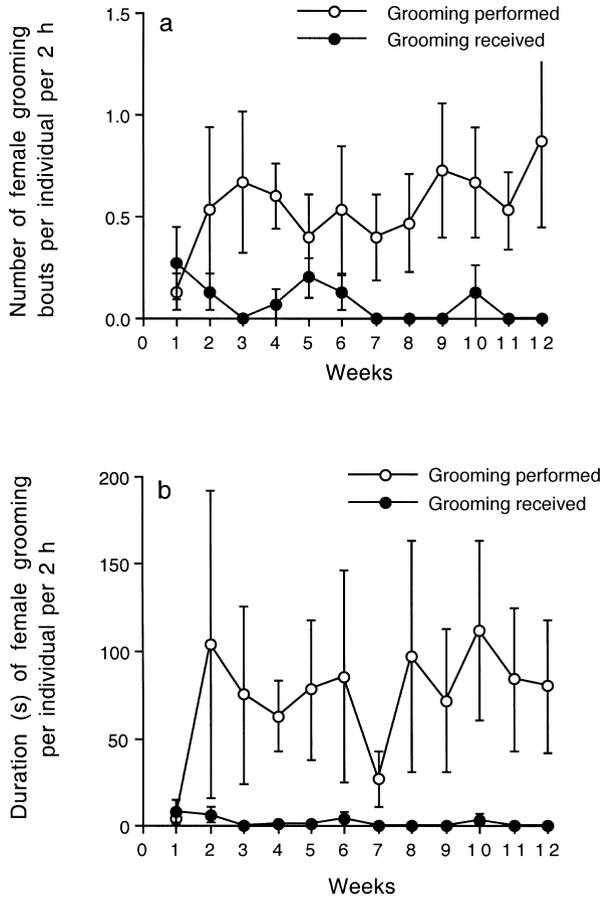


Fig. 4: a. Number of grooming bouts ($\bar{x} \pm SE$) performed and received by females over the 12 wk of lactation. b. Duration of grooming ($\bar{x} \pm SE$) performed and received by females over the 12 wk of lactation. Data refer only to male–female interactions

Male–Female Interactions in Relation to Male Characteristics

Repeated-measures ANOVAs revealed statistically significant differences among the six males for all the behavioral measures considered (Table 2). Post-hoc tests revealed that the alpha male Te received more approaches, contacts, and grooming (both in frequency and in duration) from females than all the other males. The fourth-ranking male Qe, however, had the highest scores for approaches and contacts made, frequency and duration of grooming, and frequency of infant handling. The subadult male BI received more aggression and avoided females more than all the other males. The fifth-ranking male Ii was the least involved in interactions, affiliative or agonistic, with females. Although the ANOVA indicated an overall significant difference among the males in terms of aggression performed

Table 2. Behavioral scores for the five adult males and the subadult male and results of the ANOVAs comparing behavior among the six males. Although the ANOVAs were run with frequency and duration data, the behavioral scores for the males are presented in terms of percentage of the total

Behavior	ID of male										ANOVA, p
	Total score	Te	Oh	Ji	Qe	Ii	Bl				
Approaches	252	24.21	17.06	7.94	42.86*	1.19	6.74				F = 28.52, p < 0.001
Approaches received	76	65.79	*7.89	0	10.53	1.31	14.47				F = 12.27, p < 0.001
Contacts	19	5.26	0	5.26	89.47*	0	0				F = 2.60, p < 0.05
Contacts received	92	83.69	*8.69	2.17	5.43	0	0				F = 6.14, p < 0.001
Grooming F ¹	13	7.69	0	15.38	76.92*	0	0				F = 2.86, p < 0.05
Grooming D ¹	359	17.27	0	13.65	69.08*	0	0				F = 2.45, p < 0.05
Grooming received F ¹	98	80.61	*7.14	2.04	10.20	0	0				F = 6.28, p < 0.001
Grooming received D ¹	13189	82.14	*9.18	2.67	6.00	0	0				F = 8.95, p < 0.001
Aggression	44	22.73	38.64	22.73	2.27	0	13.64				F = 2.60, p < 0.05
Aggression received	21	0	0	4.76	9.52	9.52	76.19*				F = 9.21, p < 0.001
Avoidance	10	0	0	0	0	0	100*				F = 7.00, p < 0.001
Avoidance received	54	14.81	24.07	22.22	33.33	0	5.55				F = 4.48, p = 0.01
Submission received	87	29.88	16.09	21.84	31.03	1.15	0				F = 4.25, p < 0.01
Infant handling	29	10.34	10.34	3.45	65.52*	3.45	6.89				F = 2.28, p < 0.051

*Significantly higher (p < 0.05) than scores for all other males (Bonferroni–Dunn post-hoc test).

¹F = frequency; D = duration (s).

and avoidance and submission received, the post-hoc individual comparisons between males were not statistically significant.

Discussion

This study reports the occurrence of both affiliative and agonistic interactions between adult males and lactating females in a captive group of pigtail macaques. The data on bodily contact and grooming suggest that, with the exception of the fourth-ranking male Qe, the males present in this group showed little or no interest in initiating affiliative interactions with lactating females. In fact, the vast majority of the interactions involving contact and grooming were initiated by the adult females. In contrast, adult males approached females more than vice versa. Male approaches to lactating females may have reflected curiosity in their infants. With the exception of Qe, however, the adult males showed little or no infant handling. Moreover, the presence of infants in general seemed to have a negligible effect on male-female interactions. For example, male-female interactions showed little or no variation in relation to infant age, the only exception being that females avoided males less frequently as lactation progressed. Thus, the higher frequency of male approaches to females is unlikely to have resulted from interest in infants and may simply reflect a sex difference in activity levels.

Dominance rank had a clear influence on female behavior. Most affiliative interactions with adult males were initiated by high-ranking females and directed to the alpha male. In fact, the alpha male received more approaches, contacts and grooming (both in frequency and in duration) than all the other males. These findings are consistent with the hypothesis that adult females view the alpha male as an attractive social partner and that competition among females for proximity, contact and grooming with the alpha male result in him being monopolized by high-ranking females (Seyfarth 1977). The finding that females with sons approached the adult males more than females with daughters was probably due to the fact that two high-ranking females who approached males with a high frequency happened to have male infants.

The relation between high dominance rank and male-female affiliative relationships has also been reported for other macaque species. In *Macaca fuscata* and *M. mulatta*, friendships during the birth season are concentrated among high-ranking males, and high-ranking males tend to associate with older and/or high-ranking females (Oki & Maeda 1973; Grewal 1980; Takahata 1982; Furuichi 1985; Chapais 1983, 1986; Hill 1986; Manson 1994; but see Kaufmann 1967 who found no relation between male rank and rank of female friends in rhesus macaques). In Japanese macaques, friendships involving middle- and low-ranking males have only occasionally been reported (Takahata 1982). The strong influence of dominance rank on male-female friendships during the birth season in rhesus macaques led Chapais (1983, 1986) to conclude that such relationships are mainly due to two factors: the attraction of adult females to the high-ranking males and the attractiveness of the alpha female to the high-ranking males.

The adult male pigtail macaques in this study showed little evidence of being

attracted to high-ranking females. In fact, the affiliative interactions between high-ranking females and the alpha male were so dependent on the female's initiative as to question whether they can be referred to as friendships. Because female grooming was generally not reciprocated by the alpha male, it is plausible to assume that females obtained other benefits from their association with him. One possibility is that adult females exchanged proximity and grooming with support and protection from the alpha male against other group members. Although no data on agonistic support were available in this study, previous research has shown that in pigtail macaques the alpha male frequently intervenes in intragroup conflicts and plays an important role when the group faces external challenges (Smith 1973; Oswald & Erwin 1976). In rhesus macaques, Chapais (1983, 1986) reported that the most attractive males were the least aggressive to females and that aggressive males affiliated little with females. In the current study, the least aggressive male was the fourth-ranking one and not the alpha male. Thus, females who frequently interacted with the alpha male and other high-ranking males risked being attacked by them. This was particularly evident in the case of one female (Dt) who had very high scores of affiliation with males as well as high scores of aggression received.

Although female dominance rank was a good predictor of variation in female affiliative behavior, it was a poor predictor of differences in male behavior. Specifically, there was no significant correlation between female dominance rank and any of the measures of male behavior considered, including approach, contact, grooming, aggression, avoidance, and infant handling. The five adult males and the subadult male, however, differed from each other in all of these measures. Differences in aggression and avoidance were mostly due to the behavior of the two lowest-ranking males. Male affiliative behavior towards lactating females and their infants, however, was mostly accounted for by the fourth-ranking male, Qe. Although this male displayed a high frequency of approaches, contacts, and grooming towards most lactating females and their infants, he appeared to have a preference for one middle-ranking mother–infant dyad.

The behavior of Qe is interesting in the light of data on mating success during the previous year. The paternity of 13 infants born in the study group during the year prior to the beginning of this study was assessed by Gust et al. (1996) using a DNA profile analysis. Eight of 13 infants were sired by the fourth-ranking male Qe, three by the second-ranking male Oh, and two by the fifth-ranking male Ii. The alpha male Te, the third-ranking male Ji, and the subadult male Bl did not sire any offspring. Semen analysis of Te revealed that the alpha male was sterile, whereas sperm counts for other males fell into the normal range (Gust et al. 1996).

Assuming that Qe was the most reproductively successful male also in the following year, his behavior can be interpreted in one of the following ways. One possibility is that affiliation with lactating females and mating success were causally related. This could be the case if male–female affiliation increased the probability of subsequent mating, when females returned to estrus. Alternatively, it is possible that previous mating interactions resulted in the subsequent maintenance of strong social bonds when infants were born, without any consequence for future mating activity. According to this hypothesis, however, the male's affiliative efforts have

no clear adaptive function and amount to little more than a waste of time. Finally, male affiliative behavior could be interpreted as a form of parental investment. It may be argued that by supporting the females who were likely to have conceived his offspring, the male may have indirectly contributed to enhance the probability of offspring survival. This helpful behavior may have been associated with a specific mechanism of offspring recognition (e.g. phenotype matching), or a general rule of thumb linking previous mating activity with confidence of paternity. Previous studies of macaques have failed to provide evidence of preferential interactions between fathers and offspring (e.g. Berenstein et al. 1981; Gust et al. 1996). Moreover, if the parental investment hypothesis were correct, it is not clear why an adult male with high confidence of paternity would not engage in more direct forms of parental care such as infant carrying. Even the adult male who was most interested in infants, however, did not show interactions with them other than brief touching. Thus, the low involvement of pigtail macaque males in infant handling makes the parental investment hypothesis improbable. Overall, although non-adaptive explanations of the behavior of the fourth-ranking male cannot be ruled out, his affiliative efforts are perhaps best viewed as part of a mating strategy (e.g. Berard et al. 1994). Thus, by displaying high affiliation and low aggression towards lactating females and their infants, this male may have increased his subsequent chances of mating success.

In conclusion, this study confirms previous research (Maestriperieri 1998) indicating that adult male pigtail macaques show little interest in young infants and fails to provide strong evidence that adult males and lactating females form intense and reciprocal social bonds (i.e. friendships). Although some females and males showed a preference for a particular individual of the opposite sex, such a preference was generally not reciprocated. The general tendency of females to be attracted to the alpha male is best interpreted as an attempt to gain his agonistic support or protection, while the unusual affiliative behavior shown by one of adult males is probably best viewed as part of a social strategy aimed at maximizing future mating success.

Since this study focused only on lactating females during the first 3 mo postpartum, it cannot be ruled out that male–female friendships similar to those observed in baboons and in rhesus and Japanese macaques also occur in pigtail macaques, but are limited to relationships between males and non-lactating females. Likewise, it cannot be ruled out that strong bonds between specific pairs of individuals could be more apparent over periods of time longer than the current study period. However, it is also plausible that the negative findings of this study reflect a true difference between macaque species, which could perhaps be accounted for by differences in morphological, reproductive or behavioral traits. For example, sexual dimorphism in body size and aggression among pigtail macaques relative to rhesus and Japanese macaques (Fooden 1975; Bernstein et al. 1979) could potentially result in male–female friendships being less likely to occur in the former than in the latter species. Alternatively, the fact that pigtail macaques are non-seasonal breeders would imply that adult males have access to some sexually receptive females at any time during the year and therefore may be less

motivated to affiliate with lactating females. Future studies are needed to address these questions in pigtail macaques, as well as to further investigate the determinants and function of friendships in other Cercopithecine primates.

Acknowledgements

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