Why are infants so attractive to others? The form and function of infant handling in bonnet macaques

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Female macaques and baboons are intensely interested in other females' infants, but provide little direct care for them. The selective factors that shape this strong attraction to neonates may differ from those that shape alloparental care in other taxa. The attraction to neonates may have evolved because (1) it enhances young females' acquisition of maternal skills, (2) it is a form of reproductive competition among females, or (3) it is a by-product of selection for appropriate maternal care. I studied patterns of infant handling in a large group of bonnet macaques, *Macaca radiata*, at the California Primate Research Center at the University of California, Davis. Infant handling was generally gentle and nonintrusive, although females sometimes tugged on infants. Females were more strongly attracted to infants than were males, regardless of their age. Adult females handled infants as often as subadult females did. Male and female infants were handled at equal rates, and rates of handling towards all infants declined sharply as infants matured. Infants were handled by related females at higher rates than by unrelated females, and at higher rates by higher-ranking females than by lower-ranking females. The data provide little support for the 'learning to mother' hypothesis, because older females were as interested in infants as were subadult females. Although mothers were reluctant to allow their infants to be handled, the data do not support the reproductive competition hypothesis because patterns of infant handling did not match patterns of harassment of infants. The data provide a better fit to the by-product hypothesis. Females were most strongly attracted to infants when maternal care was most critical for infant survival and females of all ages were strongly attracted to infants. Taken together, these data suggest that a strong attraction to infants is favoured by selection because females that are highly responsive to infants make good mothers.

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Mammalian young are costly to rear because they must be fed, carried, groomed and protected from predators over a long period. A parent's investment in its present offspring limits its ability to produce additional offspring, creating a potent force shaping the reproductive strategies of males and females (Trivers 1972). Despite the high costs of rearing offspring, alloparental care is common among mammals, occurring in at least nine orders and 120 species (Riedman 1982; Gittleman 1985; Packer et al. 1992).

Several different processes may have shaped the evolution of alloparental care among mammals. Alloparental care may have been favoured by kin selection, where alloparents typically care for closely related young, as jackals, hyenas and wild dogs do (van Lawick & van Lawick-Goodall 1971; Moehlman 1980 cited in Riedman 1982; Owens & Owens 1989). Alloparental

care may also be a form of reciprocal altruism if alloparents receive help in raising their own offspring in return, as may be the case for some mongoose species (e.g. Rood 1978) and lions, *Panthera leo* (Schaller 1972; Packer & Pusey 1984). In other cases, alloparental care may be favoured by natural selection as a means to enhance the alloparent's own parenting skills, a factor that may play a role in some pinniped and primate species (Riedman 1982; Fairbanks 1990). If alloparents harm their charges, as they sometimes do, alloparenting may be a form of reproductive competition (Hrdy 1976, 1978; Silk 1980; Wasser & Barash 1981; Wasser 1983; Gittleman 1985; Maestripieri 1994a). Finally, alloparental interactions may not always be adaptive. Thus, alloparenting may represent a 'reproductive error' which occurs when individuals who are primed to provide parental care encounter alien offspring and are unable to distinguish them from their own (Reidman 1982). Alloparental care may also be a side effect of strong selection for appropriate maternal

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behaviour that favours high responsiveness to infants (Quiatt 1979).

Alloparental interactions are common among primates. In some cases, alloparents provide substantial amounts of care for infants. For example, in the small-bodied marmosets and tamarins, mothers receive extensive assistance from other group members in carrying, feeding and protecting their offspring (e.g. Goldizen 1987a; Tardif et al. 1993; Garber 1997). Group members frequently handle infant langurs, beginning when they are only hours old (e.g. Hrdy 1976; McKenna 1979; Dolhinow & Murphy 1982; Vogel 1984; Sommer 1989; Stanford 1991, 1992). In their first month of life, capped langur, *Presbytis pileata*, infants spend nearly as much time with allomothers as they do with their own mothers (Stanford 1992). Infant cebus monkeys are frequently carried and sometimes nursed by individuals other than their mothers (*Cebus* sp.: O'Brien & Robinson 1991; Perry 1996; Manson 1999). Alloparental care is also common in vervets, *Cercopithecus aethiops*, where young females are most active in holding and carrying young infants (Lancaster 1971; Fairbanks 1990; Meaney et al. 1990). In these species, mothers are generally tolerant of alloparental interactions.

Although the costs and benefits of alloparental care have not been worked out in detail for most species, there is evidence that mothers sometimes benefit from the care that their infants receive from alloparents. Among marmosets and tamarins, alloparental care apparently enhances female fertility, enabling breeding females to produce twins twice per year (Goldizen 1987b). Female capped langurs feed more efficiently when their infants are held by others than when they hold them themselves (Stanford 1992). Female vervet monkeys whose infants receive the most care from others have shorter interbirth intervals than females whose infants receive less care (Fairbanks 1990).

There is also some evidence that alloparents themselves benefit from providing care for infants. In marmoset and tamarin groups, helpers are often kin and may enhance their inclusive fitness by caring for infants (Goldizen 1987b). Young females tend to handle infants more clumsily, becoming more adept as they become older and more experienced (Hrdy 1977; Meaney et al. 1990). Helping enhances the likelihood that female cottontop tamarins, *Saguinus oedipus*, will raise their first infant successfully (Tardif et al. 1993). In addition, juvenile vervet monkeys that frequently care for other females' infants are more likely to rear their firstborn infants successfully than females that have less contact with infants (Fairbanks 1990).

Strong attractions to newborn infants are not always coupled with care giving in primates. This is particularly characteristic of macaques and baboons. In these species, group members show an intense interest in young infants, but provide little direct care for them. Group members crowd around new mothers, attempting to greet, touch, cuddle, nuzzle, sniff and inspect newborn infants while they are in contact with their mothers (e.g. Gouzoules 1975; Altmann 1980; Silk 1980; Small 1990; Bauers 1993; Paul & Kuester 1996). These kinds of interactions are collectively labelled 'infant handling' (Maestripieri 1994a). Most macaque and baboon mothers receive virtually no direct help in feeding, carrying, grooming, or protecting their offspring from predators (Nicolson 1987). Macaque and baboon mothers never initiate alloparental interactions and respond warily to efforts to handle their infants (Altmann 1980; Nicolson 1987). Although juvenile females often show the most active interest in handling infants (Clarke 1978; Caine & Mitchell 1980; Hiraiwa 1981; Nicolson 1982, 1987; Small 1982; Paul & Kuester 1996), older females also handle infants.

To understand the evolution of alloparental interactions among macaques and baboons, we need to understand why infants are so attractive to others. The selective factors that have shaped 'natal attraction' (Small 1991; Mann & Smuts 1998) in baboons and macaques may be quite different than the selective factors that have shaped alloparental care in langurs, vervets, marmosets, tamarins and capuchins. Because mothers seem to be reluctant to allow others to handle their infants and alloparents provide little direct care for infants, it seems unlikely that natal attraction or infant handling are beneficial to mothers or infants. This rules out functional explanations based upon kin selection and reciprocal altruism.

We can also rule out the possibility that natal attraction is a kind of 'reproductive error' (Reidman 1982) for several reasons. Because parental care is costly, we would expect this kind of reproductive error to be rare. In fact, rates of infant handling interactions are often very high, suggesting that natal attraction is quite common. Moreover, if natal attraction is a reproductive error, then it should be limited to parous females, perhaps to females that have recently given birth. However, immature females are strongly attracted to infants (references above).

Natal attraction may enhance maternal skills by providing young females with opportunities to observe mother–infant interactions and handle newborn infants. The main prediction, which can be derived from the 'learning to mother' hypothesis (Lancaster 1971), is that immature females will show the most active interest in infants and handle them at the highest rates (Maestripieri 1994a; Paul & Kuester 1996). Moreover, an immature female's contact with infants is expected to influence her subsequent reproductive success. Females with more extensive contact with infants are expected to rear their firstborn infants more successfully than females that have had less extensive contact with infants. Finally, while young females may not always handle infants competently, they are generally expected to treat them gently. Rough and overtly abusive forms of infant handling should be uncommon.

The reluctance of mothers to allow newborn infants to be handled suggests that these kinds of interactions may be harmful to infants. While some forms of infant handling in baboons and macaques are gentle and unintrusive, alloparents sometimes pull vigorously on infants, interrupt suckling bouts and cause distress to infants (Maestripieri 1994a). If these interactions are harmful or abusive, then natal attraction may be a form of

reproductive competition among females (Hrdy 1976; Silk 1980; Wasser 1983; Maestripieri 1994a). If this is the case, then the form and pattern of infant handling should reflect the pattern of reproductive competition among females. A number of predictions follow from this line of reasoning. Females should handle infants at higher rates than males do. Rough and overtly abusive forms of infant handling are expected to occur often. Moreover, adult females are expected to handle infants more often and more roughly than younger females do. Natal attraction is also expected to mirror more overt forms of aggression towards immatures. In some groups, adult females harass juvenile females at higher rates than juvenile males and aggression is mainly directed towards offspring of unrelated, lower-ranking females (Dittus 1977; Silk et al. 1981a; Maestripieri 1994b). Thus, females should be most strongly attracted to female infants and the infants of unrelated, lower-ranking females. Finally, as infants mature and become more serious competitors, harassment should intensify. Thus, rates of alloparental interactions, particularly rough forms of infant handling, should rise as infants mature.

Finally, natal attraction may simply be a side-effect of selection for appropriate maternal behaviour if females who are highly responsive to infants make good mothers. Because natural selection is likely to favour benign treatment of infants by their mothers, infant handling behaviours are generally expected to be gentle and nonabusive. Females are expected to handle infants more often than males. This hypothesis also predicts that adult females will remain interested in other females' infants, even when they are old enough to have infants of their own. Responsiveness to infants is likely to be most advantageous when maternal solicitude is most critical for infant survival. Thus, females are expected to be most strongly attracted to infants in their first weeks of life when they are most dependent upon their mothers for care. Females are expected to be equally attracted to male and female infants. However, social conditions may influence females' access to particular infants and opportunities to handle them. Females spend much of their time in proximity to maternal kin, so females may handle related infants at higher rates than they handle unrelated infants.

Predictions derived from these three hypotheses, which are summarized in Table 1, can be tested with data from a well-established group of bonnet macaques, *Macaca radiata*, housed at the California Primate Research Center. This group was typical of other cercopithecine groups in many ways. Females formed a stable, linear dominance hierarchy in which related females typically occupied adjacent ranks (Silk et al. 1981b). High rank conferred reproductive advantages upon females, as survivorship among the offspring of high-ranking females was higher that of low-ranking females (Silk et al. 1981c; Silk 1988). Infants and juveniles were vulnerable to harassment, and some juvenile females were seriously harmed by other group members (Silk et al. 1981a). Both adult (Silk 1980) and immature females (Clarke 1978; Caine & Mitchell 1980; Small 1982) showed considerable interest in other females' infants.

Table 1. Summary of predictions derived from hypotheses for natal attraction

Hypothesis 1: natal attraction enhances young female maternal skills.
  1. Females will handle infants at higher rates than males.
  2. Immature females will show strongest interest in infants.
  3. Immature females that handle infants most often will be most likely to rear their firstborn infant successfully.
  4. Rough and abusive forms of handling will be rare.

Hypothesis 2: natal attraction is a form of reproductive competition among females.
  1. Females will handle infants at higher rates than males.
  2. Rough and abusive forms of handling will be common.
  3. Adult females will handle infants more roughly than younger females.
  4. Females will handle female infants at higher rates than male infants.
  5. Females will handle related infants less often than unrelated infants.
  6. Females will handle lower-ranking females' infants at higher rates than higher-ranking females' infants.
  7. Rates of handling, particularly rough forms of handling, should rise as infants grow older.

Hypothesis 3: natal attraction is a by-product of selection for appropriate maternal care.
  1. Females will handle infants at higher rates than males.
  2. Gentle forms of handling will be common.
  3. Adult females will handle infants as often as younger females.
  4. Females will handle infants at the highest rate when they are youngest.
  5. Females will be equally attracted to male and female infants.
  6. Females will handle related infants more often than unrelated infants.

METHODS

Study Population

Observations were conducted over a 4-year period in a large and stable group of bonnet macaques housed at the California Primate Research Center in Davis, California. The study group was established in 1970–1971 and maintained for behavioural research over the next two decades. Management policies were designed to replicate demographic features of free-ranging groups. No unfamiliar females were introduced into the group after it was initially established. Maturing males were periodically removed from the group to simulate emigration, and mature males were introduced occasionally to simulate immigration. Due to natural recruitment, the group grew in size and eventually exceeded the capacity of the enclosure. One year before the present study began, the group was divided. In an attempt to mimic fission in free-ranging macaque groups (Chepko-Sade & Sade 1979), a number of the lowest-ranking females and all of their immature offspring were moved to another enclosure.

When the present study began, the group contained 45 monkeys. When the study ended, the group contained 59 monkeys. During the study, the group was composed of 17–21 adult females (>4 years), 6–12 adult males (>7 years) 1–4 subadult females (3–4 years), 3–7 subadult males (5–7 years), and 12–15 juveniles (females: 1–3 years; males: 1–5 years). Annual birth cohorts ranged from 9 to 15 liveborn infants.

Reproduction in this group was seasonal. Most females conceived between September and February and infants were born between March and August (Silk 1989). Most females conceived for the first time when they were 3.5 years of age, and produced their first infant at the age of 4 years (Silk et at. 1981c). Interbirth intervals following surviving births typically lasted 13 months, while interbirth intervals following nonsurviving births were slightly shorter (Silk 1988).

Subjects

The subjects of this study were 40 infants, including one pair of twins, which survived their first 6 weeks of life. The sample included 19 males and 21 females. These 40 infants were born to 16 females. Mothers varied widely in age (4–17 years), parity (0–12 previous pregnancies), maternal experience (0–11 previous live births), and dominance rank (0–100% of females dominated). Although a relationship between maternal rank and infant sex has previously been documented in this population (Silk et al. 1981c), there was no consistent relationship between maternal rank and infant sex in this sample (chi-square test: $\chi^2_1=1.37$, two-tailed $P=0.242$).

Data Collection

This report focuses upon behaviour directed towards infants when they were on or near (within 3 m of) their mothers during the first 6 months of life. The analysis is based upon information derived from focal observations of mothers. During focal observations of mothers, all interactions directed towards the focal subject's infant by other group members were recorded. For all interactions, the nature of the interaction, the identity of the partner, and the direction of the interaction were noted. For practical reasons, it was only possible to monitor interactions that took place in proximity to (within 3 m of) the mother.

The following forms of infant handling were recorded during focal observations: greet, muzzle, touch, groom, inspect, pull, carry and hold. Females greeted infants by approaching, bending down and raising their eyebrows as they leaned towards the infant. Greetings were often accompanied by low grunts. Muzzling occurred when one individual placed its face very close to another individual's face or body. Touching was recorded when one monkey made manual contact with another monkey in a nonaggressive context. Inspections involved peering, touching, or smelling the genital area. Pulling was recorded when an infant was in contact with its mother and was vigorously tugged away from the mother. In most cases, pulling did not result in mother–infant contact being broken. Carrying was recorded when non-mothers transported infants ventrally or dorsally. Holding was scored when one monkey held an infant in its ventrum. The term infant handling will be used to refer to this group of behaviours collectively. This analysis does not include overt forms of aggression (threaten, hit, bite, drag, chase) towards infants, partly because these kinds of interactions were very uncommon when mothers were nearby.

Analysis

In the analyses reported below, the infant is the unit of analysis. I computed hourly rates of interactions towards infants by dividing the number of interactions directed towards the infant by the number of hours the mother was observed. The number of hours of observation per mother ranged from 1.5 to 17.25. This variation is due in part to the fact that some infants did not survive their first 6 months of life, and in part to changes in the sampling regime over the course of the study. In the first year of the study, focal data were collected approximately 6 h/day. In subsequent years, focal data were collected approximately 3 h/day. For some analyses, I computed the hourly rate of interactions per partner by dividing the number of interactions by the number of hours observed and the number of potential partners.

The results reported here are based on events that took place when infants were on or near their mothers. This would generate a biased description of infant handling behaviour if (1) females behaved differently towards infants when the infants' mothers were nearby and far away, or (2) there was systematic variation in the amount of time that infants spent near their mothers. However, there is good reason to believe that the results are broadly representative of infant handling interactions in this group. First, infants in this group spend relatively little time out of proximity to their mothers in their first 6 months of life (Silk 1991). During the first 2 months of life, when handling was most common, infants spent less than 5% of their time out of proximity to their mothers. At 6 months of age, they still spent approximately 60% of their time in proximity to their mothers. Second, previous analyses demonstrated that maternal dominance rank, parity, experience and age had no effect on proximity between mothers and their infants (Silk 1991). Third, I repeated a number of analyses taking into account the proportion of time that each infant spent in proximity to its mothers. None of the results was altered.

Sample sizes varied in the analyses because not all infants could be included in all comparisons. Five of the 39 infants did not have maternal kin in the group, reducing the sample for analysis of the effects of kinship to 34 infants. All members of the same matriline were treated as kin in these analyses. When I compared rates of handling from unrelated females in higher- and lower-ranking lineages, I excluded infants in the highest- and lowest-ranking lineages, reducing the sample to 28. Comparisons of rates of handling from related females and higher-ranking, unrelated females were limited to a
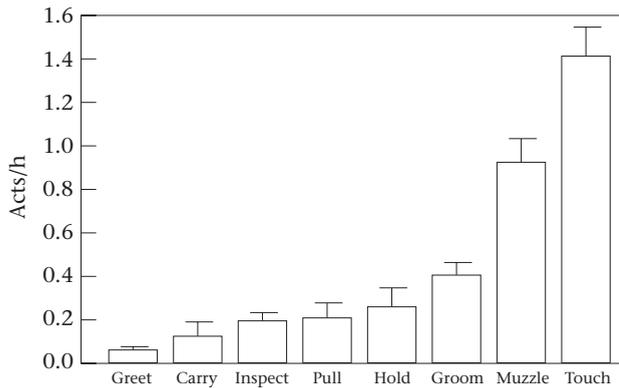
Figure 1. The mean (+SE) rates (acts/h) of different forms of infant handling. (See Methods for definitions of behaviours.)

Figure 2. Mean (+SE) rates of handling received by infants from each age class. Rates are based on the number of hours of observation and the number of partners in each age–sex class.

sample of 25 infants. Infant handling received from kin could not be computed for the five infants without kin or the two infants that were never handled, leaving 32 infants in the sample. All the significance tests cited below were two-tailed.

One pair of female twins was born in the course of the study. For the purposes of this analysis, the twins were treated as a single infant. The decision to treat the twins as a single infant did not substantially affect any of the results reported below.

RESULTS

The Form of Infant Handling

The distribution of infant handling behaviours is shown in Fig. 1. Muzzling and touching were the most common elements of infant handling, while greetings were the least common elements. Infants typically did not play an active role in initiating any of these interactions.

These behaviours can be tentatively ranked along a continuum from gentle/nonintrusive to rough/intrusive. Greetings, which involved no contact at all, were presumably the least intrusive forms of behaviour directed towards infants. Muzzling, touching and grooming all involved gentle contact. Inspections were slightly more intrusive as the handler sometimes grasped one of the infant's legs and lifted it away from the mother's ventrum to smell and/or inspect its genitals visually. But in other cases, handlers simply bent over the infant and peered at
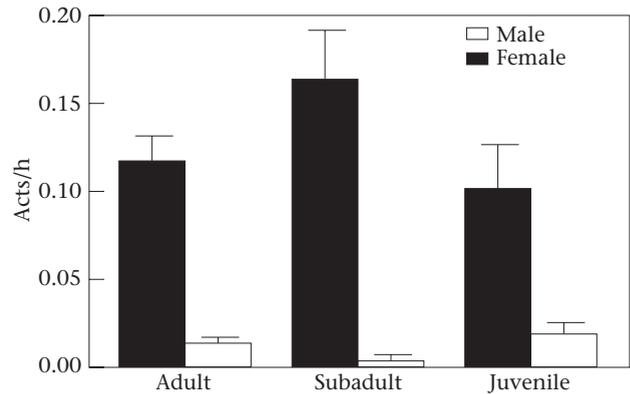
its genitals or gently touched and sniffed the genital area. Pulling was rougher and more intrusive than inspections because the handler vigorously grasped and pulled the infant while its mother was clasping it. Two behaviours cannot be readily ranked along this continuum: carrying and holding. Infants were usually not treated roughly when they were held and carried, but they were sometimes handled awkwardly. Infants were also kept out of contact with their mothers. Thus, these behaviours could have been intrusive, but they did not seem to be rough.

Sex Differences in Interest in Infants

In this group, females were considerably more active than males were in handling infants (Fig. 2). Comparisons based upon the hourly rate per potential partner showed that disparities in the rates of handling by males and females were quite consistent among adults, subadults and juveniles (Table 2).

Age Differences in Handling by Females

On average, infants were handled at higher rates by subadult females than by adult females (Fig. 2). Infants were also handled at slightly higher rates by adult females than by juvenile females. However, there were no consistent differences in the rates of handling by adult and subadult females (Table 3). Infants were handled at significantly higher rates by subadult females than by

Table 2. Infant handling by males and females

	Number of cases (N=39)			Wilcoxon signed-ranks test	
Age class	Females> males	Females< males	Females= males	Z	P*
Adults	36	0	3	−5.232	<0.001
Subadults	26	1	12	−4.517	<0.001
Juveniles	27	6	6	−3.842	<0.001

*Two-tailed.

Table 3. Infant handling by adult, subadult, and juvenile females

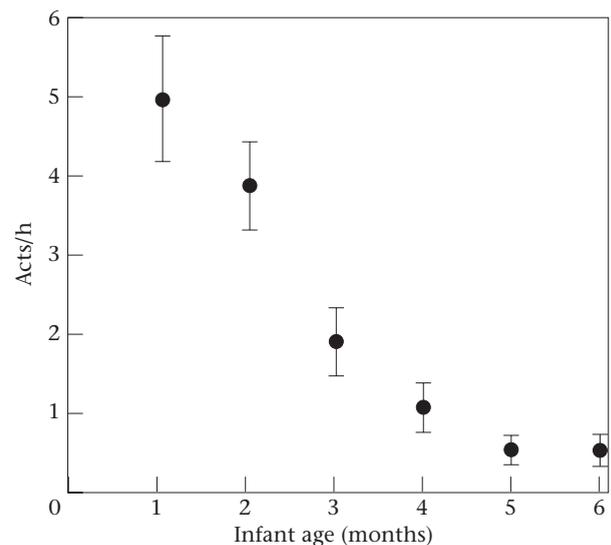|	Number of cases (*N*=39)			Wilcoxon signed-ranks test	
Age class	Older> younger	Older< younger	Older= younger	*Z*	*P**
Adult versus subadult	16	20	3	−1.508	0.131
Adult versus juvenile	24	12	3	−1.846	0.065
Subadult versus juvenile	23	11	5	−2.522	0.012

*Two-tailed.
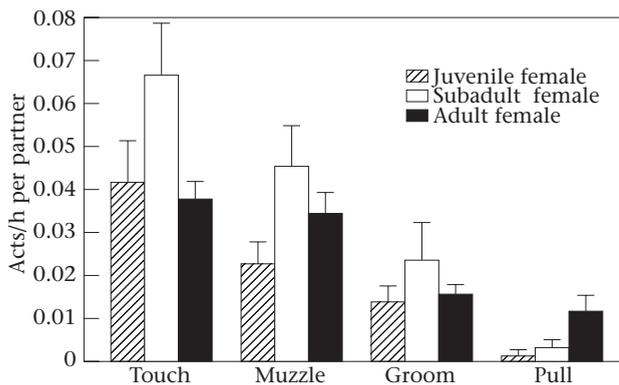
Figure 3. Mean (+SE) rates of handling received by infants from juvenile, subadult and adult females. Rates are based on the number of hours of observation and the number of female partners in each age class.

Figure 4. Mean (+SE) rates of handling received by infants of different ages.

juvenile females, but differences in the rate of handling by adult and juvenile females were not statistically significant.

Quality of Infant Handling by Mature and Immature Females

To determine whether the quality of infant handling received from immature and mature females differed, I compared the rates of several different forms of handling received from adult, subadult and juvenile females (Fig. 3). Infants were more likely to receive rough treatment (pulling) from adult females than from younger females (Wilcoxon signed-ranks test: adult versus subadult, $Z= -2.84$, $P=0.005$; adult versus juvenile, $Z= -3.42$, $P=0.001$; subadult versus juvenile, $Z= -0.74$, $P=0.461$).

Gentler forms of infant handling did not follow the same pattern (Fig. 3). Infants were touched gently at lower rates by adult females than by subadult females ($Z= -2.11$, $P=0.035$) and were touched at the same rate by adult females and juvenile females ($Z= -0.704$, $P=0.481$). Infants were muzzled by subadult and adult females at about the same rate ($Z= -0.90$, $P=0.368$), and were muzzled at lower rates by juvenile females than by adult or subadult females (adult versus juvenile: $Z= -2.69$, $P=0.007$; subadult versus juvenile: $Z= -2.12$, $P=0.034$). Infants were groomed at approximately equal rates by females of all ages (adult versus subadult:

$Z= -0.43$, $P=0.666$; adult versus juvenile: $Z= -1.20$, $P=0.229$; subadult versus juvenile: $Z= -0.63$, $P=0.528$).

Effect of Infant Age

Infants were most attractive to females when they were very young. The hourly rate of handling declined sharply as infants matured (Fig. 4). In their first month of life, infants were handled on average approximately five times per hour by adult and subadult females. By 3 months of age, infants were being handled only twice per hour, and at 6 months of age, the average rate of handling dropped to 0.6 per h. All forms of handling followed the same trajectory.

Effects of Infant Sex

There was no evidence that infant sex influenced the overall rate of infant handling. On average, the 20 female infants were handled 4.0 times/h and the 19 male infants were handled 4.1 times/h (Mann–Whitney test: $U=171.5$, $P=0.603$). There were no consistent differences in hourly rates of rough forms of infant handling (pulling) for male and female infants ($U=183.0$, $P=0.857$) or in the
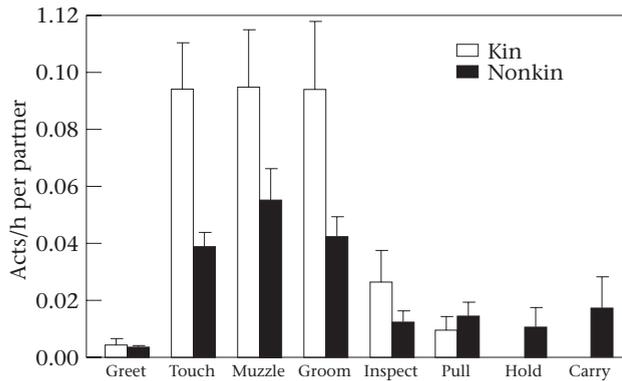
Figure 5. Mean (+SE) rates of various forms of handling by kin and nonkin. See Table 4 for results of significance tests.

proportion of rough handling received (pulling/all handling: $U=170.0$, $P=0.603$).

Effects of Kinship

Infants were handled at higher rates by kin than non-kin overall (Wilcoxon signed-ranks test: $Z=-2.150$, $P=0.032$, $n_1=22$, $n_2=10$). On average, infants were handled 0.33 times/h by each of their mature female kin

and 0.20 times/h by each of the unrelated females in the group. The effects of kinship were particularly pronounced for touching, muzzling and grooming (Fig. 5, Table 4).

Effects of Dominance Rank

When infants were handled by unrelated females, they were more likely to be handled by females that outranked their mothers than by females that were of lower rank than their own mothers. This difference was highly significant when all forms of handling were considered collectively (Wilcoxon signed-ranks test: $Z=-3.34$, $P=0.001$). On average, infants were handled 0.32 times/h by each unrelated, higher-ranking female and 0.14 times/h by each unrelated, lower-ranking female in the group. The effects of rank extended across all forms of handling. Infants were muzzled, inspected and pulled at significantly higher rates by unrelated, higher-ranking females than by unrelated, lower-ranking females (Table 5). For touching, grooming, carrying and holding, the pattern was the same, but the differences were not statistically significant. Thus, rank seemed to influence the patterning of both gentle and rough forms of handling.

Kinship and high rank generally enhanced females' access to infants to a similar extent. There was no

Table 4. Handling by related and unrelated females

Behaviour	Number of cases* (N=34)			Wilcoxon signed-ranks test	
	Kin> NK	Kin< NK	Kin= NK	Z	P*
Greet	3	11	20	−0.847	0.397
Touch	20	12	2	−2.954	0.003
Muzzle	19	12	3	−1.999	0.046
Groom	15	14	5	−1.935	0.053
Inspect	8	14	12	−0.341	0.733
Pull	6	13	15	−0.523	0.601
Hold	0	11	23	−2.936	0.003
Carry	0	4	30	−1.826	0.068

NK: Nonkin.
*Two-tailed.

Table 5. Handling by unrelated, higher-ranking and unrelated, lower-ranking females

Behaviour	Number of cases* (N=28)			Wilcoxon signed-ranks test	
	HR>LR	HR<LR	HR=LR	Z	P*
Greet	3	6	19	−0.296	0.767
Touch	15	8	5	−1.430	0.153
Muzzle	20	6	2	−3.670	<0.001
Groom	13	10	5	−0.821	0.412
Inspect	13	4	11	−2.154	0.031
Pull	12	5	11	−1.823	0.068
Hold	7	2	19	−1.599	0.110
Carry	5	1	22	−1.572	0.116

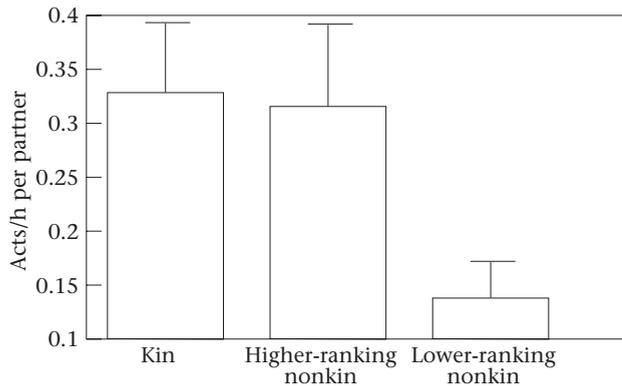HR: High rank; LR: low rank.
*Two-tailed.

Figure 6. Mean (+SE) rates of handling received from kin, higher-ranking nonkin and lower-ranking nonkin. Rates are based upon the number of acts/h per potential partner.

difference in the overall rate of handling received from kin and higher-ranking, unrelated females (Fig. 6). Infants tended to be held and pulled at lower rates by related females than by unrelated, higher-ranking females, but there were no consistent differences in the rates at which infants were touched, muzzled, groomed, or inspected by related females and higher-ranking, unrelated females (Table 6).

Impact of Handling on Young Females' Future Reproductive Success

Ten females that were observed as juveniles and subadults later gave birth. For these females, it is possible to examine the relationship between contact with infants and subsequent reproductive performance. Five females were observed as 2- and 3-year-olds, and gave birth at the age of 4 years. One female, who produced her first infant at the age of 4 years, was observed only as a 3-year-old. Two females that gave birth for the first time after the age of 5 years were observed between the ages of 2 and 4 years. For each female, I tallied the number of infant handling interactions observed during these years. This sum was divided by the number of hours that mothers were observed during the same years.

Three of the 10 females' firstborn infants survived to 6 months of age. Two females rejected apparently healthy firstborn infants and provided no care for them; both infants died within days of birth. The remaining five females' firstborn infants died within 30 days of birth.

The extent of females' contact with infants had no consistent impact on the outcome of their first pregnancies (Mann–Whitney test: survive versus not survive: $U=4.0$, $P=0.183$). The three females whose firstborn infants survived actually handled infants less often on average than the seven females whose infants died or were rejected within the first month of life (mean $\pm$ SE: survived: 0.098+0.021; died: 0.185+0.030).

DISCUSSION

The female bonnet macaques in this group were strongly attracted to young infants, much as are other primates. While bonnet females were attracted to infants, they did not often provide care for them. Most interactions with infants were very brief, and infants were not often held or carried by alloparents. The form and patterning of infant handling interactions in this group provide insight about the evolution of natal attraction.

The learning to mother hypothesis was not well supported by the results of this study. The learning to mother hypothesis predicts that immature females will be most strongly attracted to infants. This pattern is commonly observed in baboon and macaque groups (Clarke 1978; Caine & Mitchell 1980; Hiraiwa 1981; Nicolson 1982, 1987; Small 1982; Paul & Kuester 1996). However, in this study, infants were handled at the same rates by subadult and adult females. This does not necessarily disprove the learning to mother hypothesis because it is possible that young females and older females were attracted to infants for different reasons. The fact that juvenile and subadult females handled infants more gently than adult females provides some support for this view. It is not clear why infants were handled at higher rates by subadult females than by juvenile females. Juvenile females may have been less strongly attracted to infants than subadult females, or they may have been unable to gain access to infants as readily as subadult females.

Table 6. Handling by kin and higher-ranking, unrelated females

	Number of cases (N=25)			Wilcoxon signed-ranks test	
Behaviour	Kin>HR	Kin<HR	Kin=HR	Z	P*
Greet	0	7	18	−2.371	0.018
Touch	11	10	4	−1.199	0.230
Muzzle	8	13	4	−0.400	0.689
Groom	7	10	8	−0.166	0.868
Inspect	3	11	11	−1.287	0.198
Pull	2	12	11	−1.915	0.056
Hold	0	5	20	−2.023	0.043
Carry	0	3	22	−1.604	0.109

HR: High rank.
*Two-tailed.

The learning to mother hypothesis also predicts that early contact with infants will enhance subsequent reproductive performance. In this group, there was no evidence that contact with infants enhanced females' subsequent reproductive success. Although the sample of immature females was very small, the three females that reared their firstborn infants successfully had less contact on average with infants than females whose firstborn infants did not survive. Paul & Kuester (1996) also found no evidence that infant handling by immature Barbary macaque, *Macaca sylvanus*, females affected their subsequent reproductive performance.

Three of the predictions derived from the hypothesis that natal attraction is a form of reproductive competition among females were supported by the results. First, females handled infants at higher rates than males. Second, infants were handled more roughly by adult females than by younger females. Similar patterns have been observed in other groups (Altmann 1980; Hiraiwa 1981; Nicolson 1987; Maestripieri 1993a). Third, infants were handled at higher rates by females that outranked their mothers than by females that were subordinate to their mothers. The effects of dominance rank on infant handling in studies of other groups are inconsistent. Some studies have found that handling is typically directed down the hierarchy (Altmann 1980; Silk 1980; Wasser 1983; V. Bentley-Condit, unpublished data), but there are also groups in which dominance rank has no consistent impact on handling (Maestripieri 1994b; Paul & Kuester 1996).

While some results support some of the predictions derived from the reproductive competition hypothesis, the data do not support other predictions derived from this hypothesis. Thus, females generally handled infants gently; the most common forms of infant handling involved gentle, nonintrusive behaviours. Moreover, adult females handled infants as often as subadult females, and they did not selectively handle infant females or unrelated infants. Finally, rates of handling, including pulling, declined sharply as infants grew older.

The data provide a better fit to predictions derived from the hypothesis that natural selection favours natal attraction because females that are responsive to infants make good mothers. Most infant handling interactions were gentle and unintrusive. There was no direct evidence that females actually harmed infants when they handled them, even when they pulled on them roughly (see also Paul & Kuester 1996). Adult females remained interested in infants, and rates of infant handling among subadult and adult females did not differ consistently. Females were most strongly attracted to very young infants, and the sex of the infant had no effect on the rate of handling. Finally, infants were handled at higher rates by kin than nonkin. All of these results are consistent with predictions derived from the by-product hypothesis. Paul & Kuester (1996) also concluded that the pattern of alloparental interactions in Barbary macaques was most consistent with the hypothesis that females' attraction to young infants is a by-product of selection for appropriate maternal care.

The by-product hypothesis is also supported by evidence that females' hormonal status may influence their attraction towards infants. Maestripieri & Wallen (1995) have reported that female pigtail macaques, *Macaca nemestrina*, handle infants most often during early and middle pregnancy, and during lactation. Paul & Kuester (1996) also found high rates of infant handling among lactating female Barbary macaques, but not among pregnant females. However, they point out that highly synchronized breeding in this population may provide pregnant females with few opportunities to interact with infants.

The by-product hypothesis seems to provide a plausible explanation for why females nuzzled, carried, held, groomed, inspected and touched infants gently, but it may not explain why they tugged on them and attempted to pull them away from their mothers. The by-product hypothesis also does not explain why mothers were so reluctant to allow their infants to be handled or why handling was mainly directed down the hierarchy. These results seem more consistent with the reproductive competition hypothesis. Maestripieri (1994a) argued that when experienced females handle other females' infants more roughly than they handle their own infants, 'some intentionality in harming or distressing the infant must be inferred' (page 537). He suggested that rough or abusive handling should be considered to be a form of harassment.

Although I was among the first to suggest that rough infant handling is a form of female–female competition (Silk 1980) and have documented severe aggression towards juveniles in this bonnet macaque group (Silk et al. 1981a), I am not convinced now that females' attraction to infants is a product of reproductive competition among females. Perhaps the interactions classified here as rough handling (pulling) occur when females persist in attempting to handle infants in the face of determined maternal resistance. Mothers' resistance may reflect the dangers that their infants encounter when they are out of their reach, rather than the harm that infants will incur when they are being handled. If infants are in danger when they are away from their mothers, then mothers may avoid other females' efforts to handle their infants. In this group, mothers had real reason for concern. Infants were chased, threatened, attacked and bitten by adult females, and they were more likely to be harassed when they were away from their mothers (Silk 1991). At least 15 of the 39 infants included in this study (38%) were wounded during their first 6 months of life. Seven of these 15 infants sustained multiple injuries, and two infants, which were repeatedly and severely wounded, died from their injuries.

Alloparental interactions in this group, and in other groups of baboons and macaques, may reflect a conflict of interest between alloparents and mothers. Females are strongly attracted to infants, and this motivation is a product of selection for responsiveness to infants. In macaque and baboon groups, females are freer to express this attraction towards the infants of lower-ranking females than towards those of higher-ranking females because of the hierarchical nature of social relationships.

High-ranking females can also pursue their objectives with less finesse than low-ranking females because they have little fear of mothers responding aggressively. At the same time, mothers are concerned about the safety of their infants when they are out of reach and anxious to maintain control of their infants. In groups like this one, where other females pose a threat to infants, maternal protectiveness is likely to be favoured by selection. This may be why mothers resist efforts to pull infants away from them, creating vigorous tugs-of-war over infants.

This explanation does not imply that alloparental interactions will never be harmful to infant baboons and macaques. There are a number of examples in the literature of infants that starved or became severely dehydrated as a result of extended contact with allomothers (reviewed by Kohda 1985; Thierry & Anderson 1986; Maestripieri 1994a; Paul & Kuester 1996). However, even though these interactions sometimes have deleterious consequences, it does not necessarily mean that they are maintained by selection because they cause harm to infants. Thus, there are also examples of infants that have survived extended contact with allomothers. Although we generally label extended allomothering episodes with negative outcomes as 'kidnappings' and those with positive outcomes as 'adoptions', it is not clear that different proximate factors motivated females to maintain extended contact with other females' infants in these situations or that different selective factors favoured the evolution of these interactions.

Similarly, this line of reasoning does not imply that selection always favours benign interactions towards infants in these species. There is plenty of evidence that infants and juveniles are sometimes the target of aggression from other group members in cercopithecine groups (e.g. Gouzoules 1975; Dittus 1977; Kurland 1977; Hiraiwa 1981; Silk et al. 1981a; Simpson 1988; Maestripieri 1993a, b). I would argue, however, that females are attracted to infants for reasons other than to harass them.

Monkeys' vocalizations may provide useful insights about the nature of various types of alloparental interactions. A growing body of evidence suggests that monkeys use vocalizations to signal their intention to behave benignly (E. Kaldor, J. B. Silk, R. Boyd, unpublished data). Grunts facilitate affiliative interactions among adult female baboons and are effective in reconciling conflicts with former opponents (Cheney et al. 1995; Silk et al. 1996). Similarly, rhesus macaques, *Macaca mulatta*, often grunt and girney before they groom other adult females (Kaldor 1996). The same kinds of calls often precede infant handling (Bauers 1993; Cheney et al. 1995; Kaldor 1996). Thus, by monitoring vocalizations, we might be able to assess females' intentions. If handling is a form of harassment, then females are not expected to grunt to infants before they handle them, particularly when they handle them roughly. If, on the other hand, infant handling is a by-product of females' responsiveness to infants, then females are expected to grunt to infants before they handle them, even when they pull on them vigorously.

Natal attraction seems to have deep roots in the primate order, although the form and frequency of infant handling differs considerably across taxa. Although females may be strongly attracted to all infants across the primate order, the expression of their attraction to infants (that is, the form and frequency of alloparental interactions) may be influenced by the social and demographic conditions in which females live (McKenna 1979; Silk 1980; Wasser & Barash 1981; Thierry & Anderson 1986; Stanford 1992; Maestripieri 1994b; Clarke et al. 1998). Females' willingness to provide costly care for other females' infants may depend in part on the presence of close kin or the opportunities for reciprocity. Mothers' responses to attempts to handle their infants may also be influenced by the social environment. When potential care givers pose little threat to infants, then mothers may be tolerant of infant handling. In such situations, mothers may take advantage of other females' interest in their infants, and profit from opportunities to forage unfettered (Hrdy 1976; Jones 1980; Vogel 1984; Stanford 1992), develop stronger bonds with group members (Hrdy 1976; de Waal 1990), test social bonds (Manson 1999), enable their infants to cultivate relationships with prospective caretakers (McKenna 1981; Dolhinow & Murphy 1982) or enhance infant safety in times of sudden danger (Hrdy 1976; Zucker & Kaplan 1981). When the social environment is hazardous, mothers may be protective and restrictive of their infants. In these situations, access to infants is likely to mirror females' priority of access to valued resources, and to favour relatives and higher-ranking females.

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