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Mother-infant relationships and infant development in captive grey-shanked douc langurs (*Pygathrix cinerea*)

Nolan N. Bett

Columbia University, Department of Ecology, Evolution and Environmental Biology

10th floor, Schermerhorn Extension, 1200 Amsterdam Avenue, New York, NY 10027, USA <nnb2112@columbia.edu>

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Summary

An infant's relationship with its mother influences the development of social bonds throughout the rest of the infant's life, and can have a significant effect on its long-term fitness. The majority of research conducted on this relationship has focused on a limited range of primate taxa. In this study, I observed mother-infant relationships in three dyads of grey-shanked douc langurs (*Pygathrix cinerea*), a critically endangered colobine that is endemic to Vietnam. Such a study broadens our understanding of social relationships amongst primates, which are known to vary significantly among taxonomic groups, and provides information that can improve captive management and potential reintroduction of grey-shanked douc langurs. The three infants varied in age from 7 weeks to 25 months. The two older infants spent significantly more time further away from their mothers than the 7-week old, although all three infants spent a similar amount of time nursing. The majority of the older infants' contact time with the mothers was used for nursing, whereas the 7-week old infant engaged in other activities such as climbing upon and holding onto his mother. There was also evidence of weaning conflict in the oldest infant, who was rejected by his mother more often than the younger two infants. Also, the effect of living without any other infants or juveniles manifested itself in attention-seeking behaviours, such as grabbing at the face and body of the mother, which was particularly prevalent in the middle-aged infant. Suggestions for future studies and their applications to the conservation of grey-shanked douc langurs are discussed, with an emphasis on the potential importance of captive breeding and reintroductions to their survival as a species.

Mối quan hệ Mẹ-Con và sự phát triển của con non trong điều kiện nuôi nhốt ở loài chà vá chân xám (*Pygathrix cinerea*)

Tóm tắt

Mối quan hệ của con non và mẹ có ảnh hưởng quan trọng đến sự phát triển mối quan hệ xã hội của con non trong cuộc đời chúng, và có thể ảnh hưởng đáng kể đến sức khỏe lâu dài của chúng. Trước đây có nhiều nghiên cứu về mối quan hệ này, tuy nhiên chỉ tập trung vào một số loài nhất định. Trong nghiên cứu này, tôi đã quan sát ba cặp mẹ và con của loài chà vá chân xám, một loài khỉ ăn lá đặc hữu của Việt Nam. Nghiên cứu này đã góp phần mở rộng những hiểu biết của chúng ta về mối quan hệ xã hội của các loài thú linh trưởng vốn được biết đến là rất đa dạng. Nghiên cứu cũng đã cung cấp những thông tin cần thiết nhằm nâng cao chất lượng chăm sóc, quản lý các cá thể nuôi nhốt và việc tái thả các cá thể này vào tự nhiên. Ba cá thể con non từ bảy (7) tuần tuổi đến 25 tháng tuổi đã được quan sát. Kết quả cho thấy, hai cá thể nhiều tuổi hơn thường xuyên rời xa mẹ hơn là cá thể 7 tuần tuổi, cho dù cả ba cá thể có

cùng khoảng thời gian bú mẹ. Phần lớn thời gian hai cá thể nhiều tuổi hơn bên mẹ là dành cho việc bú, trong khi cá thể 7 tuần tuổi thường xuyên leo trèo và ngồi trong lòng mẹ. Nghiên cứu này đã thu thập được bằng chứng cho thấy mối xung đột giữa con non lớn nhất và mẹ của nó trong quá trình cai sữa. Đồng thời nghiên cứu cũng ghi nhận các tập tính như cào mặt và cơ thể con mẹ nhằm lôi kéo sự chú ý ở cá thể con non lớn thứ hai. Đây có thể là ảnh hưởng của việc con non phải sống một mình mà không có những cá thể anh em khác. Những gợi ý cho việc tiếp tục nghiên cứu trong tương lai và vận dụng những kết quả vào công tác bảo tồn loài chà vá chân xám sẽ được thảo luận, đặc biệt là chương trình nhân nuôi và tái thả.

Introduction

The relationship between an infant and its mother is one of the strongest bonds in social mammals (Mateo, 2009). It is critical to the infant's immediate survival, and shapes many of its future relationships, which can have a significant effect on long-term fitness (Altmann, 1980; Förster & Cords 2002; Hinde & Spencer-Booth, 1967; Horwich, 1974; MacKinnon, 2007). Primates have a longer period of infancy than all other mammals of similar size (Pereira & Fairbanks, 1993), and rely on their mothers not only for nutrition and protection, but also for transport (Strier, 2000). The mother-infant relationship is therefore particularly influential in a primate's development, and it has been an important focal point in the study of social behaviour.

Many external factors can influence mother-infant relationships, such as group composition and the physical environment, as can life history characteristics such as the length of infancy (Förster & Cords, 2002; Maestripieri, 2009; Nicolson, 1991). The relationship between infants and mothers also varies with taxonomy and body size (Nicolson, 1991; Strier, 2000), and therefore broad generalizations across distant taxa are unreliable. Research on infant development in primates has been biased toward macaques, baboons, and vervet monkeys (Maestripieri, 2009). Aside from the work of Dolhinow on *Semnopithecus* (e.g. Dolhinow 1982; Jay 1965), Asian colobines are a group of primates that have received less attention. Furthermore, few studies of colobine infants have tracked their subjects through to social independence. Instead, many end within the first year of the infant's life, at which point locomotor and nutritional independence has been achieved, but rarely social independence (e.g. Brent et al., 2008; Horwich and Manski, 1975; Rapaport & Mellen, 1990).

This study explores the mother-infant relationship of the grey-shanked douc langur (*Pygathrix cinerea*), an Asian colobine that inhabits evergreen forests in central Vietnam. Although their relationship to other langurs is questioned, doucs are referred to as douc langurs in this paper because this is the term that is most familiar to individuals outside the fields of primatology and systematics. The grey-shanked douc langur was only recently identified (Nadler, 1997), and very little is known about its behaviour and ecology. Research on the grey-shanked douc langur will not only help to fill our current gap in knowledge of infant development in colobines, but is also important for improving our broader understanding of the behaviour of this species. Grey-shanked douc langurs are classified as Critically Endangered (IUCN 2010), and face serious threats from deforestation and hunting (Nadler et al., 2003). Research on their behaviour and life history is necessary to make population viability assessments, and is therefore critical to long-term conservation efforts.

The total population of grey-shanked douc langurs is estimated at fewer than 1000 individuals (Ha Thang Long, 2007). In addition to being rare, douc langurs are almost entirely arboreal, and prefer the upper canopy (Lippold, 1998), making them very difficult to observe in the wild. Studies of captive animals are often used in behavioural research, as they allow for a controlled

environment and remove the difficulties associated with tracking and watching animals in the field. Douc langurs are difficult to maintain in captivity, largely because of their specific dietary needs (Hick 1972; Hill 1972). The Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park, Vietnam, is currently the only facility in the world that houses grey-shanked douc langurs. Most individuals at the EPRC were confiscated from poachers, and in recent years they have been bred at the center. The goal of the center is to reintroduce endangered Vietnamese primates back into their natural habitat. Studies on the social behaviour of these animals may improve the chances of successful reintroductions. A better understanding of infant development, for example, can help us ascertain how best to reintroduce family groups with young offspring. These studies will also help determine the most suitable group sizes and compositions for captive douc langurs, and may inform other colony management decisions such as when to separate offspring from their parents.

I observed the frequency of a wide variety of behaviours (see Appendix) of three mother-infant pairs of grey-shanked douc langurs at the EPRC over a period of six weeks. I also tracked the spatial relations of infants and their mothers. This is the first study on mother-infant relationships in this species, and I compare the observed behavioural patterns to those of other Asian colobines. I also address the potential conservation applications of these results.

Methods

Subjects

From June 23rd to July 25th, 2010, I observed three captive mother-infant dyads of grey-shanked doucs at the EPRC (see Table 1 for information on individuals). The three mothers had been confiscated from poachers, while their infants were born at the center. The three infants were 1.75 months, 15 months and 25 months old at the start of the study. The precise dates of birth for the mothers are unknown.

Table 1. I.D., sex, age, and source of grey-shanked douc mothers and infants at EPRC.

I.D.	Infant Sex	Date of arrival at EPRC (m/d/y)	Birth date (m/d/y)	Age at start of study	Source
Mot1	M	10/19/2006	?/?/2000	10 years	Confiscated
Inf1		05/06/2010	05/06/2010	1.75 months	born EPRC
Mot2	F	11/09/2005	?/?/?	?	Confiscated
Inf2		03/08/2009	03/08/2009	15 months	born EPRC
Mot3	M	12/15/2001	?/?/1997	13 years	Confiscated
Inf3		05/05/2008	05/05/2008	25 months	born EPRC

The study animals lived as family units (parents plus infant) in separate outdoor cages. The Mot1/Inf1 family included a male juvenile (born 10/10/07) that was an older full sibling of Inf1. Each 10 m x 5.5 m x 3.5 m cage was fully enclosed with wire mesh fencing (Fig. 1). The cage floor was concrete, above which three levels of bamboo and wood supports simulated tree branches. Cages were spaced roughly 8 m apart from one another. The douc langurs were therefore able to see human visitors and other monkeys in adjacent cages. Adult males occasionally reacted to sounds made from adjacent cages, while mothers and infants did not appear to alter their behaviour. None

of the individuals appeared to be affected by the presence of visitors. There were 20 staff members at the EPRC who frequently walked along the adjacent footpaths and entered cages to clean them and feed the animals. The center was also open to tourists from 0900-1100 h and 1300-1600 h. During the period of the study, visitor presence was low (5-10 visitors per day).

Fig.1. A typical cage at the Endangered Primate Rescue Center, Vietnam. Photo: Nolan Bett.

The animals were fed three times daily (at 0630-0700 h, 1030-1100, and 1300-1500 h) with bundles of leaves from local tree species. Approximately 10 bundles were spread out in each cage at every feeding. Cage cleaning usually coincided with feeding or occurred shortly before.

Data Collection

I observed the animals six days per week during the study period from 0530-1030 h, and again from 1300-1500 h. A time budget assessment during the week preceding the study determined the douc langurs were most active during these periods. I conducted focal samples of a mother-infant dyad, and made instantaneous records at 20 sec intervals of the behaviour of both the infant and the mother, as well as their proximity. I did not record data when keepers entered the cage, but resumed immediately afterward.

Each of the three dyads was sampled every day: one from 0530-0800 h, another from 0800-1030 h, and the third from 1300-1500 h. The time at which the dyads were sampled was rotated

from one day to the next such that the dyads were observed for the same overall amount of time during each sampling period. I developed an ethogram before starting the behavioural data collection (Appendix). I scored proximity in five categories: 0 m (touching), greater than 0 m and less than or equal to 0.5 m, greater than 0.5 and less than or equal to 1 m, greater than 1 m and less than or equal to 2 m, and greater than 2 m.

Data Analysis

I pooled the observations for each dyad by day, expressing values for individual behaviours as percentages of total daily instantaneous records (expressed as proportion of time). I used these daily proportions to compute mean percentage of time spent on each behaviour. I tested the daily proportions for normality using the Shapiro-Wilk test, and used either ANOVA, (if the distributions were normal) or the Kruskal-Wallis test (if the distributions were not normal) to compare data among subjects/dyads. When the resultant p-value was ≤ 0.05, I used the Tukey HSD test (if distributions were normal) and the post-hoc test provided by Siegel & Castellan (1988; if distributions were not normal) for multiple comparisons between subjects/dyads.

I measured the mothers' rejection rate by dividing the number of times they rejected their infants' attempts to establish nipple contact by the sum of the rejections and acceptances. I considered a series of one or more consecutive sampling points in which the infant was in contact with its mother's nipple as a single nursing bout, and I demarcated each nursing bout as one acceptance from the mother. I therefore assumed that infants did not stop and resume nipple contact between two sample points within a bout. Sample points were recorded at a high frequency, and therefore any gaps in nipple contact between consecutive points would be very brief.

I calculated a weighted average distance between the infants and their mothers by converting proximity categories into a distance index, using the middle value of each proximity range (e.g. 0-0.5 m was averaged to 0.25 m, 0.5-1.0 m was averaged to 0.75 m, and so on). Using the distance index, a mean distance was calculated for each sample day. The mean distances were normally distributed, and I used ANOVA to compare the daily mean distances between mothers and infants in the different dyads. All p-values are two-tailed. Results are displayed as box plots with medians and inter-quartile ranges when non-parametric analyses were used, and as bar charts with means and standard errors when parametric analyses were used. I used the statistical software R (2.11.1) for all analyses.

Results

There was a total of 27,005 sample points over 150 hours of observation, spread evenly across the three dyads. The three infants differed from one another in several aspects of their behaviour. These included the proportion of time spent holding onto, sitting in the lap of, and climbing on their mothers (respectively: Kruskal Wallis; $X^2 = 46.852$, d.f. = 2, $P < 0.001$; $X^2 = 31.276$, d.f. = 2, $P < 0.001$; $X^2 = 51.096$, d.f. = 2, $P < 0.001$). Post hoc comparisons indicated Inf1 spent more time doing each of the three behaviours than Inf2 and Inf3 (Fig. 2a-c). The infants also differed in the proportion of time spent grooming their mothers, sharing food with their mothers, and grabbing at their mothers' faces and bodies (respectively: $X^2 = 19.841$, d.f. = 2, $P < 0.001$; $X^2 = 16.612$, d.f. = 2, $P < 0.001$; $X^2 = 19.048$, d.f. = 2, $P < 0.001$). Post hoc comparisons revealed Inf2 spent more time engaged in each of these behaviours than Inf1 and Inf3 (Fig. 2d-f).

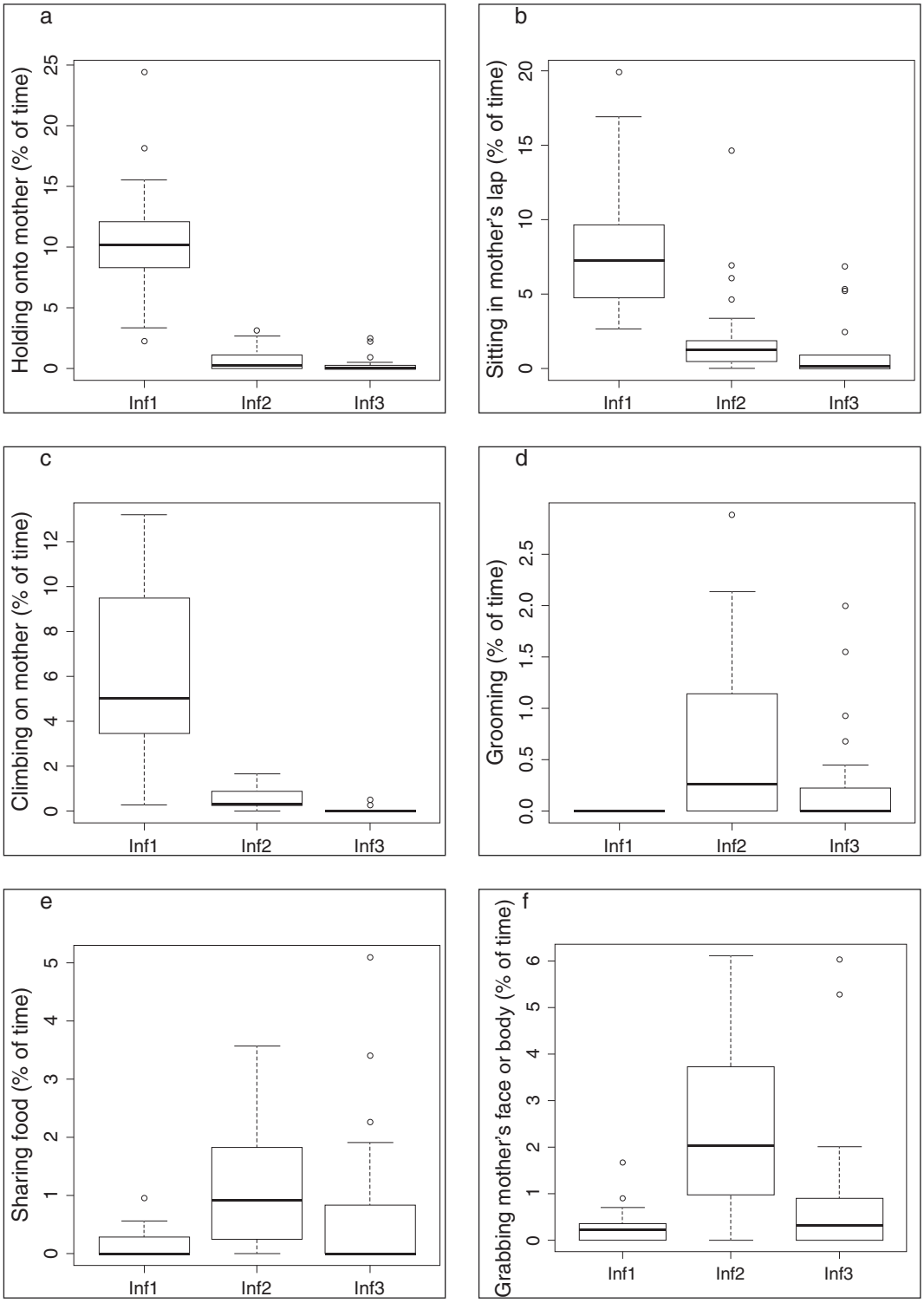

Fig.2. Proportion of time spent by infants a) holding onto their mothers, b) sitting in their mothers' laps, c) climbing on their mothers, d) grooming their mothers, e) sharing food with their mothers, f) grabbing their mothers' face or body.

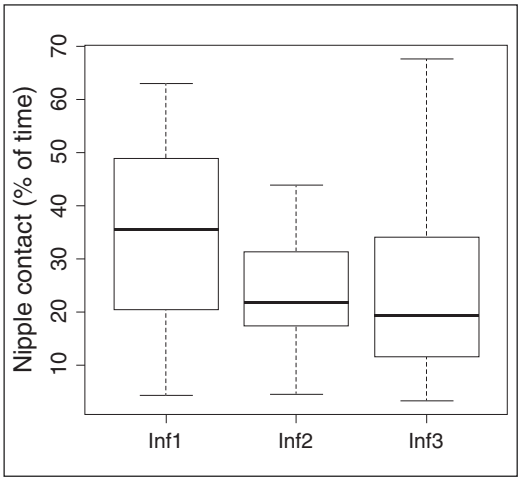

Fig.3. Proportion of time spent by infants in contact with their mothers' nipples.

The three infants did not differ significantly in the amount of time they spent in contact with their mothers' nipples (Kruskal Wallis; $X^2 = 5.7926$, d.f. = 2, $P = 0.055$) (Fig 3). This was the most common behaviour for each of the infants: Inf1 spent 36 ± 8% (n = 22, 95% C.I.), Inf2 spent 23 ± 5% (n = 22) and Inf3 spent 27 ± 9% (n = 22).

The three mothers differed in the amount of time they spent physically supporting their infants' weight (ANOVA; F = 74.235, d.f. = 2, $P < 0.001$), and post hoc comparisons revealed Mot1 spent more time than Mot2 and Mot3 (Fig. 4a). The mothers did not differ significantly in the amount of time they spent grooming their infants (Kruskal Wallis; $X^2 = 5.280$, d.f. = 2, $P = 0.071$) (Fig. 4b).

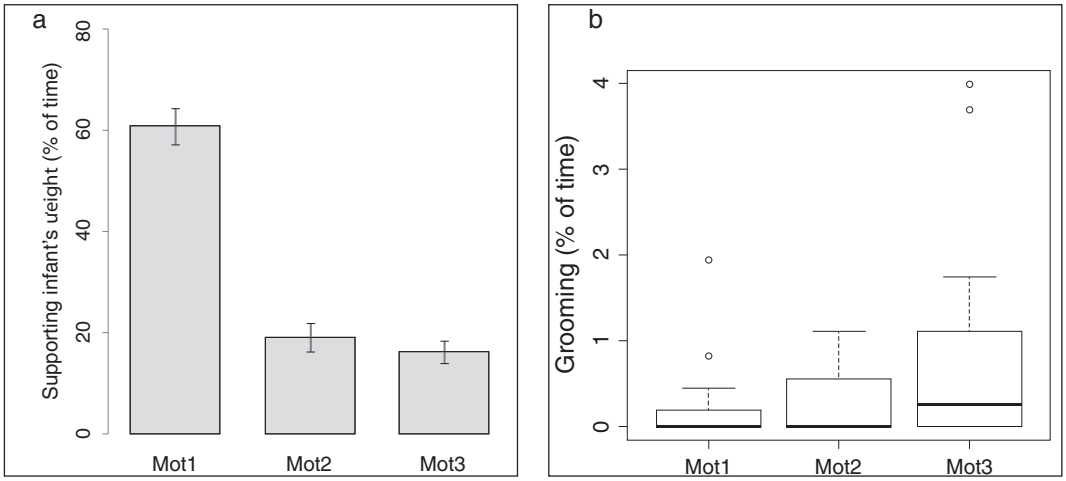

Fig.4. Proportion of time spent by mothers a) supporting their infants' weight, b) grooming their infants.

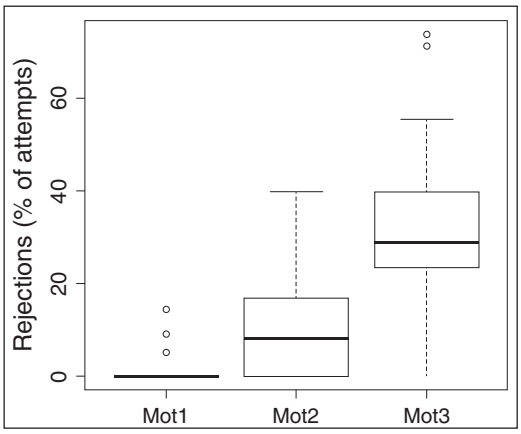

Fig.5. Percentage of attempts to establish nipple contact in which the mother rejected the infant. Total number of nursing attempts, successful or unsuccessful, by infants: Inf1 = 205, Inf2 = 251, Inf3 = 267.

The rate of infant rejection differed across the three mothers (Kruskal Wallis; $X^2 = 32.394$, d.f. = 2, $P < 0.001$). Post hoc comparisons revealed that Mot3 rejected her infant more often (32% ± 9, n = 22, 95% C.I.) than Mot1 (2% ± 2, n = 22) and Mot2 (10% ± 5, n = 22) (Fig. 5).

The proximity between the infants and their mothers differed significantly (ANOVA; F = 109.740, d.f. = 2, $P < 0.001$). Inf1/Mot1 were in physical contact with one another most of the time, and the amount of time they spent in different proximity categories decreased as the proximity range increased (Fig. 6). Inf2/Mot2

and Inf3/Mot3, on the other hand, were most often either in contact with one another, or more than 2 m apart. They spent very little time at distances between these two extremes.

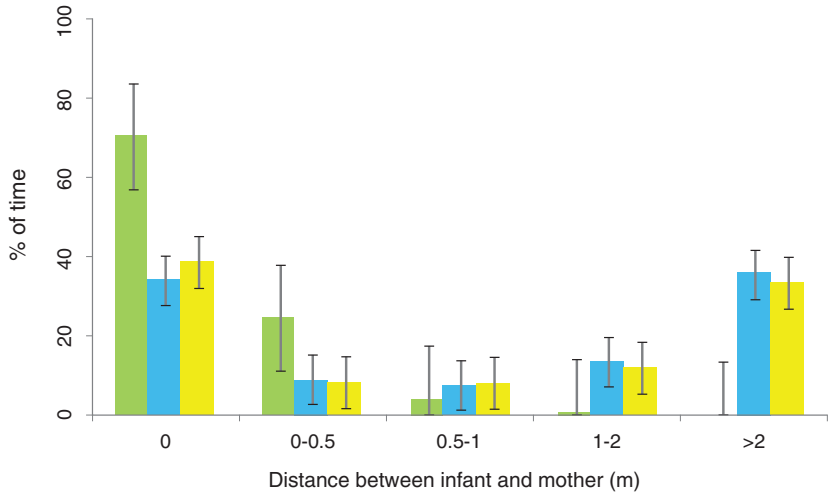

Fig.6. Proximity between mother and infant. Green = Inf1/Mot1, blue = Inf2/Mot2, yellow = Inf3/Mot3.

Discussion

In douc langurs, there appear to be several shifts in behaviour between the ages of 2 and 25 months. One of the most striking differences is in mother-offspring proximity. The older infants, Inf2 and Inf3, spent more time further away from their mothers than Inf1, and spent little time interacting with their mothers aside from nursing. They rarely, for example, held onto, climbed upon, or sat in the lap of their mothers. The youngest infant, Inf1, by contrast, rarely ventured farther than 1 m from his mother—most of his time was spent in physical contact, interspersed with brief exploratory journeys <2 m away. Brief exploratory journeys were reported for similar-aged captive red-shanked douc langurs (*Pygathrix nemaeus*) (Hick, 1972; Ruempler, 1998), which are the grey-shanked douc langurs' closest relatives (Roos et al. 2007), although not all infants make these trips so young (Brockman & Lippold, 1975). Yeong et al. (2010) observed four infant red-shanked douc langurs from their birth until an age of 18 months. The proportion of time these infants spent in physical contact with their mothers decreased dramatically during the first two to four months of life, after which the time spent in contact remained fairly constant. The proportion of time the 1-2 month old red-shanked douc langurs spent in contact with their mothers (60-90%) was similar to Inf1, and the proportions of time 18-month olds spent in contact with their mothers (20-60%) was similar to Inf2 and Inf3.

Each of the infants spent a relatively large amount of time on its mothers' nipples, but the rate of rejections by the mothers increased with infant age. This pattern of rejection presumably reflects different stages of the weaning process, which is often gradual. In the Nilgiri langur (*Trachypithecus johnii*), for example, the process begins as early as 14 weeks after birth, at which point the mother leaves her infant consistently, and alternates between accepting and rejecting her infants' attempts to nurse (Poirier, 1968). The process then continues, with the rejections increasing in frequency and severity, until the infant is over a year old. At this point, the mother regularly rejects the infant's attempts to nurse, until eventually the infant no longer seeks contact with its mother's nipple.

Maternal effects on infant development in primates act through many different factors; a mother's social partners, diet, physiology, and daily activities can all have profound and lasting effects on her offspring (Altmann, 1980; Förster & Cords, 2002; Hinde & Spencer-Booth, 1967; Mateo, 2009). In addition, there is a great deal of individual variation in growth rates, weaning age, and behavioural development, even in individuals that live in the same environment (Maestripieri, 2009; Pereira & Leigh, 2003). Infant development in primates is therefore an exceptionally complex process that can be influenced by a combination of maternal effects, social surroundings, physical environment, and individual variation.

Differences in wild and captive environments likely have a strong effect on infant development, and studies of colobines have confirmed that rates of infant independence differ in captivity and in the wild. Zhao et al. (2008) found that wild white-headed langur (*Trachypithecus leucocephalus*) infants are weaned at a younger age than captive infants. In red-shanked douc langurs, however, the opposite may occur, with captive infants undergoing accelerated maturation. In the wild, weaning begins at roughly 12-13 months of age, and continues until the infant is 2 years old (Lippold, 1995). In captivity, mothers begin to reject their infants' attempts to suckle when the infants are 4-10 months old (Yeong et al., 2010). The age at which captive infants no longer spend time on their mothers' nipple is unknown, however, because studies have not continued long enough to observe independence. Infant red-shanked douc langurs have been observed nursing through the ages of 7 months (Hick, 1972), 13 months (Brockman 1976), 17 months (Kavanagh, 1978), and 18 months (Yeong et al., 2010). The latest known age of an infant on its mother's nipple was 24 months (Ruempler, 1998), and this is likely an underestimate since the behaviour still occurred when observations stopped. In this study, the oldest infant was 25 months old, and continued to spend time on its mother's nipple at a rate that was similar to the 2-month old infant. By this advanced age, during which the individual is consuming a full diet of leaves, nipple time is no longer nutritional (and should therefore not be considered nursing), but is probably done for comfort. This study provides a snapshot of infant behaviours beyond one year of age, which is when many infant studies end. To better understand behaviours such as weaning in the grey-shanked douc langurs, however, field studies that track continuously the infants through to independence are needed. Additional captive studies are also necessary to determine how the captive environment alters infant development, particularly studies with a larger sample size.

The time course of weaning also depends on how quickly the mother gives birth again. In primates, weaning often ends with the birth of a younger sibling (Nicolson, 1987; Strier, 2000). Through extensive observations of the North Indian langur (*Semnopithecus entellus*), for example, Jay (1965) found that mothers regularly give birth to a second infant approximately two years after the first offspring was born, at which point she severs all nursing ties with the elder infant. In my study, Inf1's older brother (20 months) rarely interacted with his mother, and I never saw him attempt to establish nipple contact, even though he was 5 months younger than Inf3, who established nipple contact frequently. Also, of the four infants that Yeong et al. (2010) observed, the two that had younger siblings were weaned earlier than the two who did not. The birth of a younger sibling seems to lower the age at which an infant is weaned, and may even affect other social interactions. For example, female *Cercopithecus mitis* groomed older offspring less often when younger siblings were born (Cords, 2000).

Other behavioural differences existed among the infants, although it is difficult to ascertain whether these differences arose from social factors, which can affect many aspects of maternal behaviour and infant development (Förster & Cords 2005; Hinde & Spencer-Booth, 1967;

Maestripieri & Call 1996; Spencer-Booth, 1968) or are simply individual idiosyncrasies. Inf2 spent a significantly greater proportion of her time grooming her mother than the other two infants. Cords (2000) suggested that grooming may be more important to developing long-term relationships in female *C. mitis* than in males, and a similar sex difference could occur in douc langurs, which, like *C. mitis*, are female-philopatric (Wenting Liu et al. 2008). Such a sex difference could account for the variation in time spent grooming. Also, Inf2 spent a relatively large amount of time grabbing her mother's face and body, which could reflect the absence of other infants or juveniles with whom she could play. Captive red-shanked douc langur infants, for example, exhibit less social play when they are housed with only their parents in comparison to infants that live with other infants and juveniles (Yeong et al., 2010). Arguing against such an interpretation, however, is Inf3, who lived in a similar social environment to Inf2, yet did not "play" extensively with its mother. Further studies of infants in varying social environments could help clarify the effect of environment on behaviours such as grooming and social play.

Conservation Implications

Studies of social behaviour on captive individuals also have the potential to guide conservation management. The mother-infant relationship affects the survival abilities of infants, and to a lesser degree the mothers as well, and therefore can influence the success of reintroductions of captive individuals into the wild. We can assume that to maximize the likelihood of infant survival, the relationship in captivity should be similar to what is seen in the natural environment. This can be best ensured by imitating the douc langurs' natural social and physical environment as effectively as possible in captivity. For example, grey-shanked douc langurs currently live in groups of <20 individuals, with an average group size in the range of 8-15 (Ha Thang Long, 2004). These groups generally include multiple infants and juveniles, which provide opportunities for bonding and play. Behaviours such as the face and body grabbing exhibited by Inf2 towards her mother may result from a lack of playmates, which could affect the infant's ability to form future social bonds and therefore to integrate into a group in the wild. Also, if infant development is accelerated or delayed in captivity, the timing at which mothers and infants are reintroduced should be adjusted accordingly. If infants are reintroduced too soon, for example, they may not adjust well to the shift in setting, or may be an extra burden on their mothers, which could exacerbate the pressures of switching to a natural environment. Rosenblum and Andrews (1994) found that a mother's ability to foster normal infant development decreased when she was confronted with an unpredictable environment. Minimizing the changes from captive to natural environments could therefore be critical to maintaining a stable relationship between mothers and their infants. Creating a captive environment that imitates the natural one is especially important for species such as the grey-shanked douc langur, which is critically endangered (IUCN 2010), and may rely on successful reintroductions in the future.

If deforestation and hunting continue to reduce grey-shanked douc langur population sizes, the species' reliance on captive-breeding programs will increase. The EPRC is currently the only location to house captive grey-shanked douc langurs, which are likely just as difficult to sustain in captivity as their sister taxa, the red-shanked douc langurs, have proven to be (Hill, 1972; Hick, 1972; Ruempler, 1998). Captive behaviour studies on grey-shanked douc langurs can be used to improve their maintenance, welfare and breeding success, ensuring a stable captive population.

This is the first study on social relationships in captive grey-shanked douc langurs, however, and their relationships in the wild are equally understudied. Additional studies, both in captivity and

in the wild, will allow us to compare their behaviours in these different environments. This information can be used to increase the likelihood that captive-bred individuals will thrive in their natural environment, which could prove to be vital to their long-term conservation.

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