Natal Attraction in Adult Female Baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana

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Abstract

Mammalian females are strongly attracted to infants and interact regularly with them. Female baboons make persistent attempts to touch, nuzzle, smell and inspect other females' infants, but do not hold them for long periods, carry them, or provide other kinds of care for them. Mothers generally tolerate these interactions, but never initiate them. The function of these brief alloparental interactions is not well understood. Infant handling might be a form of reproductive competition if females' interest in infants causes distress to mothers or harm to their infants. Alternatively, infant handling might be the product of selection for appropriate maternal care if females who are highly responsive to infants are the most successful mothers. We test several predictions derived from these hypotheses with data collected in a free-ranging group of baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve of Botswana. Infants were most attractive when they were very young. Mothers of young infants were approached by other adult females on average once every 6 min, and other females attempted to handle their infants approximately once every 9 min. By the time infants were a year old, their mothers were being approached only once every 30 min and infants were being handled only once every 5 h. Females were more strongly attracted to other females' infants when they had young infants of their own, and their interest in other females' infants declined as their own infants matured. Females seemed to be equally attracted to all infants, but had greater access to offspring of their relatives and subordinate females. Females nearly always grunted as they handled infants. As in other contexts grunts are a reliable predictive signal that non-aggressive behavior will follow, the use of grunts before handling suggests that these interactions were not a form of deliberate harassment.

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Introduction

In many mammalian species, females interact regularly with other females' infants (e.g. elephants: Lee 1987; lions: Packer & Pusey 1984; dolphins: Mann & Smuts 1998; sperm whales: Whitehead 1996; rodents: D'Amato 1993; primates: Mitani & Watts 1997; bats: Wilkinson 1992; mongoose: Clutton-Brock et al. 2001). A variety of functional hypotheses have been offered to explain these interactions, with benefits proposed to accrue to different parties. For example, alloparents may benefit directly if their interactions with others' offspring enhance their own parenting skills (Riedman 1982; Fairbanks 1990; Mann & Smuts 1998). Mothers might also benefit if allomothers hold and carry their infants for extended periods, permitting them to feed more efficiently (Stanford 1992), while infants could benefit if allomothers allow them to nurse (Packer et al. 1992), protect them from predators when their mothers are out of proximity (Whitehead 1996), or 'adopt' them when their own mothers disappear (Thierry & Anderson 1986). All parties might benefit if efforts to provision and protect young augment the size and competitive power of the group (Clutton-Brock 2001).

In this paper, we explore the pattern and possible function of females' attraction to other females' infants in baboons. Like other female mammals, female baboons and macaques are strongly attracted to the infants of other group females, making repeated attempts to greet, sniff, inspect, and touch other females' infants (Altmann 1980; Silk 1980, 1999; Maestripieri 1994a; Paul & Kuester 1996; Bentley-Condit & Smith 1999; Paul 1999). Efforts to account for these brief interactions, collectively labeled infant handling, have considered a variety of functional explanations with no clear consensus (Maestripieri 1994b). In fact, the benefits of allomaternal interactions in baboons and macaques are not immediately obvious.

Although females in these species are strongly attracted to other females' infants and attempt to handle them at high rates, they seldom hold, carry or nurse them, or otherwise feed or provide long-term care for them. In addition, mothers seem wary of others' efforts to handle their infants and do not generally initiate these interactions (Altmann 1980; Maestripieri 1994a,b; Silk 1999). These observations suggest that neither mothers nor their infants actually benefit from these interactions. Handling other females' infants does not seem to increase primiparous female macaques' reproductive success. Moreover, experienced mothers who have successfully raised their own infants continue to express strong interest in other females' infants (Paul & Kuester 1996; Silk 1999). This combination of results suggests that allomothers do not themselves benefit directly through increased maternal experience.

Taken together, the details of allomaternal interactions in these species suggest a more limited set of possible explanations. Given the sometimes competitive tenor of adult female relationships in these species and the apparently one-sided interest in infant handling between mothers and handlers, one possibility is that infant handling represents a form of reproductive competition that causes distress to mothers or their infants (Hrdy 1976; Silk 1980;

Wasser 1983; Maestripieri 1994a). Reproductive competition among females is expected to occur when there is density-dependent mortality and reproductive opportunities are therefore limited. In these circumstances, females may attempt to limit the reproductive success of other females by harassing their offspring (Silk 1983). Hence selection might actively favor females who are strongly attracted to other females' infants. We call this the harassment hypothesis.

Alternatively, the attraction to other females' infants might arise as a generalization of selection on infant responsiveness in the service of providing appropriate maternal care (Quiatt 1979; Paul 1999; Silk 1999). If females who are highly responsive to infants are the most successful mothers, then a strong, general attraction to infants might evolve as a product of selection acting on maternal responsiveness. We call this the natal attraction hypothesis.

To test these alternative functional hypotheses for infant attraction, we examine the pattern of infant handling by adult female baboons in the Moremi Reserve, Botswana. These data complement and extend previous work on infant handling in macaques and baboons conducted at other sites. Our analysis focuses on the variables that influence infants' attractiveness and accessability to other females, and the variables that influence females' attraction and access to infants.

Methods

Study Group and Subjects

The study was conducted in the Moremi Reserve in the Okavango Delta of Botswana. One group of baboons at this site has been observed since 1977. The animals were fully habituated to humans on foot and could be identified individually [for more details about the study population see Rendall et al. (1999), Silk et al. (1999)].

Our data come from two study periods, Aug. 1992–Jun. 1993 and Apr. 1996–Feb. 1997. Data from the first study period were collected by JBS, DLC, and RMS, and data from the second study period were collected by DR. During the 1992–93 study period, 19 adult females were present. Fourteen of these females survived until 1996 and 10 juvenile females reached adulthood by 1996. Twenty-three adult females were present during the 1996–97 study period.

The maternal kinship relationships of all animals born in the group since 1977 were known. The ages and parities of females who were present in the group when demographic monitoring began in 1977 were estimated based upon the assumption that they were at least 6 yr old when their first known infant was born.

Here, we use the term 'kin' to refer to all females related through the maternal line. Paternal kinship was not known to observers, although paternal kinship relationships may influence behavior (Widdig et al. 2001, 2002) in Cercopithecine groups.

Behavioral Sampling

We conducted focal observations on each of the adult females in the group. During focal observations, we recorded all social interactions and vocalizations involving the focal animal, noting the identity of the partner, and the identity of the individual who was responsible for initiating the interaction. We also monitored all approaches to and from adult members of the group. During the 1992–93 study period, focal observations lasted 10 min; during the 1996–97 study period, focal observations lasted 60 min; 595 h of focal observations were collected in 1992–93 and 733 h of focal observations were collected in 1996–97.

The analyses of infant handling are based on interactions that took place when infants were on or near their mothers (within 2 m). Our results are thus limited to females' attraction to infants under these conditions. This decision could distort the overall description of infant handling if females interact in qualitatively different ways toward infants when they are near and far from their mothers. However, we believe that our results are broadly representative of infant handling interactions in this group because baboon infants spend most of their time on or very near their mothers during their first months of life (Altmann 1980; Nicolson 1982).

Dominance Hierarchy

Female dominance rank was determined from the pattern of supplants observed during focal observations and ad libitum. All females were placed in a square matrix and ordered so as to minimize the number of entries (reversals) below the diagonal. The females in this group formed a stable and linear dominance hierarchy and matrilineal kin occupied adjacent ranks. Although there was considerable turnover in the cohort of adult females between 1992 and 1997, the relative ranks of surviving females did not change.

Analysis

The analysis is based on observations of 27 mothers and 37 infants (1–12 mo of age); 10 females had infants during both study periods. Table 1 provides information about maternal age, rank and parity, infant sex and the age span of infants included in the study. In the analysis of the effects of infant age on the rate of interactions received by and performed by mothers, the mother is the unit of analysis. In the analyses of the factors that influence the attractiveness and availability of infants, the mother–infant dyad is the unit of analysis. The sample thus includes five females who were observed in both study periods with different infants between the ages of 1 and 6 mo. We elected to present the results based on mother–infant dyads for three reasons. First, because the two study periods were 3 yr apart, the females who produced infants in both study periods experienced changes in their age, parity, dominance rank, and the number of adult kin in the

Table 1: Subjects

Mother	Infant sex	Maternal rank	Maternal age	Maternal parity	Study period*	Age range (mo)
AC	M	19	7	1	II	1–7
AL	F	17	14	5	I	7–12
AL	F	20	17	8	II	1–7
BL	F	21	8	2	II	5–12
BT	F	3	16	8	I	1–3
BT	M	5	19	11	II	6–12
CD	M	19	8	3	I	10–12
CD	F	23	11	5	II	8–12
CT	F	7	7	1	II	4–12
HL	M	5	6	1	I	1–6
HL	F	8	9	3	II	1–5
HN	M	6	7	1	I	3–12
HN	F	9	10	3	II	9–12
JL	F	10	7	1	I	2–11
JN	F	22	10	3	II	1–8
LE	M	11	8	1	I	7–12
LE	F	14	11	3	II	8–12
LK	F	12	8	1	II	9–12
LX	M	4	8	1	II	3–12
MC	M	6	8	1	II	2–6
MR	M	15	12	4	I	1–11
MR	M	18	15	6	II	7–12
NI	M	15	8	2	II	1–6
NN	M	13	11	4	I	1–4
NT	M	17	14	7	II	5–12
RS	M	16	11	2	II	7–12
SH	M	7	15	6	I	1–8
SH	F	10	18	8	II	4–12
SL	F	1	7	1	II	4–11
SR	M	3	7	1	II	4–12
SS	F	8	8	2	I	1–10
SS	F	11	11	4	II	1–6
ST	F	1	18	8	I	1–8
SY	M	2	11	4	I	3–12
SY	F	2	14	6	II	7–12
WR	F	9	15	6	I	3–12
WR	M	13	18	8	II	1–2

*I = 1992–93; II = 1996–97.

group. Secondly, four of these five females had one male and one female infant, making it impossible to combine them in the analysis of the effects of infant sex. Thirdly, we replicated the analyses using individual mothers as the unit of analysis, and this had no substantive effect on the results. For the sake of consistency, then, we report results of the analyses by dyad throughout.

To assess the effects of infants' age on their attractiveness to other females, we computed the mean rate of interactions with mothers of infants aged 1–12 mo. For each female, we computed the hourly rate of approaches, grunts, and grooming received by focal females during each of the first 12 mo of their infants' lives. We also computed the hourly rate of handling that infants received while they were on or near their mothers during each of the first 12 mo of life. For each mother, we computed the correlation between the rate of interaction and infant age. We report the mean (and standard error) of the value of the correlation coefficients and their distribution.

To assess the effects of infant sex and maternal rank on rates of interaction, we combined data from the first 6 mo of life for each mother–infant dyad. We computed the hourly rate of interactions by dividing the number of interactions received during the first 6 mo by the number of hours observed during the first 6 mo. We used the Mann–Whitney U-test to determine whether infant sex influenced the rate of interaction over the first 6 mo. We computed Spearman correlations to assess the relationship between maternal rank and hourly rate of interactions over the first 6 mo of life.

To determine whether mothers were equally likely to interact with (or infants were equally likely to be handled by) higher and lower ranking females, we computed the number of interactions per available female in each category. We followed the same procedure to compute the average number of interactions with relatives and non-relatives. We used the Wilcoxon signed rank tests to assess the effects of relative rank and kinship on the average number of interactions per available female.

We initially analyzed data from the two studies separately, but found that the analyses produced virtually identical results. For simplicity, we present below only the combined results from the two study periods.

Results

Infant Age

In our study group, females' interest in mothers and their infants was most pronounced when infants were very young. Mothers were approached most often and received the most grunts from other adult females when their infants were 1–2 mo old. This is also when infants were handled most often. Rates of approaches, grunts, grooming, and infant handling all declined as infants matured (Fig. 1). These patterns were quite consistent across mothers (Table 2). Mothers of 1-mo-old infants were approached about 10 times per hour and were grunted to 19 times per hour, while mothers of 12-mo-old infants were approached twice per hour and were grunted to only once per hour. The rate of grooming mothers received dropped by a third over the first year of their infants' life. Rates of infant handling declined from nearly seven acts per hour in the first month of life to 0.2 acts per hour in month 12.

Characteristics of Infants and their Mothers

If infant handling is an early form of reproductive competition, then females will handle female infants at higher rates than male infants. This sex bias in infant handling is expected because density-dependent mortality generates competition among females for reproductive opportunities. In species with matrilocal social organization such as baboons, females become permanent group members, while males disperse when they reach adulthood. Thus, females represent a more enduring source of competition than males, and young females are expected to be harassed at higher rates than males (Silk 1983). The handling-as-harassment hypothesis also predicts that females will selectively handle (and thereby harass) the offspring of lower ranking females and will handle unrelated infants more often than they handle related infants.

The natal attraction hypothesis suggests that females should be equally attracted to all infants, but social factors may constrain their *access* to certain infants. Thus, infants are expected to be handled more often by females that outrank their mothers than by females that are subordinate to their mothers. High rates of association among maternal kin may also lead to high rates of handling among relatives.

Here, we examine the effects of infant sex, maternal age and parity, maternal rank, and maternal kinship on the hourly rate of interactions with mothers and their infants during the first 6 mo of life. We restrict these analyses to interactions over the first 6 mo because this is the period when infants were most attractive to other females. Twenty-seven mother–infant dyads, which were observed when infants were between 1 and 6 mo old, are included in these analyses. We assume that the rate of approaches, vocalizations, and grooming directed to mothers provides an index of the *attractiveness* of the mother and her infant, while rates of handling provide a measure of the infants' *accessability* to other females.

Infant sex had no consistent effect on the mother–infant dyad's attractiveness or the infant's accessability. Mothers of male and female infants were approached (Mann–Whitney $U = 11.0$, $p = 0.310$), grunted to ($U = 15.0$, $p = 0.699$), and groomed ($U = 10.5$, $p = 0.240$) at the same rates. In addition, male and female infants were handled at the same rates during the first 6 mo of life ($U = 32.0$, $p = 0.800$). Maternal age and parity are highly correlated in our sample ($r = 0.968$, $p < 0.001$; $n = 27$), but neither variable has any influence on the rate of approaches, grunts, or grooming received by mothers, or the rate of handling received by their infants ($p > 0.150$ for all correlations).

Maternal dominance rank had little effect on the attractiveness of mother–infant dyads, but it did affect the accessability of their infants. Mothers' dominance rank was uncorrelated with the rate of approaches ($r = 0.173$; $p = 0.217$, $n = 27$), grunts ($r = 0.245$, $p = 0.217$, $n = 27$), or grooming received ($r = -0.119$, $p = 0.553$, $n = 27$), but low ranking females' infants were handled at higher rates than high ranking females' infants ($r = 0.452$, $p = 0.018$, $n = 27$).

(a) Approaches received

(b) Grunts received
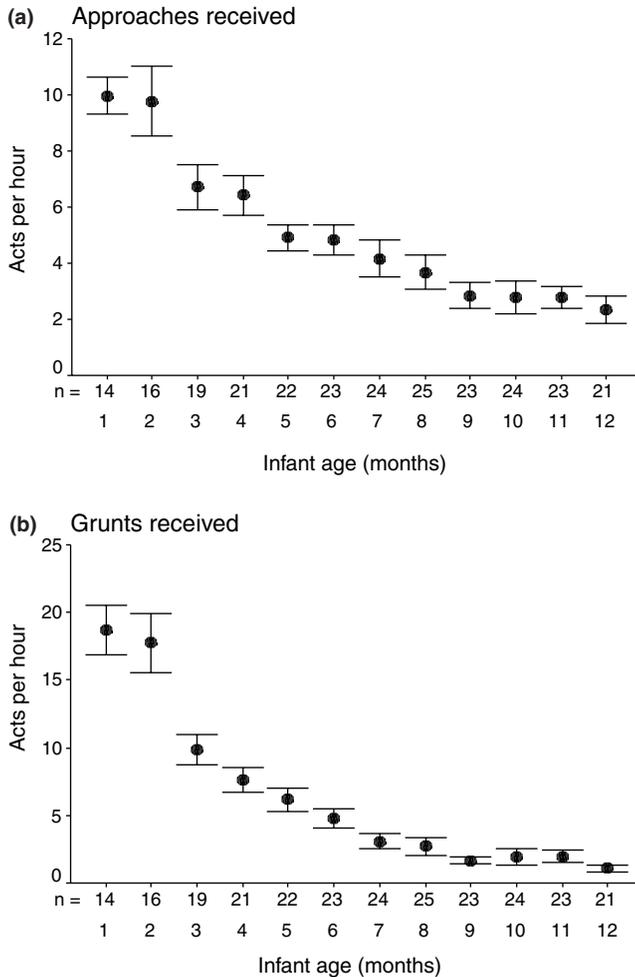
Fig. 1: These figures show the rate of approaches, vocalizations, and grooming interactions received by mothers and the rate of handling directed toward their infants at different ages. Means and standard errors are shown; the number of mother–infant pairs observed at each age is shown below the x-axis

Most infant handling is directed down the hierarchy. Infants were handled by females who outranked their mothers 75% of the time. Infants were handled more often on average by females that outranked their mothers than by females that were lower ranking than their mothers. This pattern was very consistent across mother–infant pairs (Wilcoxon signed rank tests: $Z = -4.265$, $p < 0.001$; Fig. 2). However, this does not entirely account for the effects of maternal rank on infant handling. The offspring of low ranking females were handled more often on average than the offspring of higher ranking females by both higher ranking females ($r = -0.831$, $p < 0.001$, $n = 26$) and by lower ranking females ($r = -0.534$, $p < 0.006$; $n = 25$).

(c) Grooming received

(d) Handling received
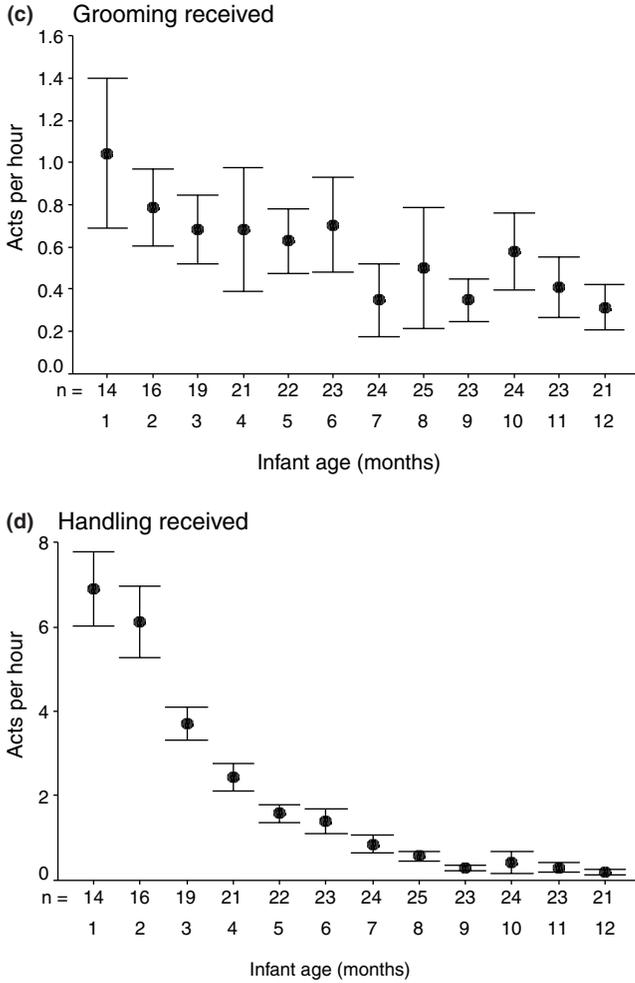
Fig. 1: Continued

Maternal kinship enhanced both the attractiveness of mothers and their infants and the accessability of their infants. On average, mothers received more approaches and grunts from related adult females than from unrelated females (approach: $Z = -2.938$, $p = 0.003$; grunt: $Z = -2.841$, $p = 0.004$), and they were groomed by related females much more often on average than they were groomed by unrelated females ($Z = -3.718$, $p < 0.001$). Infants were also handled by related females much more often than by unrelated females ($Z = -2.875$, $p = 0.004$; Fig. 2).

Both relative rank and kinship appear to influence females' access to infants. However, these categories overlap. To tease apart the effects of dominance rank and kinship on infant handling, we compared the average number of handling

Table 2: Summary of correlations between infant age and rate of interactions

Type of interaction	Correlation coefficient (mean ± SE)	Negative correlations		Positive correlations		No data
		p < 0.05	p > 0.05	p > 0.05	p < 0.05	
Approaches to mother	−0.5541 ± 0.0574	10	11	1	0	0
Grunts to mother	−0.6761 ± 0.0443	10	12	0	0	0
Grooming to mother	−0.2743 ± 0.0652	2	17	2	0	1
Handling to infant	−0.7091 ± 0.0562	13	8	1	0	0
Handling by mother	−0.4506 ± 0.0455	5	17	0	0	0
Handling to mother × Handling by mother	0.4076 ± 0.0674	6	12	4	0	0

For each of the 22 females who were observed with infants < 6 mo old, we computed the relationship between the monthly rate of interactions and infant age. The mean and standard error of the correlation coefficients is given along with the distribution of significantly negative (p < 0.05), non-significantly negative, non-significantly positive, and significantly positive correlation coefficients. Sample sizes for individual correlations ranged from 4 to 17. Ten females were observed with two infants, and 12 females were observed with one infant.
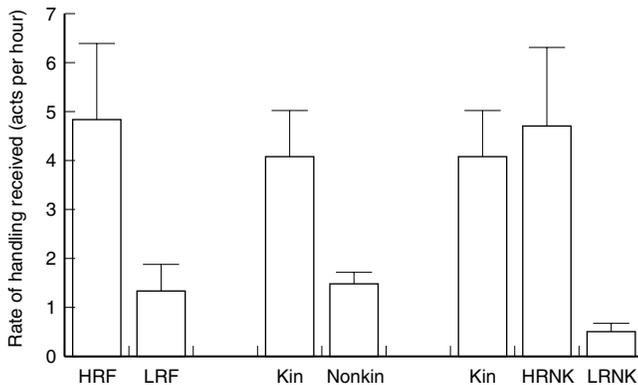
Fig. 2: Infants were significantly more likely to be handled by females that outranked their mothers than by females that their mothers outranked, and were also more likely to be handled by related females than unrelated females. Differences in the amount of handling received from higher-ranking and lower-ranking kin were not consistent among females, nor were differences in the average amount of handling received from kin and higher-ranking non-kin. Infants were handled by both kin and higher-ranking non-kin more than by lower ranking non-kin

interactions received from higher ranking kin, lower ranking kin, higher ranking non-kin, and lower ranking non-kin. There were no consistent differences in the average number of handling interactions received from higher- and lower-ranking kin ($Z = -1.355$, $p = 0.176$), so we combined these categories for comparison with higher- and lower-ranking non-kin. Infants were handled with equal frequency by kin and higher ranking non-kin ($Z = -0.523$, $p = 0.601$), but were handled more often by kin than by lower ranking non-kin ($Z = -3.197$, $p < 0.001$; Fig. 2).

Mothers' Interest in other Females' Infants

Mothers handled other females' infants most when they had young infants of their own (Fig. 3), and their interest in other females' infants declined as their own infants matured. During the months in which their infants were handled at the highest rates mothers also handled other females' infants at high rates (Table 2). Thus, mothers were most attracted to other females' infants when their own infants were most attractive to other females.

These results might simply reflect the fact that mothers of young infants spent much of their time together, and therefore had many opportunities to interact with young infants. We suspect that this was not the case because females did not often handle each others' infants during the same encounter. Fig. 4 shows that when one mother of a young infant approached another mother of a young infant, the approaching mother was usually the only one who engaged in infant handling. Moreover, the fact that handling is generally directed down the
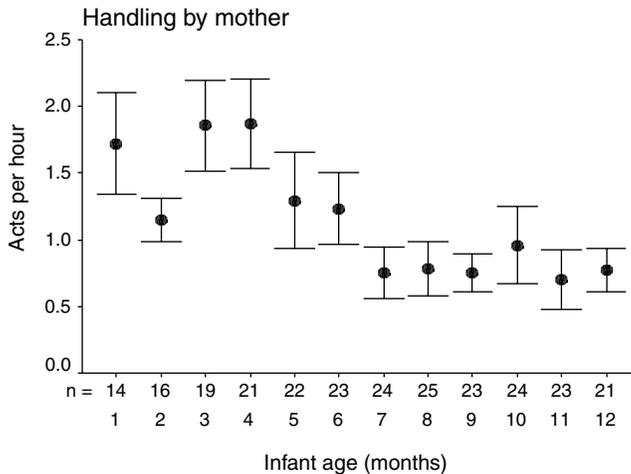

Fig. 3: The rate of infant handling by mothers is plotted against the age of their own infants. Mothers were more active in handling other females' infants when their own infants were young. Mean values and standard errors are shown; numbers of mother–infant pairs observed at each age are shown below the x-axis
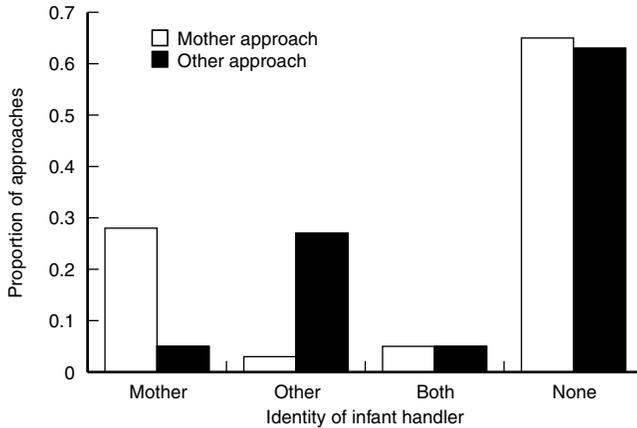
Fig. 4: The white bars show the proportion of approaches by focal females who had young (1–6 mo-old) infants to other mothers of young infants that were followed by handling by the focal mother, the other mother, both mothers, or neither mother. The dark bars show the proportion of approaches received by focal females who had young infants from other females with young infants that were followed by handling by the focal female, the other mother, both mothers, or neither. In both cases, the pattern is the same. The approaching mother was more likely to handle the other mothers' infant than vice versa; and handling was rarely reciprocated in a single encounter

hierarchy largely eliminates the possibility that females handled one anothers' infants. Mothers had very limited access to the infants of the females who handled their own infants.

Grunts Preceding Infant Handling

Grunts preceded infant handling 92% of the time. The decision tree in Fig. 5 depicts the sequence of events that preceded handling. About half of the approaches to mothers of young infants (55%) were accompanied by grunts from the approaching female. When approaching females grunted, they proceeded to handle the infant 57% of the time. When females did not grunt as they approached, they subsequently handled infants only 6% of the time. Thus, grunting greatly increased the likelihood that handling would occur. This pattern characterized 25 of the 27 mothers in our sample ($Z = -4.469$, $p < 0.001$).

Discussion

Adult females in Moremi were strongly attracted to newborn infants, and they made persistent attempts to smell, nuzzle, touch, and inspect them. Females' interest in infants was a function of the age of the infant and their own reproductive status. Mothers of young infants were approached by other adult females on average once every 6 min, and other females attempted to handle their infants approximately once every 9 min. By the time infants were a year old, their
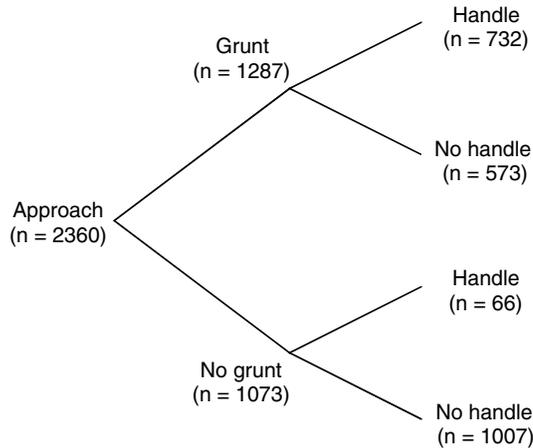
Fig. 5: This decision tree depicts the sequence of events that followed approaches to mothers of young (1–6 mo-old) infants. In some cases females grunted to mothers after they approached. Grunts led to infant handling about 57% of the time. Approaches that were not followed by grunts led to infant handling only 6% of the time

mothers were being approached only once every 30 min and infants were being handled only once every 5 h. Females were more strongly attracted to other females' infants when they had young infants of their own, and their interest in other females' infants declined as their own infants matured. While females seemed to be uniformly attracted to all infants, their *access* to infants was related to maternal rank and kinship. Females were more likely to handle infants if they outranked the mother or they were related to the mother. One consequence of this fact is that the offspring of the lowest ranking females were handled approximately six times as often as the offspring of the highest ranking females.

These data fit only one of the predictions derived from the handling-as-harassment hypothesis—that females will selectively handle offspring of lower ranking females. In other populations of macaques, females also handle infants of lower ranking females more often than they handle those of higher ranking females (Paul & Kuester 1996; Silk 1999). Although high rates of handling of lower ranking females' infants might be construed as a form of harassment, females in Moremi nearly always grunted before they attempted to handle infants. Female macaques also vocalize before they handle infants (Bauers 1993; Silk et al. 2000). Although it is obviously impossible to infer the motivational intent of grunting females, in other contexts grunts are a reliable predictive signal that non-aggressive behavior will follow and are effective in reconciling conflicts with former opponents (Cheney et al. 1995; Silk et al. 1996; Cheney & Seyfarth 1997). Hence, the use of grunts before infant handling suggests that these interactions are not a form of deliberate harassment.

The handling-as-harassment hypothesis fits certain features of infant handling observed in other populations of baboons and macaques. First,

mothers are sometimes anxious or distressed when other females attempt to handle their infants, and usually hold firmly to their infants when others attempt to pull them away. Secondly, infants are sometimes pulled roughly (Altmann 1980; Silk 1980, 1999; Maestripieri 1994a,b; Paul & Kuester 1996). However, these instances are generally uncommon, even in groups in which severe aggression to infants is observed in other contexts (e.g. Silk 1999). Macaques and baboons maintain rigid dominance hierarchies, and very rarely challenge higher ranking females, but females are nevertheless sometimes able to handle the infants of higher ranking females (Altmann 1980; Silk 1980, 1999; Wasser 1983; Maestripieri 1994b; Bentley-Condit 1996; Paul & Kuester 1996). In some groups, rates of infant handling are higher among kin than non-kin (Paul & Kuester 1996; Silk 1999), a pattern we would not expect to observe if handling is a form of harassment.

The natal attraction hypothesis provides an explanation for primate females' particular attraction to very young infants (Paul 1999), a pattern that was clearly evident in our data as well. As very young infants are completely dependent on their mothers for nourishment, transport, and protection, selection may act to make females particularly responsive to newborns.

The natal attraction hypothesis may also explain why we found that mothers' interest in other females' infants mirrored in time other females' interest in their own infants. As baboons do not breed seasonally, natal attraction by mothers is not due to synchronous changes in the availability of young infants. Moreover, rates of handling by mothers are not an artifact of high rates of association with other mothers of young infants. As handling is typically directed down the hierarchy, mothers were usually unable to handle the infants of females who handled their own infants.

Natal attraction may be mediated by the same proximate motivational processes that underlie appropriate maternal responsiveness. In mammalian females, responsiveness to infants is linked to endocrine changes during pregnancy and lactation (Maestripieri 2001). In macaques, estrogen treatment increases females' responsiveness to infants (Maestripieri & Zehr 1998), and lactating macaque females handle other females' infants more than non-lactating females (Maestripieri & Wallen 1995; Paul & Kuester 1996).

The natal attraction hypothesis cannot explain why mothers are so reluctant to allow their infants to be handled or why females have such limited access to the offspring of higher ranking females. If females' attraction to infants is a product of selection for good maternal care, we would expect most handling to be gentle (rather than rough) and mothers to tolerate efforts to handle their infants. In baboons, infant handling is generally outwardly gentle (Altmann 1980; pers. obs.), but mothers are anxious about these interactions nonetheless. Mothers' reluctance to allow their infants to be handled may simply reflect the stresses or anxieties associated with close proximity to higher-ranking females, regardless of the manner in which their infants are handled. Such reluctance might also reflect the dangers that infants face when they are out of contact with their mothers. Infant baboons in this population are highly vulnerable to

infanticidal attacks by adult males (Palombit et al. 2000) and rates of predation are high (Busse 1980), so natural selection may have favored high levels of maternal protectiveness.

It is possible that natal attraction may have evolved as a product of selection for appropriate maternal care, but has also been favored by natural selection because it causes distress to mothers and their infants. Clearly, we cannot rule out this possibility based on the available data. However, one crucial distinction here would seem to be that the harassment hypothesis predicts that females will *only* try to handle infants if it generates stress and anxiety in mothers and their infants, while the natal attraction hypothesis predicts that females will try to handle infants *regardless* of the impact on the mother and infant. There is some evidence that primate females are strongly attracted to infants even when it does not produce stressful responses in mothers. For example, natal attraction is coupled with relaxed maternal responses to infant handling in a number of primate species, including capuchins (Manson 1999), howlers (Clarke et al. 1998), and langurs (Hrdy 1976; McKenna 1979; Stanford 1992).

According to the natal attraction hypothesis, females have a general interest in all newborn infants which stimulates their attempts to handle other females' infants and to provide appropriate care for their own infants. This raises an important question: Why has not natural selection designed mothers to be more selective in their attraction to infants? The answer may be related to the kinds of kin recognition mechanisms that operate in primates. In general, primates do not seem to recognize their own infants at birth, and require some time to learn their infant's identity (e.g. Jensen 1965; Klopfer 1970; reviewed in Rendall, in press). This exposure constraint might favor mothers who are strongly motivated to interact with infants, thereby learning their own infant's identity and how to distinguish it from others (Mann & Smuts 1998; Maestripieri 2001). A general attraction to very young infants might thus result from strong positive selection on maternal responsiveness combined with proximate mechanistic constraints that preclude immediate selective discrimination of one's own infant.

At least one additional aspect of infant handling interactions remains unexplained. Although females occasionally interact with infants when they are on their own, they generally seem most interested in infants when they are on their mothers. This might mean that infant handling is primarily directed at mothers, not their infants, and support the handling-as-harassment hypothesis. It may also reflect the fact that infants are seldom out of contact with their mothers during the months when they are most attractive to other females. It is also possible that females may be attracted to infants when they are with their mothers because they use association patterns to learn the identity of infants and their relationship to other group females. If females are unsure of the identity of very young infants when they are off their mothers, they may be reluctant to risk provoking higher ranking females by handling their infants. More systematic information about females' interactions with infants on and off their mothers will be needed to resolve this issue.

Overall, our data provide only limited support for the handling-as-harassment hypothesis, and better support for the natal attraction hypothesis. The natal attraction hypothesis may explain why primate females are so strongly attracted to newborn infants generally, but it does not account for the great diversity in the form of alloparental interactions across the primate order (Mitani & Watts 1997; Paul 1999). Strong natal attraction may provide a powerful stimulus that motivates females to interact with infants. However, the selective factors that influence the kinds of interactions that females have with infants are likely to be different than the selective factors that shape females' general attraction to infants.

Acknowledgements

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