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Costs and benefits of allomothering in wild capped langurs (*Presbytis pileata*)

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Summary. Data from a 15-month field study of the capped langur monkey, *Presbytis pileata*, in Bangladesh indicate that allomothering behavior is restricted to particular female-infant dyads. Primary allomothers were all parous adult females; nulliparous females rarely allomothered, Newborn infants were transferred from the mother to other females within a short time of birth, as reported for some other colobine species, but over the first 3 months of life each neonate's contact with nonmothers was largely restricted to a single allomother in each of five study groups. Capped langur mothers with newborn infants spent more time feeding when the infant was being allomothered than when it was in the mother's care. The model of allomothering as a selfish behavior by nulliparous or pregnant females used to enhance maternal skills at the expense of mothers is not supported by this study. Rather, allomothering may have adaptive significance as altruistic behavior among group females, in that it enables lactating females to increase feeding time. Capped langur allomothering is best interpreted as a low-cost behavior that can benefit recipients that may or may not be related.

Introduction

The relationship between female nonhuman primates and newborn infants varies widely within the primate order. Hrdy referred to this spectrum of mother-infant relations as the "nurture – abuse continuum" (Hrdy 1976). Small (1990) recently discussed the spectrum of female-infant relationships for the genus *Macaca*, noting that some species exhibit permissive mothering with infant transfer while in other species the infant rarely has contact with other females. The most intensive affiliative relationships between infants and non-mother females is found in the Old World monkey subfamily Colobinae, in which newborns may be passed among the females of the social group within minutes of birth. Infant transfer or allomothering has been seen as a major social adaptation characterizing this group; the adaptive significance of allomothering behavior has been hypothesized as a means to enable females to maximize foraging efficiency (Jones 1980; Vogel 1984), as a way to increase the likelihood of adoption in the event of mother loss (McKenna 1981), as a means of insuring proper socialization of infants (McKenna 1981), and as practice mothering behavior by immature females (Lancaster 1971; Hrdy 1976; Quiatt 1979) that may enhance reproductive success in adulthood. The entire suite of behavioral and anatomical adaptations of colobines to folivory have even been posited as related to allomothering (McKenna 1979).

Some authors have observed that excessive or incompetent allomothering, particularly by immature females, is detrimental to the survival of an infant and may therefore be costly to the mother's reproductive success. Following Trivers' (1972) work on parental investment, Hrdy (1976) hypothesized that allomothering is a selfish act that prepares a young female to be be a better mother, but is potentially costly to the infant and its mother. The eagerness of pregnant and nulliparous females of some species to take infants, and the reluctance of the mother to surrender their infants to allomothers, is cited as evidence for the selfish playmothering benefits to young females (Lancaster 1971 for vervet monkeys; Hrdy 1977 for Hanuman langurs; Kurland 1977 for Japanese macaques). Kurland (1977) showed that among Japanese macaques, infants were alloparented mainly by unrelated, nulliparous females. Benefits to allomothers other than maternal experience have been suggested to include the potential to establish a closer relationship with the mother of the infant, particularly in species with strong female dominance hierarchies (Hrdy 1977).

Most assertions about the importance of allomothering among colobines are, however, based on studies of one particularly well-studied species, the Hanuman lan-

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Offprint requests to the present address gur, *Presbytis entellus*, in which allomothering is present and intensive (Hrdy 1977; Dolhinow and Murphy 1982). In this paper I present data on allomothering behavior in the capped langur, *Presbytis pileata*. The capped langur is found in eastern Bangladesh, western Burma, and parts of northeastern India (Green 1981). Green (1981) and Islam and Hussein (1982) have conducted preliminary field studies on the species, but no longterm data existed before the present study was undertaken.

I tested two predictions by Hrdy (1976) about allomothering: first, if allomothering is a selfish act performed mainly against the wishes of the mother and infant in order to enhance the allomother's maternal skills, then allomothers should be nulliparous females seeking mothering practice. Alternatively, if allomothers take infants to establish closer affiliative ties to the a particular infant's mother, then the allomother and mother should show greater levels of social affiliation after the birth than they had before the birth of the infant.

Methods

The data reported here come from a 15-month study of the behavior and ecology of a population of wild capped langurs living in Madhupur National Park in north-central Bangladesh. Madhupur is a moist-deciduous forest (Puri 1960), with a highly seasonal climate characterized by a monsoon during which 85% of the annual 2200 mm of rain falls. The rainy season lasts from May to October, and from November through April a dry season occurs during which most trees are bare of foliage. Details of the ecology and topography of the study site can be found in Stanford 1991. The study consisted of approximately 2000 contact h, and approximately 1400 h of 10-min interval scan and focal animal observation (Altmann 1974) were collected using a behavior repertoire adapted for this species from Dolhinow (1978) for Hanuman langurs. Data collection was randomized as to time of day and sequence of animal scanned.

Madhupur forest is seasonally quite open with a low canopy (average 15 m); observation conditions were excellent, and the animals were habituated to my presence and approachable to within 3 m for males and 5 m for females and immatures. Capped langurs are largely arboreal and when on the ground are preyed upon by jackals (*Canis aureus*; Stanford 1989). Five study groups were observed regularly; 69% of the observation hours come from one group. these five groups occupied home ranges that overlapped broadly. The number of immature animals, including infants, changed throughout the study as the result of births, deaths, and maturation between age classes. Allomothering data involving 12 of 14 infants are presented here; observations of the 2 other infants were too few to be included for analysis. The population dynamics of *P. pileata* at Madhupur are discussed elsewhere (Stanford 1991). Average size of Madhupur capped langur groups was 8.5 animals (including a mean of 4 adult females), and all bisexual groups were one-male. All adult males and some adult females transferred between one-male groups. All adult animals were individually identified by natural features, and infants were distinguished by size differences, facilitated by association patterns with particular animals in each group. Because capped langur births at Madhupur were clumped during 4.5 months of the year, it was possible to age immature animals with fair accuracy based on size comparisons. Geneologies of individual animals were unknown. In this study the terms infant transfer and allomothering are used interchangeably.

Infant transfers were recorded on the behavior checklist in the course of scan sampling along with the identities of both infant and mother. In this paper the terms "neonate" and "newborn" refer to an infant less than 3 months old. An allomother is any female other than the mother that actively places and keeps a young infant in her possession or her immediate proximity (≤ 1 m). A "take infant" was scored whenever a female of any age class removed an infant from the possession of another animal or took an infant that was alone. At 10-min intervals the location of a neonate was recorded as either in the possession of the mother, an allomother, or engaged in another activity. "Attempt to take infant" was scored for unsuccessful attempts to take an infant from its mother, as a way to show instances in which mothers resist attempts by allomothers to take infants. Capped langurs were considered infants until 15 months of age, but allomothering behavior nearly ceased after the first 3 months of life, so in practice all infants involved in infant transfers were neonates from birth to 3 months old and possessed the natal orange coat color. From birth to approximately 3 months old, a capped langur infant is apricot orange in color, darkening quickly after that time to the adult pattern of a gray dorsum and orange ventral surfaces.

An aspect of the study compared the dominance status of mothers with that of primary allomothers. Female dominance was measured on the basis of supplantations over food and the directionality of threat behavior. In 75000 individual behavior records, however, only 30 such female-female dominance interactions were observed. Dominance is apparently either of little importance to female capped langurs, or the mode by which it is asserted is too subtle to be distinguished.

All data were analyzed using conventional nonparametric statistical tests; measures of significance are taken at the 0.95 probability level, and all probability values are two-tailed.

Results

During the study period, 14 infants (5 males and 9 females) were born into the five study groups (Table 1). All infants at Madhupur were born from 29 December through 15 May (median birthdate = 3 March), a birth distribution that is significantly clumped (Kolmogorov-Smirnov test, $df = 11$, $P < 0.01$).

Females of all ages, including infants born the previous year, showed some interest in neonates. The frequency of female interaction with neonates varied greatly (Fig. 1), such that some neonates had intensive contact

Table 1. Infants born in the study site during the intensive study period, December 1987–December 1988

Infant's name/ Mother's name	Sex	Group	Birthdate
NN/HT	F	J	3 March 1988
IV/CE	F	J	29 April 1988
LS/EV	M	J	15 May 1988 ± 2 days
AA/HF	F	HF	21 March 1988 ± 3 days
AB/M13	F	N	29 December 1987 ± 4 days
AC/M10	M	N	7 February 1988
AD/M11	F	N	2 March 1988 ± 1 day
AG/M8	M	N	21 January 1988 ± 6 days
AE/M9	F	T	12 February 1988 ± 5 days
AF/M4	M	T	7 May 1988 ± 1 day
AP/MA	F	CT	22 April 1988 ± 3 days
AH/M3 (HF group)	F		26 March 1988 ± 5 days
AJ/no name	M		8 March 1988 ± 1 day
AK/no name	F		30 March 1988 ± 2 days

Table 2. Infant time spent with allomothers in first month of life

Infant	% time spent with allomother	% time spent with primary allomother
AP	38.6	37.33 with female M2
NN	60.0	57.75 with female EV
IV	3.5	2.92 with female BT
LS	3.3	2.80 with female BT
AB	55.0	52.50 with female M3
AC	43.9	36.3 with female M4
AA	11.1	11.1 with female M6
AD	8.00	8.00 with female M9
AE	33.3	33.3 with female M11
AF	28.6	24.5 with female M10
AG	51.4	41.0 with female M12
AH	61.0	59.9 with female M13
mean = 33.14% SD ± 22.1		mean = 30.62% SD ± 20.8

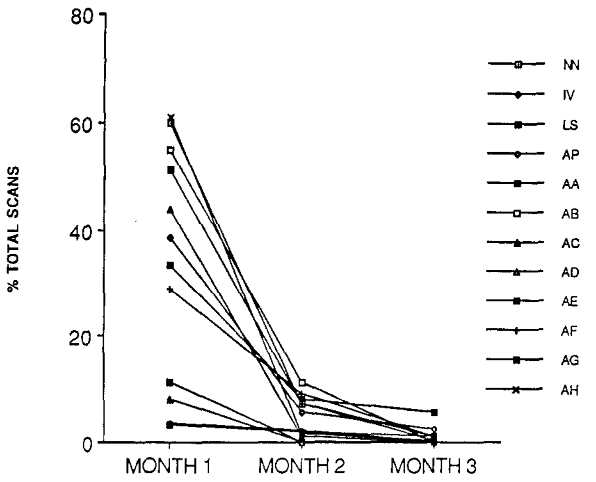

Fig. 1. Mean percentage time with all allomothers during first 3 months of life

with an allomother during the first weeks of life while others had little contact with animals other than the mother. Neonates spent an average of one-third of their daylight time (mean = 33.14%, SD ± 22.10, $N = 12$ infants) during the first month of life in the care of allomothers. After 1 month of age, the percentage of time spent with an allomother dropped markedly. No male was ever seen to interact with a newborn infant.

In contrast to the allomothering pattern in Hanuman langurs, in which the infant is typically passed among most of the group females, capped langur allomothering was characterized by a particular adult female in each group acting as a primary caregiver, while other females in the group interacted little with the infant. In each of the five study groups, 3–5 females were available as potential allomothers, but more than 90% of a newborn infant's time with an allomother was spent with the same female (92.44%, SD ± 20.82, $N = 12$ infants). This pattern was consistent among the five study groups during the infants' first month of life (Table 2). In each of the five groups, the primary allomother was an adult, multiparous female. Parity was determined either by the presence of a dependent offspring or by the presence of visible nipples. There was at least 1 nulliparous juvenile or subadult female in each of the study groups (a total of 7 nulliparous females at the conclusion of the study), but none acted as a primary allomother. Only 1 such female (BT) acted as primary allomother to more than 1 infant (IV and LS in J group), and no infant had multiple allomothers. Approximately one-half (5 of 11) of these parous allomothers had older infants of their own, born the previous birth season, but none had neonates of their own at the same time that they acted as primary allomothers. The total number of adult parous females in the five study groups exceeded the number of neonates in 1987–1988, thus there were 21 adult females that did not act as allomothers to any neonate.

Allomothers carried infants in the ventral cling position or sat cradling the infant to their abdomens. After a period of allomothering, infants were either retrieved by the mother, again without resistance from the allomother, or deposited on a substrate by the allomother from which they were retrieved within a short time by the mother. It could not be determined whether selective allomothering was due to choice of a particular infant by an allomother, or to choice by the mother of one of several females that displayed some initial interest in the neonate. The infant transfer was typically carried out without maternal resistance, however, suggesting that mothers are not very selective in their choice of allomothers. Because of the lack of genealogical data on this population, no kin relationship between group females could be established. At the age of 4 weeks, infant capped langurs began to spend increasing amounts of time away from the mother and the allomother (Stanford 1991), a somewhat shorter time at this stage than reported for Hanuman langurs (about 5 weeks of age, Dolhinow and Murphy 1982).

There was no significant difference between male and female infants in the proportion of time spent with an allomother (Mann-Whitney $U = 3$, $P > 0.10$). Because capped langur females spent little time overall (generally less than 4% of active time) in close proximity (≤ 1 m), making distinctions in the relative closeness of spatial affiliative patterns is problematic. For instance, BT was the primary allomother for CE's newborn (IV), but the amount of time spent in proximity or contact by these two females was not significantly greater than for any other female in J group. There was no significant positive correlation at the time of birth between the mother's closest spatial associate in a group and the future allomother of her infant (Rank correlation; $r_s = 0.231$, $P = 0.55$). The allomother also did not spend significantly more time in proximity to the mother of the infant whom she was allomothering ($r_s = 0.083$, $P = 0.09$). It thus appeared that the choice of allomother did not follow preparturition intragroup spatial relationships, no did an allomother associate more with the mother as a result of their relationship through the infant they shared.

During the first month after giving birth, capped langur mothers spent more time feeding when the neonate was in the care of an allomother (Fig. 2; 32.00%, SD ±

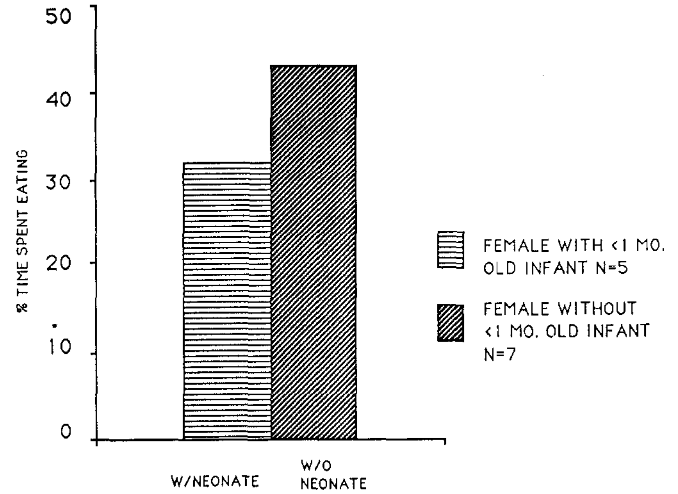

Fig. 2. Mean percentage time spent eating by mothers with and without their neonates. $t = -2.23$, $P = 0.11$, $N = 12$ infants

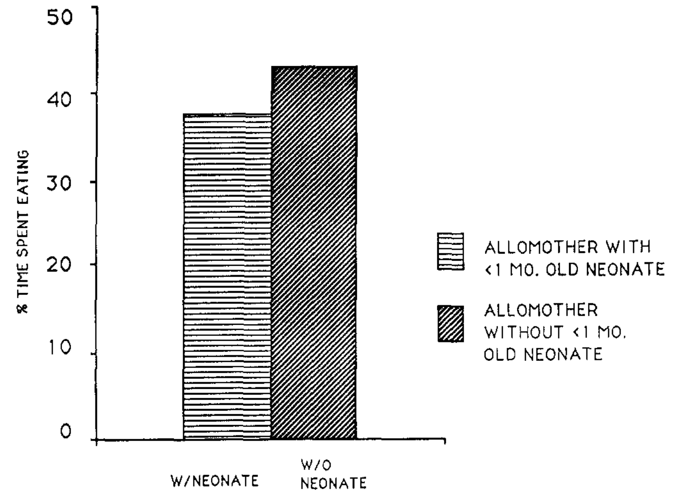

Fig. 3. Mean percentage time spent eating by allomothers with and without neonates. $t = -1.03$, $P = 0.045$, $N = 12$ allomothers

4.17 with neonate; 43.33%, SD ± 10.18 without neonate; paired t-value $= -2.23$, $P = 0.11$). A take infant was no more likely to occur when a mother was feeding than when the mother was engaged in another activity (paired t-value $= 1.05$, $P = 0.66$). Thus, when an allomother took an infant, the mother was more likely to commence feeding at that point. Upon entering a food tree with a clinging infant, a mother was approached by the allomother and gave up the infant to the other female without marked resistance. The cohesiveness of capped langur groups created a tendency for all group females to engage in the same activity in the same or adjacent trees most of the time. The activity of the allomother during the mother's freedom from infant care showed a significant positive correlation with the activity of the mother ($r_s = 0.545$, $P < 0.001$); that is, allomothers and mothers tended to both feed, rest or travel simultaneously. In spite of the strong tendency for all females in the group to engage in the same activity at the same time, allomothers spent slightly less time feeding when infants were in their care than when they were unencumbered (Fig. 3; 42.02%, SD ± 9.63 without neonate, 38.2%, SD ± 5.85 with neonate; paired t-value $= -1.03$, $P = 0.045$). Thus mothers received the benefit of added feeding time while allomothers incurred a slight cost in reduced feeding time when a neonate was in the care of an allomother.

Discussion

Allomothering behavior occurs in a variety of Old World monkey species, and in at least some species the pattern is equally permissive as it is in some colobines. Kinship may influence the likelihood of allomothering (Hrdy 1976; Riemann 1982). Kurland (1977), for example, reported Japanese macaque mothers to be more likely to retrieve infants and more likely to behave aggressively toward allomothers when the degree of relatedness between them was low. Without genealogical information little can be said about the possible influence of kinship on patterns of allomothering in capped langurs. It has been observed that female dominance relationships in the colobines are generally weaker than in cercopithecines (McKenna 1979; though there may be exceptions, *Presbytis entellus*, Hrdy and Hrdy 1976), and this weaker dominance hierarchy is believed to facilitate the evolution of infant-sharing behavior. Since intragroup dominance relationships among female capped langurs are also weak, the choice of allomother is probably not determined by dominance rank of either mother or allomother, nor can it be determined from these data whether the mother chooses the primary allomother of her infant.

Are capped langur allomothers behaving altruistically? Whitten (1982) found that vervet monkey (*Cercopithecus aethiops*) mothers obtained more food, measured in mouthfuls, when unencumbered by infants than they did while carrying infants. Under such circumstances, allomaternal caregiving should be expected to enhance a lactating female's nutritional status. According to Lancaster (1971), the opportunities for an allomother to take an infant should be expected to depend more on maternal permission than on genetic relatedness between the allomother and the mother. Capped langurs should thus not give their infants to incompetent females, an act that might prove costly to the mother's reproductive success. There was no evidence in *Presbytis pileata* that mothers resisted infant transfer by immature of nulliparous adult females, but these classes of females showed little interest in neonates. They did, however, allow parous adults to take them. It is likely, therefore, that parous females are more likely to allomother because these females gain something from the act of allomothering. Since all allomothers in this study were parous, it is unlikely that they were gaining needed maternal skills.

Allomaternal behavior in capped langurs is best viewed as cooperative alliances among group females, not necessarily close kin, in which multiparous adult females provide infant care at a slight cost to themselves, but with a relatively larger benefit to the recipient. Capped langur mothers rarely attempted to retrieve infants from allomothers, and the relationship between mothers and allomothers lacked most of the resistance and occasional aggression reported for Hanuman langurs (Hrdy 1977; Sommer 1989). The willingness of mothers to allow other adult parous females to serve as allomothers and the increased feeding time obtained by unencumbered mothers supports the view that the benefit in this relationship extends to the mother as much as it does to the allomother. The apparently low cost of allomothering – a slight reduction in feeding time – may have enhanced the likelihood of this trait spreading among individuals in the population once it arose. It might be expected that, since some female group members may be immigrants to the group, a network of reciprocal infant care would be used by new group members to establish bonds with older resident females.

In a wide range of vertebrate species, females strongly influence the form of the social system (Emlen and Oring 1977). Wrangham (1980) and van Schaik (1989) have stressed the importance of female socioecology, and in particular the reliance of related females on cooperative use of a resource base, in driving the evolution of primate social systems. That female capped langurs showed a tendency to feed more when their infants were being allomothered offers support for hypotheses by Jones (1980) and Vogel (1984) that the advantage of allomothering is that it allows the mother to enhance her nutritional status during early lactation by allowing her to feed and travel unencumbered by an infant. The adaptive significance of allomothering in at least some nonhuman primates thus may lie in a reciprocal altruistic relationship between the adult females of a group. Such intragroup cooperative behavior would add an additional benefit of the female-female bonding that is now seen as the most important element of some primate species' social systems. In a species characterized by a core of related females, the mechanism by which reciprocal infant care-giving could evolve is easily posited, in that females can expect to have ongoing relationships with a network of kin over a period of many years. Short-term costs incurred by an allomother due to lost feeding time would be compensated for by the expectation that when similarly encumbered with her own infant, the mother that is temporarily relieved of her mothering costs would later return the benefit. That allomothering to enhance social bonds with mothers was not observed among capped langur allomothers may indicate that such bonds are not important in this species, or simply may be because there were no immigrants among the sample of allomothers in this study.

Capped langur infants interacted largely with the mother and with one other adult female in the social group. This pattern of alloparental behavior is apparently unique among catarrhine primates and points to the important observation that allomothering can be a very different phenomenon in different species. The red colobus (*Procolobus badius*) and olive colobus (*Procolobus verus*), for instance, do not allomother at all (Struhsaker 1975; Oates, personal communication), nor do some of the Asian colobines (*Presbytis melalophos*; Curtin 1976). At the same time, non-colobines exhibit varying degrees of alloparent-infant relations (Chism 1978 for *Erythrocebus patas*; Lee 1983 for *Cercopithecus aethiops*; Nishida 1983 for *Pan troglodytes*). Nishida (1983) showed that among Mahale chimpanzees, nulliparous females were eager caretakers while parous females were largely uninterested in infants other than their own. Mothers exerted their choice of particular allomothers. Small (1990) showed that permissive alloparenting occurs in *Macaca sylvanus*, and it appears that the spectrum of allomothering patterns among cercopithecines may be equally varied as that found in the colobines.

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