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Attachment and Social Preferences in Cooperatively-Reared Cotton-Top Tamarins

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Abstract

In many primate species a close attachment between mother and infant provides a secure base for the infant when the infant is frightened or under stress. In cooperatively breeding primates infant carrying is divided among several individuals in the group, with the mother often doing little more than nursing. In these species it is not clear which individual would best serve as a secure base for the infant. We studied eight infant cotton-top tamarins from birth through 20 weeks of age, noting who carried the infant during the first 100 days, who transferred food with the infants, and, as infants became independent, with whom they associated during social play and affiliative behavior. From week 9 to week 20, when infants were independent of carriers most of the time, we presented families with six trials (once every 2 weeks) with a threatening stimulus (a human dressed in a lab coat and wearing an animal mask). Infants played primarily with their twin or youngest sibling and had affiliative interactions with many family members. However, in fearful situations, infants ran to those who had carried them and transferred food with them the most—their father or oldest brother (never to the mother). Although adults increased rates of mobbing calls in response to the threat, infants significantly reduced their vocalization rate. For these cooperatively breeding monkeys, the attachment object for infants is the family member that invested the most effort in carrying the infant and transferring food with the infant. These results parallel and extend results from bi-parental infant care species in which the father serves as the primary attachment figure.

Keywords

infant attachment; secure base; response to threats; cooperative breeding; cotton-top tamarins (*Saguinus oedipus*)

INTRODUCTION

The formation of an attachment or close emotional relationship between an infant and its primary caregiver is of great importance to a developing primate. Attachment behavior is expressed by the infant maintaining preferential close proximity to its attachment object, by following it or by seeking contact with the attachment object. An infant will display signs of arousal or distress through increased motor activity, vocalizations, and activation of the HPA axis when the attachment object is absent [Kraemer, 1992; Hennessey et al., 1995; Mason & Mendoza, 1998]. These signs decrease when the infant is reunited with its attachment object.

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When the infant is fearful or threatened, close contact with the attachment object reduces the infant's fear and distress [for review see Mason & Mendoza, 1998].

Most studies of attachment in human and nonhuman primates have focused on the infant–mother relationship as primary [e.g., Harlow, 1958; Coe, 1990; Kraemer, 1992; Andrews & Rosenblum, 1993] based on the fact that mammalian mothers are the sole source of nutrition for infants. However, experimental studies of nursery-reared rhesus macaques (*Macaca mulatta*) show that infants can form attachments to cloth surrogate mothers [Harlow, 1958] or to dogs with which infants are housed [Mason & Capitanio, 1988]. Peer-reared rhesus macaques display primary attachment to their peers [Higley et al., 1992]. Studies of the bi-parental titi monkey (*Callicebus moloch*), in which fathers carry infants more than do mothers, have shown that fathers are more likely to be the preferred partner for infants [Mendoza & Mason, 1986; Hoffman et al., 1995]. In a choice test infant titi monkeys preferred the father to the mother, and showed reduced stress responses when allowed access to the father. These findings support Harlow's [1958] view that the necessary nutritional contribution by mothers does not account for patterns of attachment. Rather, the individual (or object) that provides the most contact for the infant appears to become the attachment object.

Cooperatively breeding primates present an interesting complication regarding ideas of attachment. In cooperatively breeding species there are a variety of potential caretakers: mothers provide obligatory nursing, but the carrying of infants can be done by the father as well as by older siblings or non-reproductive helpers. As the number of helpers within a group increases, the amount of time fathers carry infants is reduced in various species of tamarins and marmosets [McGrew, 1988; Price, 1992; Santos et al., 1997; Washabaugh et al., in press]. Studies involving removal of the father in common marmosets (*Callithrix jacchus*) have found that infants show little distress if the infants remain with the mother [Arruda et al., 1986]. In that study, however, there were no adult helpers present, so the effects of multiple caregivers on infant response to separation could not be evaluated. Chalmers and Locke-Hayden [1986] found that common marmoset infants showed signs of distress both when infants were physically separated from their families and when the family members were treated with a tranquilizing agent that reduced responsiveness to infants.

Locke-Hayden and Chalmers [1983] reported that infant common marmosets had different rates of independence from mothers, fathers, and older siblings, and had different relationships with each type of caregiver. Cleveland and Snowdon [1984] reported that infant cotton-top tamarins (*Saguinus oedipus*) received different degrees of carrying from different family members, with fathers and adult male siblings providing the most care. As infants became independent they developed different relationships with different family members, playing most with their twin or nearest-age siblings. These results suggest two hypotheses with respect to attachment: attachment may be more diffuse in cooperative breeding primates, with many family members being able to serve as attachment figures for infants. Alternatively, strong attachments may be developed as is seen in other primate species, with the primary attachment directed toward the family member that was most involved in carrying the infant at an early age.

We studied infant cotton-top tamarins from birth through 20 weeks of age in order to understand attachment behavior in cooperatively breeding primates. Infant tamarins are carried almost continuously for the first 4 weeks, and become increasingly independent thereafter. They are carried only 50% of the time by week 8 and are almost completely independent by week 12 [Snowdon, 1996]. We used scan sampling over the first 100 days to determine which individuals carried each infant. From week 8 through week 20 we used focal animal observations to document which individuals shared food with infants, which individuals were the infants' partners during social play, and which individuals the infants associated with in

affiliative interactions. Finally, we presented a series of six experimental fear tests to the infants to determine how they would respond and to which individuals the infants would run if frightened.

METHODS

Subjects and Housing

We studied eight infant cotton-top tamarins (three twins and two singletons) born to five families. Four twins were male and four were female, and each set of twins was mixed-sex. One set of twins was the first born to its parents. Two groups (one twin, one singleton) had four older siblings present, and the other two groups (one twin, one singleton) had three older siblings present (Table I).

The small family was housed in a cage measuring $1.8 \times 1.0 \times 2.3$ m, and the larger families were housed in cages measuring $1.8 \times 3.0 \times 2.3$ m. The cages contained tree branches, ropes, and other climbing structures, and all food and water was presented 1 m or more above the floor in order to simulate the arboreal environment of cotton-top tamarins. Temperature was maintained at 26–28°C, with a 12:12 hr light cycle. Three family groups were housed individually in separate rooms. Where multiple groups were in the same room, cloth barriers prevented visual contact between cages, although animals could hear and smell other animals in the room. The two groups with infants in multiple-group rooms were housed so that they were the only group to see who entered the room. Our experience has been that groups housed in a single room under these conditions do not behave differently from groups housed in separate rooms. Monkeys were fed a cereal and vitamin mix early in the morning, with a main feed of Zu-Prem Marmoset Diet and Purina Marmoset Chow supplemented with fresh fruits and vegetables and a starch between noon and 1:30 P.M.. A high protein snack was presented in late afternoon. For further details of husbandry see Ginther et al. [2001].

Design and Procedure

For the first 100 days after infant births, scan sample data were collected at 10 A.M., Noon, 2 P.M., and 4 P.M. on which group members were observed to carry infants. At each of the time points the door to a room was opened and any animal observed carrying an infant was identified and marked on a data sheet on the outside of the door. In a previous study we showed that scan samples correlated closely with results from focal animal observations [Ziegler et al., 2000].

Beginning in week 8 and continuing through week 18, infants were observed twice weekly for 20-min sessions, one in the morning (10 A.M. to noon) and one in the afternoon (noon to 2 P.M.). In groups with twins, separate observations were made on each infant. One observation each week was made when the group had just received its primary feed between noon and 2 P.M. to observe food transfers. Food transfers are a commonly observed behavior in which an adult or older sibling offers food to infants or allows the infant to take food [Feistner & Price, 1990; Roush & Snowdon, 2001]. We made observations of the number of 30-sec intervals of infant carrying, huddling, grooming, contact, social play, and nursing. We also recorded frequencies of food transfers. These behaviors and the identity of each individual with which an infant interacted were recorded on check sheets.

Fear tests were carried out in conjunction with data collection for another study (Castro & Snowdon, 2000). To elicit fear responses and determine the response of infants, a series of six tests was presented, with one test every 2 weeks to minimize habituation. These tests were presented in late afternoon at times that did not conflict with other data gathering. After a 5-min baseline observation period, an assistant entered the room wearing a lab coat worn when monkeys had to be captured and one of three masks: one with colorful feathers, one depicting

an orangutan, and one depicting a parrot. Three masks were used in an attempt to minimize habituation to the stimuli. These stimuli constituted novel, threatening stimuli that led to arousal and attempted mobbing by adult tamarins [Castro & Snowdon, 2000]. Because the groups tested were either the only group in a room, or were the only group that could see the door opening, due to visual barriers separating other groups, only the group being tested was exposed to the assistant wearing the mask. There were 5 min of continuous exposure to the person wearing the mask, who remained standing and facing the cage throughout. The three masks worn by the assistant were presented in a Latin Square design repeated twice so that families received different orders of presentation. Two observers gathered data, one recording vocalizations and the other recording behavior. Behavioral data were dictated into a tape recorder, and the test sessions were subsequently transcribed to obtain precise temporal information. Observers were trained to meet a laboratory standard of interobserver reliability greater than 0.85. In groups with twins, both infants were observed simultaneously so that each infant would have the same degree of exposure to novel, threatening stimuli. Because our main dependent measure was time in contact with another group member, it was possible for one observer to record both infants accurately. Vocalizations were recorded using a Sennheiser ME66 directional microphone and Marantz PMD 221 monaural cassette recorder. The equipment had a virtually flat frequency response to 14 kHz. Calls were analyzed using SIGNAL RTS software for real-time spectral analysis, and calls were classified according to the descriptions of adult calls given by Cleveland and Snowdon [1982] and the descriptions of infant calls given by Castro and Snowdon [2000]. Adult calls could not be identified individually due to the intense response to the threat stimulus, so the rate per family was the unit of analysis. Infant calls were identified individually and, therefore, vocal rates for infants were analyzed by individual.

Data Summary and Analysis

Data from the scan samples of infant carrying were summarized according to the percentage of total scans each potential caretaker was observed carrying each infant. From this we identified primary and secondary caregivers. Data from the focal animal samples were summarized in three categories: 1) the rate each group member was observed to transfer food with the infant, 2) percentages of intervals of social play observed with each family member, and 3) a combined measure of affiliative behavior that included percentages of intervals with huddling, grooming, and other contact. During the fear tests, data were summarized according to the amount of time infants were being carried by or in contact with other group members during the 5 min after presentation of the fearful stimulus.

Concurrent work in our laboratory with cotton-top tamarin infants has found that averaged across all family members, twins receive similar care. However, we found no significant correlations between the behaviors expressed by twins within a litter [Washabaugh et al., in press]. Therefore, data analyses involving behavior of family members and responses to family members used the number of families ($n=5$) in analyses, averaging across twins. Infant vocal responses were analyzed using the eight infants as the sample size.

RESULTS

Based on scan samples taken 4 times a day during the first 100 days after birth, infant carrying was shared among several group members, with the father and mother being the major carriers for four of the infants, the father and oldest brother for three of the infants, and oldest brother and oldest sister for the remaining infant. Primary and secondary carriers were determined for each infant based on the percent of scans they were observed to be carrying. The mean percent of scans that the primary carrier was observed with an infant was $55.1\% \pm 12.2\%$ (mean $\pm$ SEM), and for secondary carriers it was $22.3\% \pm 3.0\%$ of scans (Table II). Males carried significantly

more than females (males $72\% \pm 7.8\%$ of scans; females $27\% \pm 7.8\%$ of scans, $t(4)=2.97$, $P=0.04$).

The mean rate of food transfers per individual was 33.5 ± 5.4 across the 12 weeks of observation. Food transfers were done primarily by the father for two infants, divided between the older brother and father for three infants, and divided between the older brother and mother, father and mother, and older sister and older brother, respectively, for the remaining infants. The mean percent of food transfers was $63.7\% \pm 11.7\%$ for the primary partner, and $23.4\% \pm 7.8\%$ for the secondary partner. Social play was done primarily with the twin (or in the absence of a twin with the nearest-aged sibling) for each infant, with a mean of $69.1\% \pm 7.8\%$ of observed time in social play being with the twin or youngest sibling. The mean time in affiliation was 85.6 ± 15.4 min out of the 480 min of observation. Affiliative social partners (for huddling, grooming, or contact) were much more diffuse. The twin was the primary affiliative partner for three infants, the oldest brother for one, the youngest sibling for another, and the father for a third. There was nearly equal division between mother and twin for one infant, and between oldest brother and twin for the last infant. The mean percent time in affiliative contact with the primary partner was $43.2\% \pm 5.5\%$.

Although infants played primarily with their twin or youngest siblings and had a wide variety of affiliative partners, their responses in fear tests were highly consistent. When the fear stimulus was presented, infants typically stopped what they were doing and (with one exception) ran toward one specific individual. In six of these cases the infants climbed on the individual in the group that had previously carried that infant and food-transferred the most with that infant. In four cases this was the father, and in two cases it was the oldest brother. For the seventh of these cases the infant (D) had received slightly more carrying and food transferring from its older sister, with the oldest brother ranking second, but in fear trials it ran most often to the oldest brother, with the oldest sister being the second most frequent target. Finally, one other infant (W) received more carrying and food transferring from its oldest brother than its father, but in fear tests responded equally toward the oldest brother and the father. The mean rate of response to the primary partner in fear trials was $81.5\% \pm 8.3\%$ of the time—a higher percentage of response directed toward one individual than was seen with any other behavior. Males were the primary targets of infant responses to fearful stimuli (males: $91.4\% \pm 6.3\%$; females: $8.6\% \pm 6.3\%$, $t(4)=8.37$, $P=0.001$). In seven of the eight infants, the percentage response to a specific individual in fear tests was marginally greater than the percentage of carrying provided by that individual in early infancy ($77.9\% \pm 8.8\%$ in fear tests vs. $49.4\% \pm 13.2\%$ in carrying, $t(4)=2.51$, $P=0.066$).

Adults gave increased numbers of type A chirps (a mobbing call [Cleveland & Snowdon, 1982]) in response to the threatening stimulus (mean 0.0 in pre-stimulus baseline, mean 2.7 ± 1.0 during the stimulus, $t(4)=3.02$, $P<0.05$). In addition to vocalizing, many adults moved to the side of the cage closest to the threat. In contrast, infants reduced their rate of “protochirps” vocalization [Castro & Snowdon, 2000] from a mean of 21.8 ± 3.8 in the pre-stimulus baseline to 8.5 ± 2.3 during the threat presentation ($t(7)=3.20$, $P<0.02$).

DISCUSSION

There was considerable variation in infant-carrying across infants. For four infants carrying behavior was distributed over several carriers, with the primary carrier doing little more than a third of the carrying. For the two infants with no older siblings, the father was the primary carrier, and for two other infants an eldest brother carried more than 75% of the scans. Despite this variation, males carried significantly more than females, as we have seen in other studies [Cleveland & Snowdon, 1984; Ziegler et al., 2000; Washabaugh et al., in press].

Similar variation was seen with food transferring. Fathers, mothers, eldest brothers, and eldest sisters all contributed substantial amounts of food transferring that varied for individual twins. Only in the twins with no older siblings did fathers engage in 100% of the food transferring. In general, males did more food transferring, confirming results found with an independent sample of infants in our colony [Roush & Snowdon, 2001], although data from another colony found food-transferring behavior was spread over more group members [Feistner & Price, 1990]. When the primary carriers of infants were combined with primary partners in food transferring, the father or oldest brother emerged as the primary caretaker for seven of eight infants. For the remaining infant there was a virtual tie between the oldest brother and oldest sister in carrying and food-transferring behavior.

When infants became independent they played most often with their twin or nearest-age sibling if there was no twin, as has been reported previously [Locke-Hayden & Chalmers, 1983; Cleveland & Snowdon, 1984]. Affiliative relationships observed in calm, undisturbed settings revealed a pattern of highly diffuse relationships. The mean percent time spent in affiliation with the primary partner was typically less than the time spent being carried by the primary partner or in play with the twin. For four infants the primary affiliative partner was also the primary play partner, whereas for the other four infants the primary affiliative partner was a parent or eldest sibling.

However, in response to the fearful or threatening stimuli, infants were highly consistent in their responses. Seven of the eight infants spent two-thirds or more time in contact with one specific individual during presentation of a threatening stimulus, and in six of these seven cases the animal that the infants ran to was the one that had been most involved in carrying and food transferring during early infancy. Infants were in contact with a male caregiver more than 90% of the time during presentation of fear stimuli. These results nicely parallel those obtained in titi monkeys, in which infants preferentially chose to be in contact with their father over their mother, and fathers appeared to provide a secure base for fearful infants [Mendoza & Mason, 1986; Hoffman et al., 1995]. However, in cooperatively breeding species, non-reproductive helpers are also actively involved in infant care and, as we have shown here, these non-reproductive helpers can also serve as a secure base when infants are frightened. We would expect similar results with other cooperatively breeding species such as Florida scrub jays, wolves, naked mole rats, and meerkats, though we are not aware of similar studies with these species.

Infants appeared to be calmed by contact with their attachment object. Although the mean rate of adult mobbing vocalizations increased significantly during fear tests, the rate of infant vocalizations declined. We noted informally that whereas adults frequently moved toward the stimulus displaying piloerection, the infants either riding on or sitting next to their attachment partner rarely showed piloerection during the tests.

Although fathers and older brothers appear to be the primary attachment objects in these natural families, there were more adult and subadult male siblings than females in our sample. In a different sample with more adult and subadult females, we would predict greater carrying and food transferring by female siblings, with a possible attachment developed toward female siblings. Arruda et al. [1986] showed that removal of fathers (the parent that did the most infant carrying) from the group had little effect on the behavior of infant common marmosets. This suggests that other family members can compensate for the absence of a primary caregiver. We have found that despite considerable variation in the behavior of individual caregivers over a broad range of group sizes and prior experience, infant tamarins receive consistent amounts of care [Washabaugh et al., in press]. One benefit of cooperative infant care is that in the face of variation in infant care, or even the loss of a major caretaker, the rest of the group can provide compensation. Similar compensation can be seen in Cercopithecine primates, in which,

following the loss of the mother, adopted infants can develop strong attachments toward adoptive parents (often males that would not normally be involved in infant care) [Thierry & Anderson, 1986].

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TABLE I**Focal Infants and Group Composition**

Infant	Birth status	Siblings
W	Singleton	Adult brother, subadult brother and sister, juvenile sister
X, Y	Twins	Subadult brother, sister, juvenile brother, sister
Z, A	Twins	None
B, C	Twins	Adult brother, subadult brother, juvenile sister
D	Singleton	Adult brother, sister, juvenile sister

Adult siblings are >21 months and post-pubertal; subadults between 14–21 months; juveniles between 7–14 months.

TABLE II
Primary and Secondary Partners With Infants in Different Contexts

Infant	Carry	Food transfers	Play	Fear
W	Father 30% Brother 24%	Brother 56% Mother 28%	Young Sib 55%	Brother 51% Father 48%
X	Father 31% Mother 26%	Father 31% Brother 31%	Twin 62%	Father 92%
Y	Father 33% Mother 27%	Father 43% Mother 32%	Twin 50%	Father 99%
Z	Father 80% Mother 20%	Father 100%	Twin 55%	Father 87%
A	Father 76% Mother 24%	Father 100%	Twin 64%	Father 64%
B	Brother 75% Father 17%	Brother 54% Father 31%	Twin 98%	Brother 89%
C	Brother 81% Father 11%	Brother 67% Father 33%	Twin 82%	Brother 94%
D	Brother 35% Sister 29%	Sister 58% Brother 32%	Young Sib 87%	Brother 76%

Brother and sister refer to eldest siblings.