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Influence of maternal dominance on mother-infant relationship and allomothering in captive stump-tailed macaques (*Macaca arctoides*)

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Abstract

The present study investigated how the maternal dominance status influences the mother-infant relationship and the interaction of females other than the mother with the group infants in captive stump-tailed macaques (*Macaca arctoides*). Nine infants were born into the group; observations were made on these infants during their first six months of life using all occurrences sampling. Eleven measures of mother-infant interaction were used for analyses: total time in contact, on nipple contact, off nipple contact, total time off contact, less than 3 feet away (touching distance), more than 3 feet away (beyond touching distance), total contact broken, leaves by mother, leaves by infant, approach by mother, approach by infant. Although the general course of development of the mother-infant relationship was similar in all mother-infant pairs, there were marked differences in regulation of mother-infant contact based on the maternal dominance status. Infants of more dominant females tend to be more secure and have greater freedom of movement within the group. High-ranking stump-tailed macaque mothers carried their offspring less than lower-ranking females. Infants born to dominant female were found to receive significantly more care contact than the infants of sub-ordinate female. The present study strongly indicated that maternal dominance status was a factor that shaped the nature of stump-tailed infants with group members.

Key words: Allomothering; mother-infant relationship; stump-tailed macaques; subordinate.

Introduction

Primate infants are born dependent on their mother[1] and mothers may play a role throughout their offspring's lives.[2] In the process of interactions with mother, infants gradually achieve independence, and develop appropriate social skills with the peer on receiving stimulus from the environment.[3] Mother not only plays an active role in promoting the infant`s independence but also regulates own interactions with the other infant and with other members of the group.[4,5] Although general course of development of mother-infant relationship is extremely

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steady across the species, individual mother-infant relationship varies substantially within groups.[6,7] Inter-individual differences in mother-infant interactions among non-human primates can often be described in terms of particular qualities of relationship[8] that is generally based on the identification of differences in one or more measures of mother-infant interaction between individual mother-infant pairs. The measures are typically those concerned with the regulation of contact and proximity between mothers and infants. Consistency at the level of individual mother-infant pairs appears to be common among Cercopithecines.[9,10]

Macaques are particularly valuable for investigating the relationship between social organizations and mothering behaviour. Considerable differences in social organization between macaques species, in particular with reference to patterns of aggression and affiliation, social cohesiveness, and kin-oriented behaviour have been documented.[11-16] Difference in social organization has been found to be accompanied by difference in mothering style, with particular reference to maternal tolerance of interactions between infants and other individuals.[11,17] The direct comparisons of mother-infant relationship between rhesus macaques (*Macaca mulatta*), pig-tailed macaques (*M. nemestrina*), and stump-tailed macaques (*M. arctoides*) showed that the three species were similar in the general course of development of the mother-infant relationship. However, there were marked differences in regulation of mother-infant contact and proximity, and in the frequencies of grooming and scratching. Stump-tailed macaques' mothers were reported to show little or no restraining and rejection of their infants and less engaged in controlling their infants` behaviour than both pig-tailed macaques and rhesus macaques.[18]

Non-mother females play important role in allomothering in certain primates.[19] Small had discussed the relationship between non-mother and infant widely in genus *Macaca* and recorded permissive mothering with infant transfer in some species while in other the infant rarely comes in contact with other adult females of the group.[20] The interest of males and of females other than the mothers in interacting with infants in macaque groups has been reported quantitatively for species such as *M. mulatta,*[4,21] *M. fuscata*,[22,23] *M. radiate*[11] and *M. sylvanus*.[24,25]Allomothering in stump-tailed macaques has been reported in certain studies [26-28] where it has been identified as key social adaptation that characterizes the group.

Quantitative information on mother-infant relationship in stump-tailed macaques is very limited.[18,29] Since it is very important to understand what influences the mother-infant relationship and how it influences the behaviour and life history of offspring, the present study aims to investigate how maternal dominance status influences the mother-infant relationship and allomothering. The knowledge of what influences mother-infant relationships in stump-tailed macaques may help planning conservation and breeding programs.

Materials and Methods

Subjects and data collection

The study was conducted on a group of captive stump-tailed macaques in the Aizawl Zoological Park, India. During the study period (January, 2009 to December, 2011), 9 infants born to 7 different mothers (Table 1). Thus, mother-infant relationship was studied on 9 mother-infant pairs. However, interaction between Neo-3 and her mother was not included in the analysis as the mother-infant pair was kept in isolation. Other members of the group include 4 adult males, 2 adult females, 3 juvenile males and 1 juvenile female. The monkeys were housed in an enclosure with 2 indoor rooms and 1 outdoor enclosure covering 850 m^2. Individuals of the study group could be readily observed at all times. Stump-tailed macaque females do not always form linear hierarchy, making it impossible to assign dominance rankings to females. Accordingly, dominance index was calculated based on the direction of aggressive and

Table 1. Different mother-infant pairs of the study group.

Name of infant	Sex	Name of mother	Maternal status	Birth date
Neo 1	Male	Nutei	Subordinate	9.6.2009
Neo 2	Female	Hnupi	Dominant	16.6.2009
Neo 3	Female	Rani	Subordinate	25.7.2010
Neo 4	Male	Dali	Subordinate	9.2.2011
Neo 5	Female	Buangi	Dominant	21.3.2011
Neo 6	Male	Seni	Subordinate	21.3.2011
Neo 7	Male	Nutei	Subordinate	2.6.2011
Neo 8	Male	Hnupi	Dominant	10.6.2011
Neo 9	Female	Mci	Subordinate	6.7.2011

submissive behaviours between all possible paired combinations of females within the group[30] which represent the relative dominance status of each female. Two females maintaining top hierarchy among the adult females were assigned dominant females while the remaining females were assigned subordinate females.

Behavioural data were collected with all occurrences sampling[31] from the day after the birth of an infant. Each mother-infant pair was focally observed in 4 weekly 60 min observation sessions for the first 6 months of infant life. Observation was also recorded for the social interactions between non-mother females and the group infants. Eleven measures of mother-infant interaction were used for analysis: total time in contact, on nipple contact, off nipple contact, total time off contact, less than 3 feet away (touching distance), more than 3 feet away (beyond touching distance), total contact broken, leaves by mother, leaves by infant, approach by mother, approach by infant. Total time in contact is the percentage of observation time the mother-infant pair spent in contact. On nipple contact was defined as movements that resulted in nipple contact whereas off nipple contact was any movement that resulted in any other body contact between mother and infant except the nipple contact. Approaches were defined as movement that brought the actor (mother or infant) within about 60 cm of the recipient (infant or mother) without making contact for at least 5 seconds. Leaves were defined as movements that caused an increase in distance from less than 60 cm to more than 60 cm between mother and infant. Leaves were recorded only if the mother-infant pair was within 60 cm proximity without body contact.[18]

Data analyses

The pair-wise variations on mother-infant relationships between infants born to mother of different dominance status was determine using Mann-Whitney test. Kruskal-Wallis test was performed to examine the variations on mother-infant relationships on a group of infants born to different mothers. Kolmogorov-Smirnov test was performed to determine the influence of maternal dominance status on the amount of care contact received by the infants from non-mother females. For all the tests, the significant level was set at 0.05 and analyses were done using SPSS 17.0.

RESULTS

A total of 864 hr of observation (96 hr for each mother-infant pair) were collected. Mann-Whitney pair-wise comparison between male infants (Neo-1, Neo-4, Neo-6, Neo-7 and Neo-8) born to females of different dominance status strongly supports the existence of maternal dominance influences on mother-infant relationship. Male infant (Neo-8) born to dominant mother was found to showed significantly more total time off contact, total contact broken, leave by infant, approach by infant and time spent >3 feet away from mother than the male infants (Neo-1, Neo-4, Neo-6 and Neo-7) born to subordinate mothers. Conversely, the total time in contact and time off nipple contact were significantly higher for male infants born to subordinate mothers (Table 2). Female infants (Neo-2 and Neo-5) born to dominant mothers were

Table 2. Pair-wise comparisons of mother-infant relationship between Neo-8 & Neo-1, Neo-8 & Neo-4, Neo-8 & Neo-6, Neo-8 & Neo-7 (Male infants born to females of different dominance status)

found to show earlier independence than female infant (Neo-9) of subordinate mother where certain measures of mother-infant interactions were significantly higher for the female infants of dominant mothers (Table 3). Furthermore, there was no significant variation on the measures of mother-infant interactions among the male infants born to subordinate mothers (Table 4).

The most frequent care contact received from non-mother females was grooming (60.6%) followed by touch-hand (17.5%), sitting-touching (15.5%) and genital manipulation (6.7%). Infants born to dominant mothers were found to receive significantly more care contact than the infants of subordinate mothers (Kolmogorov-Smirnov test: Z= 1.732, p=0.005).

Discussion

Studies conducted in captivity and in the wild have shown that monkeys mothers adjust their behaviour according to effects of socio-demographic factors such as their age and experience, dominance rank, aggression received by themselves and their infants, sex of the infant, and size and composition of their family.[32-36] Although the general course of development of the mother-infant relationship was similar in all mother-infant pairs, there were marked differences in regulation of mother-infant contact based on the maternal dominance status.

Although no single unifying concept has been found to explain all primate sociality, it seems clear that at least in certain species, dominance status has social significance.[37] There are different ways how mother's social status can influence her infant. The most direct impact is connected with food quality. It is known that higher-ranking females have access to better food, which may influence the quality of mother's milk and therefore infant nutrition.[38-40] Female's social status may also impact the nutrition and growth of older, independent offspring, because of feeding in the proximity to the mother.[41] High-ranking mothers have shorter inter-birth intervals than low-ranking mothers, no matter the gender of the previous offspring.[42] In the present study, infants of dominant females tend to be more secure and have greater freedom of movement within the group. They have less dependent on their mothers and even have more varied and greater experience than infants of subordinate females. Thus, maternal dominance status could be considered as an important factor in the ontogenetic development of social behaviour, even before the mother begins to support the infant in agonistic encounters. Male infant born to dominant mother showed the highest frequencies of total time off contact, number of total contact broken, leaves by infant, approach by infant and also spent significantly more time >3 feet away from mother as compared to infants of any sex born to subordinate mothers. These results suggest that social status of mother strongly influenced the pattern of mother-infant relationship and eventually lead to earlier independence of infants.

Allomothering is the act of an individual different from the mother holding the infant such as infant handling, play-mothering and babysitting.[2,43] There are several hypotheses and reasons why allomothering occurs in mammals. It may be due to kin selection, so individuals enhance their inclusive fitness through helping related mothers to raise their offspring. However, this does not explain infant handling among primates, because they allomother infants from other families also.[2,38,44] In primates it is likely that natural selection has favored this action to improve one's parenting skills, for example among blue monkeys (*Cercopithercusmittis*), the nulliparous females are the most active handlers.[45] Furthermore, it is shown for vervet monkeys (*Chlorocebus* sp.) that the females, who are more interested in infants as juveniles, are more likely to be successful in rearing the first live-born infant.[38,44,46,47] It is also suggested that babysitting may have a function in promoting the

Table 2. Pair-wise comparisons of mother-infant relationship between Neo-8 & Neo-1, Neo-8 & Neo-4, Neo-8 & Neo-6, Neo-8 & Neo-7 (Male infants born to females of different dominance status)

Sl. No.	Activities	Neo 8 & Neo 1		Neo 8 & Neo 4		Neo 8 & Neo 6		Neo 8 & Neo 7	
		U	p	U	p	U	p	U	p
1	Total time in contact	68.00	0.023*	64.00	0.015*	64.00	0.015*	68.00	0.023*
2	Time on nipple	80.00	0.068	80.00	0.068	96.00	0.224	80.00	0.068
3	Time off nipple	64.00	0.015*	48.00	0.002*	64.00	0.015*	64.00	0.015*
4	Total time off contact	64.00	0.015*	64.00	0.015*	64.00	0.015*	64.00	0.015*
5	Time spent < 3 F away	96.00	0.224	112.00	0.544	96.00	0.224	80.00	0.068
6	Time spent > 3 F away	64.00	0.015*	64.00	0.015*	64.00	0.015*	64.00	0.015*
7	Leave by mother	112.00	0.531	112.00	0.531	112.00	0.531	112.00	0.486
8	Leave by infant	64.00	0.015*	64.00	0.015*	64.00	0.015*	48.00	0.002*
9	Total contact broken	64.00	0.015*	64.00	0.015*	64.00	0.015*	64.00	0.015*
10	Approached by mother	96.00	0.210	88.00	0.117	80.00	0.060	96.00	0.219
11	Approached by infant	24.00	0.001*	32.00	0.001*	40.00	0.001*	32.00	0.001*

Table 3. Pair-wise comparisons of mother-infant relationship between Neo-9 & Neo-2, Neo-9 & Neo-5 (Female infants born to mothers of different dominance status)

Sl. No.	Activities	Neo-9 & Neo-2		Neo-9 & Neo-5	
		U	p	U	p
1	Total time in contact	60.00	0.01*	72.00	0.034*
2	Time on nipple	80.00	0.068	128.00	1.000
3	Time off nipple	48.00	0.002*	64.00	0.015*
4	Total time off contact	64.00	0.015*	64.00	0.015*
5	Time spent< 3 F away	56.00	0.006*	120.00	0.760
6	Time spent > 3 F away	48.00	0.002*	72.00	0.032*
7	Leave by mother	112.00	0.506	112.00	0.506
8	Leave by infant	0.00	0.001*	0.00	0.001*
9	Total contact broken	8.00	0.001*	0.00	0.001*
10	Approached by mother	80.00	0.060	120.00	0.754
11	Approached by infant	0.00	0.001*	0.00	0.001*

Table 4. Comparisons of mother-infant relationship among males born to subordinate mother.

Sl. No.	Activities	Neo - 1, 4, 6 & 7	
		χ^2	p
1	Total time in contact	0.116	0.99
2	Time on nipple	0.162	0.98
3	Time off nipple	0.093	0.99
4	Total time off contact	0.148	0.93
5	Time spent< 3 F away	1.911	0.59
6	Time spent > 3 F away	1.185	0.75
7	Leave by mother	0.162	0.98
8	Leave by infant	1.213	0.75
9	Total contact broken	1.175	0.75
10	Approached by mother	2.056	0.56
11	Approached by infant	5.33	0.14

socialization of the infant.[45] For non-human primates, the most likely explanation is the responsiveness theory,[47] which states that female primates are strongly attracted to all infants to make better mothers, because the more responsive the mother is, the higher chance that she reacts to her offspring's needs.[44,47,48] The amount of social contact and grooming received were significantly higher for infants born to dominant mothers than infants born to subordinate mothers. Grooming of infants seems to be an important conditioner for social cohesion. The grooming of infants permitted low ranking monkeys to interact safely with more dominant ones. The present study also strongly indicated that maternal dominance status was a factor that shaped the nature of the interactions of the stump-tailed infants with group members.

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