MATERNAL RESPONSE TO MOTHER–OFFSPRING SEPARATION IN THE CHIMPANZEE (*PAN TROGLODYTES*)

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For management and/or research purposes, chimpanzee mothers and their offspring are often physically separated from one another at an earlier age than they would be in the wild. Studies of the behavioural and physiological effects of mother–infant separation on infant behaviour have been conducted in both human and nonhuman primates. However, few studies have been conducted to examine the response of the mother to separation from her infant, particularly in great apes. The current study opportunistically examined the response of twelve chimpanzee mothers to separation from 15 of their offspring ranging from 1.8 to 5.4 years of age. Behavioural data (proximity of the mother to other group members, and fifteen behaviours representing six categories [agonistic, prosocial, vocalisations, abnormal, locomotor, inactive]) were collected for three weeks prior to and three to five weeks following the permanent removal of the offspring from their mothers. A repeated measures MANOVA conducted on all subjects revealed no significant change in behaviour following separation. There was a significant increase in inactivity following separation of the offspring ($F_{2,21} = 5.47$, $P < 0.05$) in a subgroup of mothers ($n = 8$) that was studied more intensively on the first day of separation. Maternal age, infant age, presence of other offspring, and past experience with mother–offspring separation had no effect on response to separation. These results contradict those of mother–infant separation studies in monkeys and indicate that most behavioural indicators of well-being are stable in chimpanzee mothers that remain in their familiar environment and social group following offspring separation.

Keywords: *animal welfare, behavioural management, chimpanzees, despair, protest, social separation*

Introduction

A considerable amount of research has been conducted on the behavioural and physiological effects of mother–infant separation in both nonhuman and human primates (Mineka & Suomi 1978). Early work with humans indicated that infants exhibit a biphasic change in behaviour following separation, characterised by an initial period of agitation referred to as the 'protest phase', followed by a 'despair phase' (Bowlby 1960). Behavioural changes of this type have also been observed in nonhuman primate infants (Hinde *et al* 1966; Kaufman & Rosenblum 1967). In studies of mother–infant separation, the infants exhibit a protest phase evidenced

by increased levels of vocalisation, locomotion and hyperactivity. This is generally followed by a despair phase evidenced by decreased levels of social behaviour and increased levels of inactivity and self-directed behaviour. In addition, physiological changes, specifically increased levels of cortisol, have been found in infants following separation from their mother (Smotherman *et al* 1977; Mendoza *et al* 1978; Vogt & Levine 1980; Coe *et al* 1983; Stanton & Levine 1985).

Whereas the response of the infant has been well documented in the literature, the response of the mother to these separations has not. Most studies of mother–infant separation focus solely on the infant and do not report on the maternal response (eg Preston *et al* 1970; Kaufman & Rosenblum 1981; Reite *et al* 1989; Laudenslager *et al* 1990). In fact, an early review of social separation in monkeys by Mineka and Suomi (1978) discussed the behavioural response of adolescent and older monkeys to peer and family separation, but made no mention of the response of the mother to separation from her infant. In addressing the lack of research on maternal response to separation, Capitanio (1986) hypothesised that the maternal response to separation would be similar to that of the infant. However, the few studies that have examined the nonhuman primate mothers' response suggest that it is somewhat different from that of the infant in that mothers display signs of protest but relatively few or no signs of despair (Jensen 1968; Kaplan 1970; Hinde & Davies 1972; Vogt & Levine 1980; Champoux & Suomi 1994). Despite the behavioural differences, there may not be a significant difference in the hypothalamopituitary–adrenal response of mother and infant to separation. For example, mother squirrel monkeys show a marked pituitary–adrenal activation when separated from their infants (Vogt & Levine 1980).

There has been very little research on mother–infant separation in the great apes. Codner and Nadler (1984) described the response of single gorilla, orangutan, and chimpanzee infants to maternal separation. As in mother–infant separation studies of monkeys and humans, the great ape infants exhibited a biphasic change in behaviour marked by increased levels of vocalisations and locomotion immediately subsequent to separation, followed by an increase in inactivity similar to despair seen in other primates. These results were corroborated by Hoff and colleagues (1994) who examined mother–infant separation in three gorilla infants. Neither of these studies examined the response of the mother to separation from her infant. In fact, there have been only two published reports of maternal response to infant separation in great apes. In a pilot study of three chimpanzee mothers' response to separation from their infants (Bloomsmith *et al* 1988), only one of the three mothers displayed behavioural changes characteristic of protest, and none of the mothers showed behavioural evidence of despair. These results were corroborated by Tarou and colleagues (2000) who described the behavioural response of an orangutan mother (*Pongo pygmaeus abelii*), which showed no evidence of protest and only a slight indication of despair following separation. The findings of these two studies suggest that mother–offspring separation in orangutans and chimpanzees may be less stressful for mothers than might be expected. However, the generalisability of these findings is compromised because of the small sample size.

The purpose of the current study is to expand upon the results of the Bloomsmith *et al* (1988) pilot study by combining those data from three chimpanzee mother–infant separations with data from twelve other mother–offspring separations that occurred for colony management purposes later in the same facility. The larger sample size allows for a more robust test of maternal response to infant separation in the chimpanzee, and is the largest sample of great apes ever studied for response to social separation. The results from this study will be useful in developing scientifically sound practices for managing chimpanzee colonies.

Methods

Subjects and their management

The subjects were twelve competent chimpanzee (*Pan troglodytes*) mothers housed at The University of Texas M D Anderson Cancer Center in Bastrop, Texas, USA. The mothers, aged 12–32 years, were housed with their youngest offspring in social groups consisting of at least two other members. During twelve of the separations, mothers had an older offspring living with them at the time that a younger offspring was separated. The social groups were housed in corrals or in conventional indoor/outdoor housing (see Riddle *et al* 1982).

Three male and twelve female offspring ranging in age from 1.8 to 5.4 years were permanently separated from their mothers. These ages represent infancy and juvenile period for young chimpanzees. These separations were carried out for a variety of purposes including removal of a youngster nearing puberty from the group containing his/her parents to prevent inbreeding, weaning of infants from nursing to increase the likelihood of the mother's returning to reproductive function, assignment of youngsters to research projects, and facilitation of the formation of other social groups. Ages of the offspring varied with the reason for the separations. To remove the offspring, the mother–infant dyads were separated from their social groups in the morning, and most were anaesthetised with ketamine hydrochloride (dosage of 7–10 mg kg^{-1}) for physical examinations. Two mothers did not require anaesthesia for separation, but all of the offspring were anaesthetised for brief physical examinations. For the mothers, this process required about one hour of chemical restraint. Each mother was then placed alone in a smaller, adjoining enclosure for recovery. After full recovery later that day, the mother was reintroduced into her social group without her infant. Three of the twelve mothers experienced two separations from offspring over the course of study, providing us with fifteen instances of mother–offspring separation.

Data collection

Behavioural and social proximity measures were collected for three weeks prior to and three weeks following mother–offspring separation. Separations took place between 1987 and 1995, during various months of the year. Twelve to twenty 15 min observations were conducted from 1987 to 1995 for each subject during each of the two experimental phases. Observation sessions were balanced for time of day and totalled 143.25 h of data. Fifteen behaviours representing six behavioural categories (agonism, prosocial behaviour, vocalisation, abnormal behaviour, locomotion, inactivity) were recorded during each session and were later analysed (Table 1). In addition, social proximity data were collected by recording the age and gender of each animal interacting with the focal subject at the sampling point and of each animal within 1 m of the focal subject. These behavioural and proximity measures were recorded using an instantaneous scan sampling technique with 10 s intersample intervals.

Data collection for the pre-separation phase began three weeks prior to the separation of the mother and her infant. The post-separation phase began on the afternoon of the separation, and observation was carried out over a three-week period. Once the mother was fully alert following the anaesthetic episode, she was reintroduced to her social group (approximately 5–7 h after initial separation). Our observations began as the mothers returned to their social groups. Two mothers did not require anaesthesia for separation and, therefore, observations on these mothers began in the morning immediately following the separation. At least one or two observation sessions were completed for each subject on the

first day of separation. The frequency of observations varied after the first day, but they were conducted at least four times per week.

A subset of eight mothers was studied more intensively on the first day of separation to explore more fully the possibility of temporary behavioural changes immediately following the separation. These mothers were observed for 1.5 h in six observation sessions on the day of separation. The subjects were not restricted to the indoor or outdoor portions of the enclosure during the observation sessions, so data were collected both indoors and outdoors.

Table 1 Definitions of behaviours measured in this study.

	Defined by/including
Agonistic behaviours	
Attack	Aggressive interaction involving physical contact. Includes hitting, tugging, grabbing, biting, stomping, rolling or repelling the other animal.
Bared teeth scream	Mouth widely opened, lips fully retracted from teeth and gums with high-pitched, intense, intermittent screams.
Prosocial behaviours	
Social play	Non-aggressive actions involving two or more individuals. Never accompanied by pilo-erection; may be accompanied by play face and/or laughing.
Social groom	Picking through hair or skin and removing debris with hands and/or mouth. Does not include pulling hair out.
Vocalisations	
Pant grunt	Rapid, rhythmic series of grunts or barks directed toward another.
Vocalisation	Includes alarm calling, food calling, shrill barking, tantrum screaming, and whimpering.
Abnormal behaviours	
Abnormal	Includes coprophagy, faeces smearing, hair pulling, and self slapping.
Locomotor behaviours	
Locomotion	Includes walking, climbing, brachiating, etc.
Receive follow	Another animal is locomoting directly behind the focal animal (within 1 m).
Move in contact	Any physical contact with another animal that is not recorded under a different behavioural category.
Follow	Locomoting directly behind another individual (within 1 m). Does not include chasing during play.
Inactive	
Nurse while resting	Another chimp is contacting the subject's nipple with an open mouth.
Rest in contact	Any physical contact with another animal that is not recorded under a different behavioural category; includes touching another animal while not moving.
Resting	Includes lying down, leaning, reclining, or apparently sleeping.
Other/inactive	Any other stationary behaviour.

Data analysis

Data were analysed using a repeated measures multivariate analysis of variance (MANOVA) to detect any differences in behaviour in each of the six behavioural categories (agonistic behaviour, prosocial behaviour, vocalisation, abnormal behaviour, locomotion, inactivity) between pre-separation and post-separation phases. Repeated measures MANOVAs were also used to determine whether there was a significant effect of past experience with infant separation or presence or absence of older offspring on the behaviour categories measured. Statistical interactions between these factors and the phase of the study (pre-separation and

post-separation) would indicate effects of these variables on the response of mothers to separation. Because main effects of these factors on the subjects' behaviour (eg behavioural differences between younger and older mothers) were not relevant for the purposes of this study, these effects are not reported. There was not a sufficient number of subjects to allow analysis of all of these factors simultaneously in a single MANOVA, so individual analyses of variance were conducted for each factor. For this reason we were not able to assess possible interactions between these factors. Regression analyses were used to determine whether there was a significant effect of maternal age or offspring age on maternal response to separation.

An analysis of variance (ANOVA) was used to determine changes in social proximity based on the mean amount of time the mother spent in proximity to other members of her group. An ANOVA was also used to determine whether there was a significant effect of the age/sex class of a group member on the mean amount of time the mother spent in proximity to other group members. The results of all analyses were considered significant if $P < 0.05$.

Interobserver reliability was maintained at greater than 90% agreement among the six categories of behaviour. One of the observers collected data in the earlier pilot study as well as in the present study, and the other observers' reliability was tested against this individual, so reliability over the entire period of the study was ensured.

Results

Behaviour of mothers prior to and after separation

The results of the behavioural observations conducted on the mothers prior to and after separation from their offspring are presented in Table 2. A repeated measures MANOVA comparing the six behavioural categories prior to and after the separation for the entire group was not statistically significant ($F_{6,23} = 0.52$, $P > 0.05$). Repeated measures ANOVAs failed to reveal significant differences in any of the individual behavioural categories between the pre-separation and post-separation phases.

Table 2 Mean percentage of behavioural scans recorded per session during the pre- and post-separation phases of the study.

Behavioural category	Phase of study	
	Pre-separation	Post-separation
Agonistic behaviours	0.09%	0.13%
Prosocial behaviours	10.3%	8.8%
Vocalisations	0.43%	0.61%
Abnormal behaviours	0.46%	0.87%
Locomotion	11.98%	11.1%
Inactivity	44.8%	49.6%

A subgroup of eight mothers was studied more intensively on the first day of separation. Table 3 presents the results of the behavioural observations prior to separation, on the first day of separation, and following the first day of separation. A repeated measures MANOVA comparing the same six behavioural categories prior to separation, on the day of separation, and during the remainder of the post-separation phase (from day two through to the end of the three-week period) was statistically significant ($F_{12,32} = 2.58$, $P < 0.05$). Repeated

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measures ANOVAs on each of the six behavioural categories revealed a significant change in inactivity ($F_{2,21} = 5.47$, $P < 0.01$). Inactivity increased significantly from 68.4% in the pre-separation phase to 80% on the first day of separation, and was at 77.3% during the remainder of the post-separation phase. Bonferroni *post hoc* tests revealed a significant difference in the mean percentage of time for which mothers were inactive between the pre-separation phase and on the first day of separation ($t_7 = –3.66$, $P < 0.05$), but not between the first day of separation and the post-separation phase. There were no significant differences in agonism, prosocial behaviour, vocalisations, locomotion, or abnormal behaviour.

Table 3 **Mean percentage of behavioural scans recorded per session in the pre-separation phase, on the first day of separation, and in the post-separation phase of the study.**

Behavioural category	Phase of study		
	Pre-separation	Day 1	Post-separation
Agonistic behaviours	0.02%	0.16%	0.02%
Prosocial behaviours	9.09%	7.61%	4.25%
Vocalisations	0.19%	1.92%	0.26%
Abnormal behaviours	0.30%	2.03%	2.34%
Locomotion	9.45%	9.16%	9.66%
Inactivity	67.03%	73.3%	72.44%

Effect of maternal age

The mothers in the study ranged in age from 12 to 32 years. Regression analyses were conducted to determine whether there was a relationship between the mother's age and the intensity of each post-separation behaviour. The results from the analysis of all mother–offspring separations revealed that there was a significant linear relationship between age and vocalisation. Older mothers exhibited less vocalisation following the removal of their offspring than the younger mothers ($r^2 = 0.3$; $F_{1,13} = 5.577$, $P = 0.034$). This trend was not observed prior to offspring separation ($r^2 = 0.089$; $F_{1,13} = 1.26$, $P = 0.28$). However, in looking at the data it was found that most mothers exhibited very low levels of vocalisation (0.0–0.26% of scans). Four of the mothers exhibited much higher levels (1.0–2.7% of scans), and it appeared that their data led to the statistically significant finding noted. There were no significant relationships between the age of the mother and any of the other behavioural measures.

Regression analyses were also used to determine whether there was a significant relationship between the ages of the mothers in the more intensely studied subgroup and their response to the first day of separation. The results showed that agonistic behaviour significantly decreased as age increased ($r^2 = 0.42$; $F_{1,8} = 5.83$, $P = 0.04$). This trend was not found prior to separation ($r^2 = 0.04$; $F_{1,8} = 0.30$, $P = 0.6$) or after the first day of separation ($r^2 = 0.089$; $F_{1,8} = 0.78$, $P = 0.4$). There were no significant relationships between the age of the mother and any of the other behavioural measures.

Effect of age of offspring

Regression analyses were used to test the hypothesis that the age of the offspring might affect the mother's response to separation. There were no significant relationships between the age of the offspring at the time of separation and the mother's response on any of the behavioural

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measures. There were also no significant relationships between the age of the offspring and the response of the mother on the first day of separation for the mothers that were more intensively studied.

Effect of presence or absence of older offspring

During twelve of the separations, mothers had older offspring that remained in the group following the removal of their younger offspring. To determine whether the presence or absence of these older offspring affected the maternal response to separation, the data were categorised into one group that had older offspring in the group (n = 12) and one group that did not have older offspring (n = 3). A MANOVA revealed no significant effects of the presence or absence of older offspring on maternal response to separation. The number of individuals housed without older offspring in the subgroup of intensively studied subjects was insufficient to conduct a similar analysis.

Effect of past history with mother–offspring separation

To examine the effect of the mothers' past history with mother–offspring separation, the mothers were divided into two groups: mothers that had had at least one offspring removed from them in the past (n = 7), and mothers that had never previously had any offspring removed (n = 8). There were no significant differences between these groups on any of the measured behaviours either in the entire subject pool or in the subgroup of more intensively studied individuals.

Effect on proximity

The mothers spent a mean of 21.5% of their time in proximity to their youngest offspring and 13.9% of their time in proximity to other group members in the pre-separation phase of the study. In the post-separation phase, the mothers spent 10.2% of their time in proximity to other members of the group. This was not a significant difference as tested by a repeated measures ANOVA.

To further examine any changes in group dynamics following separation, the other individuals of the group were classified as adult females, adult males, non-adult females, non-adult males, or other offspring of the subject. The mean amount of time spent by the mothers in proximity to each individual was estimated by determining the amount of time spent by the mother in proximity to each group member and dividing that amount by the number of individuals in the classification. A MANOVA was used to test for significant changes in this mean proximity of the mother to individuals of specific age/sex class. There were no significant changes over the course of the study.

Discussion

Separation of chimpanzee mothers from their infant or juvenile offspring was associated with few significant changes in behaviour. There were no significant changes in agonistic behaviour, prosocial behaviour, vocalisation, abnormal behaviour, or locomotion in the entire subject pool. In a subgroup of mothers studied more intensively on the first day of separation, there was an increase in inactivity during the post-separation phase of the study. This higher level of inactivity could be one symptom of despair (Bowlby 1960), although the difference was not very large (64.8% during pre-separation; 77.3% during post-separation). No other behaviours changed. There was no evidence of protest or agitation in chimpanzee mothers as a reaction to the removal of their offspring.

The chimpanzee mothers in this study reacted very differently to separation than do both human and nonhuman primate infants. Whereas chimpanzee infants exhibit behavioural changes characteristic of protest and despair following separation from an attachment object (Bard & Nadler 1983; Snyder *et al* 1984), the chimpanzee mothers in this study did not show such changes in behaviour.

The maternal response to separation observed in this study was also different from that of other nonhuman primate mothers. Previous studies have reported increases in vocalisation and locomotion indicative of protest, but relatively few or no signs of despair in mothers following removal of their infants (Jensen 1968; Kaplan 1970; Hinde & Davies 1972; Vogt & Levine 1980; Champoux & Suomi 1994). However, Suomi and colleagues (1983) observed mostly inactive behaviour in rhesus monkey mothers following separation from their infants. In their study, the mothers were allowed to remain in their home cage following separation from their infant. These results are similar to those observed in the present study in which the chimpanzee mothers were placed back into their familiar social group and environment following separation from their infant. Champoux and Suomi (1994) hypothesised that the environment in which separation takes place may play a role in determining the maternal response to infant separation in monkeys. They found that rhesus monkey mothers placed in a novel environment with other mothers also separated from their infants showed classic signs of protest following the removal of their infants. The separation environment has been shown to be a very important factor in determining the strength and duration of both the infant response to maternal separation (Mineka & Suomi 1978) and the adult response to family separation (Suomi *et al* 1975). It is therefore possible that the lack of protest observed in this study is attributable to the fact that the chimpanzee mothers were returned to their familiar social group and environment following separation from their offspring.

There were no significant differences in the time spent by the mothers in proximity to other group members overall, or to any one age/sex class in particular, as a result of the social separation. This was true even for mothers with an older offspring still present in the group. These results differ from those of our pilot study (Bloomsmith *et al* 1988), in which mothers spent significantly more time in proximity to older offspring following separation from their younger offspring. With a larger sample of subjects in the present study, mothers did not spend significantly more time in proximity to older offspring in their group.

This study also examined the effect of maternal age, offspring age, and past experience with mother–offspring separation on the behaviour of the mothers in response to the removal of their offspring. None of these factors influenced the measured responses. It was hypothesised that mothers with younger offspring would show more behavioural indications of protest and agitation following separation than mothers that had had older offspring removed, but this was not supported. None of the offspring in this study was younger than 1.8 years when removed from the mother. It is possible that the maternal response may have varied if younger offspring had been separated.

The results of this study provide further evidence that the maternal response to separation differs from that of the primate infant. Also, while studies of maternal separation in monkeys have shown that the monkey mothers exhibited protest but not despair, the present study found no evidence of protest in the chimpanzee mothers. This may be because they were housed in a familiar social group and environment and because none of the offspring was younger than 1.8 years when removed. It is important to note that research on the physiological response to mother–offspring separation indicates that lack of a behavioural

response does not necessarily indicate a lack of reaction to separation. Coe and colleagues (1983) found that both infants and mothers showed an increase in adrenal activation following separation. This increased activation remained constant even after behavioural indications of separation had disappeared. Further research on the maternal response to separation in the great apes using both behavioural and physiological measures is necessary to fully understand their response to separation from offspring.

Animal welfare implications

Captive chimpanzee mother–offspring pairs are separated from one another earlier than would occur naturally for a variety of reasons including health concerns, experimental study requirements, and facilitation of reproduction or population management. This study indicates that most behavioural indicators are stable in chimpanzee mothers that remain in their familiar physical environment and social groups after being permanently separated from their offspring. In this study, offspring were aged between 1.8 and 5.4 years, and it is important to note that there may be a different response if younger offspring are removed. The one behavioural effect that was measured was increased inactivity among those mothers that were more intensively studied on the day of separation. This may be evidence of 'despair' in these mothers, although the difference in the amount of time devoted to this behaviour was not very large. Because this study was continued for only three weeks beyond the separation, we do not know the duration of this effect.

These results have implications for the welfare and effective management of chimpanzee mothers in captivity. If mothers and offspring must be separated, the mother chimpanzees should be kept in their familiar social and physical environments to protect their welfare. We did not test an alternative technique of allowing the offspring to remain in the familiar environment and transferring the mother, but that may be worth investigating. Monitoring for individual mothers that may be inactive is appropriate during the post-separation period, but since mothers showed minimal responses, more personnel effort should be devoted to managing the welfare of the offspring when a mother–offspring separation is planned, and less to the mothers.

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