The Influence of Rearing Conditions on Maternal Behavior in *Cynomolgus* Macaques (*Macaca fascicularis*)

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We studied the influence of rearing on the adequacy of maternal behavior by comparing 20 harem-reared and 15 peer-reared primiparous cynomolgus monkeys. We used them plus 11 wild-caught females to extend this comparison to multiparous subjects and also to compare primiparae with multiparae. We observed no behavioral effect of rearing and parity. Primiparous maternal adequacy amounted to 93% in peer-reared subjects and to 95% in harem-reared monkeys. We extensively discuss theories concerning rearing effects. Leitmotifs throughout the discussion are survival value of maternal behavior immediately after parturition and predictive value of this behavior for the further course of maternal behavior. Support is accumulated for the hypothesis that certain tactile and visual experiences suffice for the development of adequate maternal behavior.

KEY WORDS: monkey; maternal behavior; delivery; parity; rearing.

INTRODUCTION

Three decades ago Harlow and co-workers published results of investigations into the influence of maternal deprivation on the development of social behavior in rhesus monkeys (Harlow and Seay, 1966; Harlow and Harlow, 1965). Female rhesus monkeys that had been reared solitarily, usually did not take care of their young. In 1976, Ruppenthal *et al.* reviewed

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the results of research into the influence of several types of social deprivation on the development of maternal behavior in rhesus monkeys. Their review shows that 76% (32 of 42) of the females that had been brought up solitarily, with or without a surrogate mother, did not take care of their firstborn young. Females, that had been reared together with peers, failed in 25% of all cases (2 of 8). Females that had been brought up by their mother but in the absence of other mothers and their young failed in <5% of all cases (n probably large). Females that had been reared by their mothers living in groups nearly all took care of their babies. It further appeared that a number of females that had failed when primiparous behaved adequately when multiparous.

In cynomolgus macaques, Kemps and Timmermans (1984) compared the maternal behavior of primiparous females reared with surrogate mothers in a peer group with primiparous females brought up by their mothers in a harem group. They found that, with respect to peripartus behavior, primiparous mothers reared in peer groups not only adequately took care of their young but also did not differ from primiparous subjects brought up by their mothers. At that time Kemps and Timmermans (1984) observed only three monkeys that had been raised with surrogate mothers in a peer group. Now we have data on 15 cynomolgus macaques that have been raised in peer groups with surrogate mothers. The aim of this report is to present data on the adequacy of maternal behavior of females from three different rearing conditions: with surrogate mothers in peer groups, by their own mothers in harems, and by their own mothers in the wild. Because the criterion, used by Ruppenthal *et al.* (1976) to determine the adequacy of maternal behavior—raising the baby independently—turned out to be a very relevant one in the study of Kemps and Timmermans (1984) we use it as the most important parameter and guideline.

The phenomenon of disturbed maternal behavior of socially deprived rhesus monkeys led to the learning-to-mother hypothesis (Spencer-Booth, 1968; Lancaster, 1971; Hinde, 1974; Hrdy, 1977; Hiraiwa, 1981), according to which observational learning and play-mothering play an important part in the acquisition of maternal behavior. Scollay and Debold (1980) questioned the adaptiveness of the learning experience and agreed with Quiatt (1979) that allomothering was not selected for improvement of care for one's own infant. Little attention was paid to verifying the learning-to-mother hypothesis experimentally, but it continued to play a part in the explanation of the ontogenesis of maternal behavior (McKenna, 1982; Coe, 1990). Fairbanks (1990) found that captive primiparous vervets that as juveniles had performed more allomothering were more successful in rearing their young. However, observations of free-ranging Japanese macaques brought Tanaka (1989) to the conclusion that primiparous females learn

to nurse on the basis of experience with their own babies. Tanaka reported that allomothering by nulliparae was rare and that on the first day after delivery primiparae often pushed their young away from the teat. Chism (1991) questioned the function of allomothering as a way of learning to handle infants. Nicholson (1991) suggested that play-mothering by nulliparae does not guarantee subsequent adequate maternal behavior when primiparous, and that to a certain degree observational learning can compensate for social deprivation. Because one of our rearing conditions, growing up with surrogate mothers in peer groups, excluded play-mothering and observational learning whereas in the other rearing condition, growing up with mothers in a harem, these experiences could occur, our experimental results can also contribute to an evaluation of the learning-to-mother hypothesis which as far as we know has not been tested experimentally.

METHOD

We investigated the influence of rearing conditions on the adequacy of maternal behavior by comparing female cynomolgus macaques that grew up with surrogate mothers in peer groups with female cynomolgus macaques that were brought up by their mothers in harem groups. Because most of the monkeys gave birth to several young, we were able to investigate the influence of repeated motherhood as well. To the group of multiparous subjects we could add a number of females, that had been caught in the wild.

Following Ruppenthal *et al.* (1976) the criterion for adequacy of maternal behavior is that the mother can raise her own baby without intervention by a human caretaker. Bringing up an infant independently is a very suitable criterion by which to evaluate the adequacy of maternal behavior because it immediately relates to the biological function of maternal care. In both nature and captivity the young is completely dependent upon its own mother. If in the wild the mother does not continuously keep her baby with her, it soon will perish. Although in captivity dangers are few, the mother also has to carry her baby with her continuously in order to keep it warm and to enable it to feed. In a cage, a suckling left to itself will get supercooled and weakens quickly. Ono *et al.* (1989) found that 2 hr after birth the body temperature of cynomolgus infants that were not cared for by the mother amounted to only 32 to 29°C. In that case intervention is indicated in order to keep the baby alive.

We consider not only the adequacy of maternal behavior but also the influence of delivery by means of cesarean section, adoption, kidnapping and the effects of mastitis. We applied cesarean section only if a mother

was in labor unsuccessfully during a long period and if the young was in breech position. We arranged adoption only if a motherless neonate as well as a lactating mother, whose baby had died recently, were available. We corrected kidnapping by returning the baby to its mother.

Every morning at 0800 and every evening at 1700, we monitored all pregnant and lactating subjects from behind a one way screen. We observed monkeys that were near term, monkeys with babies <1 week old, and monkeys with abnormal behavior or with an abnormal condition several times in the course of the day. At the day of its birth, we inspected each baby in order to ascertain that it was mature and healthy and that it displayed normal clinging behavior. Only when the baby was fully developed and healthy, did we include the data concerning maternal behavior of its mother for analysis. Also, we established whether the mother was in normal condition and lactated. Furthermore, we recorded the way she behaved toward her baby in terms of keeping it in a ventroventral position and allowing it to nurse. If a mother did not take care of her baby adequately, we postponed intervention as long as the baby stayed active. If the baby lacked initiative, we took it out of the cage, warmed it, bottle fed it, and gave it back to its mother. If after 1 day the mother still did not accept her young, we made no further attempt to keep it with her except in the case of mothers that had delivered by means of a cesarean section, for which we additionally attempted reintroduction on the next day. If a mother carried her stillborn young with her for more than 1 day we took it from her.

Subjects and Housing Conditions

During the period they grew up and during the period data were collected, the subjects lived in cages measuring either $5.0 \times 4.0 \times 2.0$ m or $5.0 \times 3.6 \times 2.4$ m. Each cage is in a separate room. All cages are furnished with horizontal and vertical wooden poles.

To prevent observational learning and allomothering in the primiparous groups during the observation period, we kept mothers with child and delivering mothers out of sight of nulliparous females by dividing cages into two equal compartments via an opaque partition. Mothers with child as well as nulliparous subjects always had the company of at least two group members.

The floors of the cages were covered with wood chips. Water was available *ad libitum* via drinking-nipples; we provided food (Hope Farms) in the morning and in the evening. Twice per week, the monkeys got cereals or apples or both. Lights were on from 0800 until 2000. Temperature ranged between 18 and 22°C.

In the investigation into the influence of rearing conditions on primiparous females, 35 subjects participated, all of which had been born and raised in our laboratory. At the time of the investigation they lived in harem groups consisting of one adult male and five to eight sexually mature females. Ages of the mothers at the moment of their first childbirth range from 4 to 6 years.

The experimental group consisted of 15 subjects that had been raised with surrogate mothers in peer groups. They and the monkeys of the control group had been used earlier in an investigation into the influence of rearing conditions on the development of phobic behavior (Timmermans *et al.*, 1994). A peer group consisted of 5–12 individuals, males as well as females. Each group lived in a separate cage. Within 1 week after birth we took the babies away from their mothers and placed them on artificial surrogate mothers. We used only young of adequate mothers. During 7 months, they were bottle-fed with Similac with iron (M&R Laboratoria, Zwolle, The Netherlands), supplemented with monkey chow and apples or cereals. Water always was available *ad libitum*. When the young were 1 year of age, the surrogate mothers, which by that time were threadbare, were removed. Details on the surrogate mothers and bottle feeding are in Timmermans *et al.* (1988). From maturity on the females were kept in harem groups together with monkeys of the same rearing condition and the same age.

The control group consisted of 20 females that grew up with their own mothers in harem groups. From the time they became sexually mature they lived—just like the females of the experimental group—in harems together with animals of the same rearing condition and the same age.

We used all females of the control group and 11 females of the experimental group as multiparous subjects. To this sample we added a group of 11 multiparous females, captured in the wild. At the beginning of the investigation the age of the multiparous subjects ranged from 5.7 to ± 8 years. All multiparous subjects lived in harems under conditions similar to those in which the aforementioned groups lived.

RESULTS

Table I contains the results on the primiparous and multiparous females from the experimental group and the control group and the results on the multiparous monkeys captured in the wild. The low frequencies of occurrence of several categories of inadequate behavior rendered statistical testing redundant.

Table I. Numbers of Full-Term Young, Born Dead and Born Alive, and Numbers of Young, Abused, Uncared for, Adopted, and Kidnapped, in Mother-Reared and Peer-Reared, and in Primiparous and Multiparous, *Cynomolgus* Monkeys

	Parity				
	Primiparous		Multiparous		
			Rearing		
	With mothers in harem (<i>n</i> = 20)	With surrogates and peers (<i>n</i> = 15)	Wild (<i>n</i> = 11)	With mothers in harem ^a (<i>n</i> = 20)	With surrogates and peers ^a (<i>n</i> = 11) ^b
Born dead	0	1	15	17	0
Born alive	20	14	76	68	27
Abused	0	1 ^c	0	0	1 ^c
Uncared for:	1 ^d	1 ^d	0	2 ^d	0
Uncared for after cesarean section	0	0	2 ^e	2 ^e	0
Adopted after stillbirth	0	1 ^f	1 ^f	0	0
Kidnapped	0	0	2 ^g	1 ^g	0

^aThe same *S*'s that were used as primiparae.

^bFour monkeys were no longer available.

^cOne *S* licked and sucked two infants to bleeding.

^dOne harem-reared *S* neglected three infants; one peer-reared *S* neglected one infant.

^eFour *S*'s neglected infants delivered by cesarean section.

^fTwo *S*'s adopted infants after stillbirth.

^gTwo *S*'s kidnapped.

We mention the numbers of young born alive and of stillborn young as frame of reference. These numbers, indeed, show that in primiparous subjects the incidence of stillbirth is much lower than in multiparous animals. In multiparous subjects, in those that had been captured in the wild, and in those reared in harem groups, stillbirth seemed to occur more often than in multiparous subjects that had been raised on surrogate mothers. This result probably is an artifact because the subjects captured in the wild and those reared in harems are older than the subjects that grew up on surrogate mothers. Inspection of the individual data showed an increase of stillbirths as a function of age. Furthermore, large interindividual differences exist in the number of stillbirths. Of 42 females, 17 gave birth to one or more mature dead babies; in 9 of the 17, the number of stillborn babies exceeded one. Most mothers carried their dead infants and offered resistance when they were taken away.

Table I does not provide indications that the other parameters were under the influence of rearing conditions or repeated motherhood. If we leave aside the mothers that underwent a cesarean section, a total of 39

of 42 mothers adequately took care of all their babies ($n = 199$). Only three mothers failed: one peer-reared mother with respect to one of her five babies, another peer-reared mother with respect to two of her nine babies, and one harem-reared mother with respect to all three of her young. We shall describe these deviant cases individually in order to allow an adequate evaluation of the part played by their background.

One peer-reared subject did not take care of her first baby. She sat apathetically near her newborn and the placenta and did not resist when her baby was taken away (the baby was afterwards adopted by a cage mate). She took care of her subsequent four babies adequately.

One peer-reared female maltreated two of her nine babies: the first and the sixth. Maltreatment consisted of excessive licking and sucking at limbs of the neonate, ultimately leading to abrasions. Already in the period immediately before delivery this monkey showed intensive staring, while she licked her lips abnormally slowly and extensively. Her other behavior was normal; she also resisted when her babies were taken away. She reared her other seven young without injuring them.

One harem-reared monkey insufficiently took care of her three babies. Although she carried and fed them occasionally, more often she pushed them away and sometimes prevented them from clinging to her. As it appeared that the young were retarded in their growth, we separated them from her. The first and the third baby stayed with the mother for 2 weeks and the second for 4 weeks before we had to separate them. The mother did not resist when her babies were taken. After her third baby she was sterilized.

Four multiparous females were found in the morning with a foot or tail of the young protruding from their vagina. A cesarean section was performed under general anesthesia. Afterward the mothers were placed in a small cage within the harem cage without their babies. When after 1 hr the effect of the anesthetic had ceased so that the mothers could walk again, they received their babies during 1 hr in their cage. None of them took care of her baby or picked it up; if the babies tried to cling to them, they pushed them away. Next day when the babies were again presented to them, their behavior was similar. The mothers did not resist when their babies were taken away. All of them previously had raised three or more babies by themselves.

Two monkeys, one primiparous and the second multiparous, permanently adopted a neonate. They had given birth to stillborn young, while in that same night other mothers refused to take care of their newborn. Both prospective foster mothers resisted when their dead babies were taken away, and they snatched up the living young, after it had been put on the floor a few meters away from their perch. The primiparous foster

Fig. 1. *Cynomolgus* macaque mother with newborn stumptailed macaque.

mother adopted the neonate of a primiparous cagemate. The multiparous foster mother adopted a neonate stumptailed macaque from another colony. (Fig. 1).

Two multiparous females kidnapped babies of cage mates. Both had already raised several young of their own. One of them stole two babies, the first one on the day of its birth and the second 1 day after its birth. The other female stole a young once, 2 days after its birth. Both resisted when the stolen young were taken away. We returned the babies to their mothers; they accepted them and took care of them. But that day the kid-

nappers took the babies again. These kidnapping females were dominant over the mothers; they sat down with the mothers, groomed them and their babies, and subsequently took the babies. In order to put an end to this behavior we separated the kidnappers from them for 2 weeks; thereafter kidnapping ceased. At the time of the kidnapping the kidnappers did not have young aging <1.5 years old, and they did not lactate. One of them was not pregnant; the other one was quite close to giving birth at the time of her first kidnapping and was pregnant in the second trimester during her second kidnapping.

After having taken care of their babies for some weeks four other multiparous mothers (not mentioned in Table I) pushed their babies away from the teat or prevented them from grasping it by keeping a forearm across the breast or by stretching the upper part of the body. The cause of this rejection appeared to be mastitis. Together with their babies, these mothers were segregated in a small cage within the harem cage. The mothers received antibiotics and the babies received supplementary feeding if necessary. Within 3 days the mothers again took care of their babies adequately.

DISCUSSION

Most subjects adequately cared for all their young; rearing condition and parity did not seem to play a part. The few mothers that failed were divided randomly among the groups and the type of failure generally did not give reason for blaming the mothers' rearing conditions.

One of the peer-reared subjects that bore nine live young injured the first and the sixth one by prolonged licking and sucking one bodily place. According to Ruppenthal *et al.* (1976), however, socially deprived females that reacted inadequately to their firstborn but adequately to the next infant remained adequate mothers thereafter. Further, one of the characteristics of inadequate mothers is indifference to the removal of their infants. Our subject, however, once relapsed to abnormal behavior after adequately caring for four young and she offered resistance when the maltreated young were taken away from her on both occasions. Further, excessive licking has not been mentioned among the abnormal behaviors imputed to maternal deprivation. So there are no reasons to ascribe the deviation of this mother to her rearing condition. The behavior of the peer-reared subject that did not accept her first infant but subsequently cared adequately for four young resembles the behavior of the indifferent motherless mother (Ruppenthal *et al.*, 1976). Probably due to exhaustion, she was apathetic after the first delivery, which also could explain her indifference. The behavior of the

harem-reared subject that neglected all three of her infants resembles a mild type of indifference, but our subject was equally indifferent to all her offspring, whereas the maternal indifference described by Ruppenthal *et al.* (1976) was most obvious in primiparous females; multiparous ones behaved much more adequately.

Four multiparous females underwent cesarean section under general anesthesia. The mothers refused to accept their infants which is in accordance with our previous findings (Timmermans *et al.*, 1981) and the findings of Lundblad and Hogden (1980) that after cesarean section under general anesthesia, only 3.5% of a great number of rhesus and cynomolgus monkeys accepted their infants.

With respect to effects of rearing conditions on the adequacy of maternal behavior, Kemps and Timmermans (1984) found peer-reared primiparous mothers not to differ in any parameter of maternal behavior from harem-reared primiparous mothers. Ruppenthal *et al.* (1976) found that peer-reared rhesus monkeys with or without surrogate mother were adequate mothers (75%) more often than subjects that grew up solitarily (24%) but that their adequacy is still well below that of laboratory-born subjects that grew up with their mothers (95%). So, our present result with peer-reared cynomolgus macaques (93%) is about the same as that which Ruppenthal *et al.* (1976) found with mother-reared rhesus macaques.

Though the ratio of adequate versus inadequate peer-reared rhesus mothers (6:2) and the small number of peer-reared subjects (8) reported by Ruppenthal *et al.* (1976) do not exclude doubts about the reliability of this result, the conclusion that peer-rearing (like solitary rearing) leads to inadequate maternal behavior has been widely accepted, prompting us to explain why 93% of our peer-reared cynomolgus macaques were adequate mothers. It seems improbable that a difference between the two species is the underlying cause because cynomolgus and rhesus are so closely related that prolific hybrids occur in the overlapping part of their habitats (Thailand) and in zoos (Fooden, 1964). The difference between the results might depend on differences between the peer conditions used. Unfortunately, a detailed description of the rearing conditions to which Ruppenthal *et al.* (1976) referred is not available (Ainsworth, 1984). It is not clear what kind of surrogates the rhesus monkeys had and how often and how long they had contact with peers. Our monkeys had heated fur-covered surrogate mothers with a pouch enclosing the infant like the arms and thighs of a mother, and peers were always present (Timmermans *et al.*, 1988). Accordingly, there seem to have been differences in opportunities for physical contact between rhesus and cynomolgus. We will elaborate the role of physical contact below after recapitulating relevant findings and suggestions.

Recapitulation of the results of studies on rearing conditions produces the following picture. In rhesus monkeys adequate maternal behavior was exhibited by 24% (10 of 42) of solitarily-reared subjects, 75% (6 of 8) of peer-reared subjects, 95% (*n* probably large) of mother-reared subjects, and $\approx 100\%$ (*n* probably large) of subjects born in the wild. Further, it appeared that if solitarily-reared monkeys were exposed to peers <1 year of age or during adolescence, the probability of becoming an adequate mother increased $\approx 50\%$ (Ruppenthal *et al.*, 1976). Maternal behavior in cynomolgus monkeys was adequate in 93% (13 of 14) of the peer-reared subjects, and in 95% (19 of 20) of harem-reared subjects. Further, there is Meier's (1965) controversial finding that solitarily-reared rhesus females (*n* = 5) adequately cared for their infants. Meier's (1965) study was not cited in Ruppenthal *et al.* (1976) and only rarely thereafter!

Meier (1965), well aware of the difference between the results of Harlow and Harlow (1962) and his own results, argued that the conditions under which his monkeys grew up provided more visual and auditory stimuli from conspecifics, infants included, than Harlow's conditions did. Seay (1966) proposed that the presence of peers probably compensated for the absence of the mother. Fedigan (1982) pointed out that solitarily-reared monkeys were deprived not only of maternal care but also of physical stimulation and suggested that lack of physical contact was the cause of abnormal behavior in socially deprived monkeys. Without mentioning maternal behavior explicitly, Suomi (1982) also suggested that physical contact is essential for the development of normal social behavior. Kemps and Timmermans (1984) agreed with Seay (1966), suggesting that growing up in a social environment suffices and specific experiences with maternal behavior are not necessary. Nonetheless, social contact, be it tactile, or visual and auditory, or all three factors, during infancy or later, seems to be most important. Meanwhile, Ruppenthal and co-workers' observation (1976) that their data did not specify how or why peer contact so strongly enhanced the development of maternal behavior has not been elaborated. We will return to this point when dealing with the role of physical contact.

It is remarkable that the question of what caused the relatively small difference in the numbers of adequate mothers among social-reared females (peer- and mother-reared—75 and 95% adequate—versus reared in heterogeneous groups—almost 100% adequate) has drawn more attention than the question of causes for the greater difference between social- and solitary-reared females (24 versus 75, 95, or 100%). This focus gave rise to the learning-to-mother hypothesis, in which observational learning and play- or allomothering (further called practice) act as learning mechanisms. The hypothesis is based on opposing two types of rearing conditions: ones that exclude observational learning and practice (solitary, with mother, with

peers) versus conditions in which observational learning and practice *could* occur (groups with mother–infant couples). Further, it is based on the observation that juvenile females play with infants.

The importance of practice was suggested by Spencer-Booth (1968) and Hinde (1974) for rhesus macaques, Lancaster (1971) for vervets, Hrdy (1977) for langurs, and Hiraiwa (1981) for Japanese macaques. However, the finding of Ruppenthal *et al.* (1976) that 95% of females reared with mother (only) became adequate mothers and the finding of Kemps and Timmermans (1984) and of our study that most peer-reared females are adequate mothers suggest that practice is of little importance. Further, Tanaka (1989) found in free-ranging Japanese macaques that allomothering was rare in nulliparous females and that primiparous mothers apparently had to learn nursing through experience with their own young. In captive vervets living in groups, Fairbanks (1990) found that primiparae that as juveniles had performed more allomothering were more likely to keep their offspring alive. Because the effects of inherent individual differences in attraction to infants could not be separated from effects of allomothering, Fairbanks suggests a combination of predisposition and experience. Chism (1991) doubted whether practice is the function of allomothering.

Though Ruppenthal *et al.* (1976) already concluded that observational learning was not necessary to “exhibit the basics of maternal care” (p. 348). We found only one attempt to assess experimentally the role of observational learning. Dienske *et al.* (1980) found that primiparous rhesus monkeys reared solitarily from about 4 months of age with a view of cages with mother–infant couples accepted their own young, though initially holding them in deviant positions, whereas most females that grew up with a view of cages with conspecifics other than mothers and infants were indifferent to their own young. Unfortunately their experiment does not answer the question whether females that accepted their infants gave a (defective) imitation of what they had seen or accepted their infants because they had become familiar with infants by seeing them. Still, without referring to new data Coe (1990) concluded that in monkeys the strong genetic base for maternal behavior in normal circumstances is completed by observational learning during the prepubertal phase.

It is curious that in speculations concerning the learning-to-mother hypothesis, the actual behavior of the mother has hardly played a part. Therefore, one should begin by inquiring what a monkey mother actually should do to preserve her newborn infant, because as we will argue below, that is the essence of maternal behavior in macaques. Next, we will evaluate what practice and observational learning could possibly contribute in acquiring the skills needed to preserve the neonate. Finally, we will suggest

why contact with peers, or more generally, social contact may play such an important part in the development of these skills.

We now restrict the discussion to periparturitional behavior because this behavioral episode is decisive for the survival of the neonate. Because of its altricial condition, the neonate is completely dependent upon the reactions of its mother immediately after birth. Another justification for the restriction to delivery behavior is that the mother's postparturient behavior is highly predictive of the further course of her relation with the infant. Our experiences with ≈ 200 deliveries of cynomolgus monkeys show that mothers that carried their infants with them on the morning after delivery kept caring for them adequately almost without exception. This corresponds with the findings of Ruppenthal *et al.* (1976) which show that there was no doubt whether a mother sufficiently cared for their newborn or that it had to be saved.

Parturient female rhesus macaques (Brandt and Mitchell, 1971; 1973), cynomolgus macaques (Kemps and Timmermans, 1982; 1984), pigtailed macaques (Goodlin and Sackett, 1983), and Japanese macaques (Negayama *et al.*, 1986) squat while straining and investigate their anogenital regions manually, and from the moment the head of the baby is crowning, they support it during expulsion (Trevathan, 1987). Mothers even are able to handle neonates at birth without visual guidance as demonstrated by 23 cynomolgus monkeys that delivered in total darkness on a pole 1.5 m above the floor and carried their infants at their ventra in the morning without any sign of an accident.

Lancaster (1971) suggested that in the laboratory, adequate mothering may involve no more than passive acceptance of the offspring. Accordingly the true test for adequate mothering should take place with free-ranging monkeys. Our data show that, even in a cage, much more than passive acceptance is involved. But we agree with Lancaster (1971) that important clues for assessing the functional adequacy of maternal behavior can be found in the natural environment.

The cynomolgus monkey preferably passes the night on branches overgrowing water (van Schaik, 1985). Like rhesus (Brandt and Mitchell, 1971), pigtailed (Goodlin and Sackett, 1983), and most other macaques (Jolly, 1972), cynomolgus macaques generally give birth at night (Suzuki *et al.*, 1990; Timmermans and Vossen, 1996). When the natural circumstances are borne in mind, the adequacy of investigating the anogenital zone and supporting the neonate at birth is obvious. In the wild, mothers that do not support their infant immediately at birth and thereafter will lose them at once.

The mother has to bring the infant into ventroventral position, whereby the neonate is nestled between the mother's thighs and arms, pro-

viding her an opportunity to lick herself and the neonate and to handle the placenta (Timmermans and Vossen, 1996). The ventroventral position gives the infant benefit of the mother's body heat and enables it to reach her teats. Further, this position permits the mother to move without having to support the infant. The importance of licking the neonate's fur dry probably depends on the prevailing temperature. It certainly seems important to free the neonate from the placenta by eating it or by biting through the umbilical cord, because a placenta dangling from the infant is a hindrance for locomotion (Timmermans and Vossen, 1996).

What role could observational learning and practice play in acquiring the basics of maternal behaviors? It is improbable that visibility at night in a leafy tree is sufficient to observe a mother's manipulations with her neonate. Furthermore, it is doubtful whether the features and the consequences of the behavior of a delivering monkey and the span between demonstration and test enable observational learning. Moreover, Visalberghi (1992) failed to teach capuchins and Japanese macaques tool-using behavior via demonstrations by conspecifics. Altogether, the probability of a nulliparous monkey learning periparturitional behavior through observational learning seems negligible.

With respect to the role of practice, it is important to know that play-mothering with neonates can hardly occur in macaques (or in baboons and chimpanzees) because mothers do not permit it (Nicolson, 1986). Moreover, Sackett and Ruppenthal (1974) found that nulliparous rhesus females reared under free-ranging conditions do not find neonates attractive and, Holman and Goy (1980) and Gibber (1986) established that nulliparous rhesus females are unwilling to retrieve sucklings. No doubt, the ability to handle infants will be enhanced by practice with older infants. However, this ability would have to be generalized to handling neonates. Pryce (1995) notes that play-mothering and mothering differ in that a juvenile female responds to the complex mother+infant, whereas the primiparous mother must respond to her infant. Moreover, this generalization has to occur in external and internal circumstances that strongly deviate from the situation in which practice took place (Kemps and Timmermans, 1984) and at a moment inescapably dictated by parturition. In short, the primipara in labor for the first time, sitting in the dark on a branch, without delay has to seize and hold a slimy baby that slips out of her pelvis.

We still have to answer questions posed by Ruppenthal *et al.* (1976) about how and why social contact as provided by peer rearing or later social housing so strongly enhanced the development of maternal behavior. A young monkey normally spends the greatest part of its first half-year in physical contact with its mother. The experiences with physical contact in mother-reared and peer-reared monkeys are twofold. The young cling to

mothers or to surrogates and peers and are held by mothers or by peers (Dienske *et al.*, 1980). Some of the solitarily-reared monkeys described by Ruppenthal *et al.* (1976) had surrogates, but it is not clear which type, and others had no surrogate, so we do not know to what they were clinging; they were not held.

Being held generally is considered indispensable for normal behavioral development because it meets a basic need of the infant, but being held also is an experience that could bring about habituation of being clung to. A mother needs to possess considerable tolerance for physical contact because she has to accept the strongly clinging neonate. Ruppenthal *et al.* (1976) reported that most solitarily-reared mothers avoided being clasped by their offspring, and Holman and Goy (1980) and Gibber (1986) found that nulliparous rhesus avoided neonates, which demonstrates that being clasped initially is an aversive experience. In a model of the regulation of maternal motivation in mammals, Pryce (1992) distinguishes four factors, two of which are aversion and fear of novelty evoked by the neonate. Meier (1965), who found no negative effects of solitary rearing until 60 days of age, daily handled (weighed) his subjects, which were quite tractable. This could indicate that they were habituated to tactual stimulation.

Next to being deprived of physical contact, the solitarily-reared monkeys to which Ruppenthal *et al.* (1976) refer may have been more or less deprived of seeing conspecifics. Meier (1965) and Dienske *et al.* (1980) suggested that seeing and hearing infants may facilitate the development of maternal behavior. The cages in Meier's laboratory were much closer together than those in the Wisconsin laboratory to which Ruppenthal *et al.* (1976) refer and visual and auditory stimuli from infants were abundant every day. Accordingly, there seem to exist considerable differences among rearing procedures, concerning opportunities to see and hear conspecifics and being handled by caretakers. The reason 76% of solitarily-reared females did not take care of their offspring (Ruppenthal *et al.*, 1976) could have been that after delivery the females suddenly were confronted with two impressive novel experiences: a more or less unfamiliar living being in their living space that was clasping them.

Regarding opportunities for social contact (visual and auditory as well as tactual), the features of the surrogate mothers that we used and the continuous presence of peers made our peer-rearing much more like mother-rearing than the peer-rearing (with part-time peers and probably less sophisticated surrogate mothers) to which Ruppenthal *et al.* (1976) refer. This could be the reason 93% of our peer-reared subjects were adequate mothers but only 75% of the peer-reared females that Ruppenthal *et al.* (1976) described were. A rank order of the rearing conditions according to the percentage of adequate mothers—rhesus solitary, 24%; rhesus with part-

time peers, 75%; cynomolgus with surrogates and full-time peers, 93%; rhesus with mother, 95%; and rhesus and cynomolgus in heterogeneous groups, $\pm 100\%$ —parallels that of opportunities for social contact. Heterogeneous groups excepted, there was no opportunity for observational learning and practice, nevertheless the frequency of adequate mothers in the other condition varied between 24% and 95%. There is little variance to be explained by observational learning and practice, which is in accordance with the argument that it is highly improbable that these mechanisms of learning play an important part in the development of periparturitional behavior.

In conclusion, the suggestion of Seay *et al.* (1964) that the inadequate behavior of solitarily-reared females does not mean that maternal behavior is of necessity learned but that inadequate early experiences block its expression is affirmed, with the addition that inadequate early experiences probably can be compensated by social housing later on (Ruppenthal *et al.*, 1976). Fundamental social experiences in the realm of tactile, visual, and perhaps auditory stimulation seem to be most important and sufficient for the emergence of maternal behavior at delivery. Of course, this does not mean that learning-to-mother can play no part in acquiring maternal abilities enhancing the survival of offspring. We underscore that maternal behavior immediately postpartum is obligatory if the neonate is to survive, that this behavior already contains the basics of maternal care and is highly predictive of the adequacy of subsequent maternal care, and that it is highly improbable that postpartum behavior is acquired through play-mothering or observational learning.

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