Maternal Behavior of Laboratory-born, Individually Reared Long-tailed Macaques (*Macaca fascicularis*)

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To investigate maternal behavior in laboratory-born, individually reared monkeys, we carried out a statistical analysis of 896 long-tailed macaques (*Macaca fascicularis*) based on breeding records of the Tsukuba Primate Research Center (National Institute of Biomedical Innovation, Ibaraki, Japan). Data were obtained from 3266 cases of normal delivery between 1982 and 2004. In each case, maternal behavior was classified as either adequate or inadequate. We examined the effects of parity and the sex of the infant on maternal behavior. We also investigated the similarity of maternal behavior between mothers and their daughters and the effect of quality of maternal care received in infancy on maternal behavior as an adult. The results showed that only the mother's number of deliveries had a significant effect on maternal behavior. The greatest improvement of maternal behavior was observed at second delivery, and the incidence of improvement kept being above 0 thereafter. Our results suggest that, as reported previously, parity is an important factor in the adequacy of maternal behavior in individually reared monkeys.

Abbreviations: IR, improvement ratio; IA, individual adequacy; SPF, specific pathogen-free; TPRC, Tsukuba Primate Research Center

The Tsukuba Primate Research Center (TPRC; National Institute of Biomedical Innovation, Ibaraki, Japan) was established in 1978. The original purpose of monkey breeding in the TPRC was to supply the laboratory-bred monkeys for national vaccine safety testing performed in the National Institute of Infectious Diseases. All monkeys in the TPRC breeding colony were free from measles virus by 1982, and the breeding colony became free *Shigella*, *Salmonella*, *Mycobacterium tuberculosis*, *Mycobacterium bovis*, simian varicella virus, and herpes B virus by 2002.

The TPRC now has expanded its function to provide monkeys to medical researchers in a broad range of fields, such as infection and hyperimmunization restraint. These research areas often need monkeys that are specific-pathogen free (SPF) at its highest level. To effectively maintain and supply SPF monkeys and monkey fetuses that are appropriate for each experiment, the TPRC uses individual rearing. Monkeys are separated from their mothers 5 to 6 mo after birth and receive pair-rearing with an age-matched cagemate until 2 y of age. Thereafter, they are kept in individual cages except during mating periods. Even though TPRC monkeys always have visual, auditory, and olfactory contact with their conspecifics living in the same room, their social experience is quite limited compared with that of wild or group-reared captive monkeys.

Many previous studies indicated that monkeys with limited or no social experience show abnormal social behavior. The most extreme cases are reported in a particular series of studies.[1,7,8,19,20] For the duration of their infancy, monkeys were housed without their mothers and with little or no opportunity to interact with other monkeys. As a result, they had difficulty forming normal social relationships in many interactive situations, such as playing,[1,8,20] mating,[7] and mothering.[1,7,20] The abnormal maternal behavior of these monkeys evoked interest among researchers. Some of the females that had poor social experiences as infants abused or neglected their own infants, in some cases so severely that the infants died.[20]

Many of the cited studies were observations of monkeys reared under more severe circumstances than those in a normal breeding colony. Even in normal breeding colonies, most researchers observe only a portion of the colony animals.[12,14-17,21] No large-scale investigation has examined the effects of individual rearing on the maternal behavior of the monkeys. Here we report the statistical analysis of data accumulated over a period of 20 y on the maternal behavior of more than 3000 cases involving approximately 900 monkeys that were individually reared for most of their lives.

Materials and Methods

Rearing and breeding conditions of the TPRC. The rearing and breeding conditions of the TPRC have changed somewhat over time, depending on prevailing regulations and practices. However, what has never changed is the individual rearing of monkeys and the length of time during which monkeys are reared with their mothers or age-mates.

The rearing and breeding conditions were fixed as follows from 2005. Monkeys in the TPRC breeding colony are reared in individual cages (0.5 m wide × 0.8 m high × 0.9 m deep; stainless steel mesh). The breeding rooms are rectangular, and the individual cages are installed on the long sides of the room. Each room contains at least 90 cages. Most (90% to 95%) cages are occupied continuously. Therefore, monkeys can always make visual, auditory and olfactory contact with their room-mates. Ambient temperature in the rooms is kept about 25 °C, and humidity is set at 50% to 60%. The air is replaced 12 times hourly.

Lighting is on for 12 h, from 0700 to 1900. Monkeys are provided with apples in the morning, and monkey chow is given to them twice in the afternoon. Water is available ad libitum.

Monkeys in the breeding colony are inspected daily by experienced animal technicians. When any abnormality is found, a veterinarian examines the monkey promptly and applies the appropriate treatment. Moreover, the monkeys are medically examined under anesthesia at least once every 2 y. The medical examination consists of body weight measurement, tuberculin test, blood sample, stool test, examination of the fundus, and a medicated bath.

Monkeys are separated from their mothers 5 to 6 mo after birth and receive peer-rearing with an age-mate until 2 y of age. After that, they are reared individually except during the mating period. The mating period begins 11 d after menstrual bleeding is observed, which is 1 d before the estimated ovulation. The monkey is anesthetized and moved to the cage next to the mating partner at least 1 d before the start of the mating period. The mating period is begun by removing a partition between the cages. After 3 d the partition is replaced.

Pregnancy diagnosis is conducted by the ultrasonography under anesthesia 5 wk after the end of the mating period. If the female is not pregnant, she begins the next mating period around the presumed ovulation day. During pregnancy, females are reared individually. After delivery, the dam and her infant are reared together for about 6 mo, after which they are separated. The offspring begin peer-rearing with an age-mate, and dams are reared individually again.

These rearing and breeding conditions are approved by the Institutional Animal Care and Use Committee of National Institute of Biomedical Innovation, Japan.

Laboratory procedures. Subjects were 896 laboratory-born long-tailed macaques (*Macaca fascicularis*) in the breeding colony of the TPRC. Data were obtained from breeding records collected between March 1982 and March 2004. Individual monkeys gave birth from 1 to 12 times (mean ± SD, 3.7 ± 2.3). The total number of normal births was 3266.

Animal technicians determined the adequacy of maternal behavior on the basis of daily inspection from the infant's birth to separation of mother and infant, about 6 mo.

Breeding records reported whether a dam showed inadequate maternal behavior, regardless of duration or frequency. Moreover, even if a mother that was once judged to be 'inadequate' never again showed inadequate behavior to the same offspring, the record was never changed. In short, only the cases in which inadequate maternal behavior was *never* observed by the animal technicians were recorded as adequate.

Inadequate maternal behavior was defined as rejection of the infant, holding an infant incorrectly, refusal to nurse, or violence against the infant. The dam's avoidance of, or escape from, physical contact with her infant was considered rejection of the infant. Holding an infant incorrectly means that the dam held her infant on her ventral side upside down. Refusal to nurse means that the dam held her infant correctly but prevented the infant's access to her nipples. Violence against the infant was physically hitting or stepping on her offspring.

When a dam showed inadequate maternal behavior, she and her infant were separated, and food and medical treatment were given to the infant as needed. If the infant regained his or her health, he or she was returned to the mother. In most cases, the infant was returned to the dam only once. The animal technician observed the pair for about 10 min, and if the dam took care of her infant normally, the infant was allowed to remain. If inadequate maternal behavior was observed at that time or at the inspection thereafter, the infant was separated from the mother again and was never returned to her.

If the infant was in poor physical condition for more than 2 to 3 d, or if the dam showed inadequate mothering after the infant's return, the infant was reared by artificial nursing or by foster mothers.

Consistency in adequacy of maternal behavior. Multiparous monkeys were classified into 4 groups based on changes in their adequacy of maternal behavior: good, improved, poor, and inconsistent. Monkeys that showed adequate care for all their offspring were classified as having good maternal behavior. The monkeys belonging to the improved group showed inadequate maternal behavior at the first delivery or between the first and a certain delivery number, but they never had inadequate behavior thereafter. Note that our definition of improvement is based on the change in maternal behavior between deliveries, not on a change with the same infant. Monkeys that showed inadequate maternal behavior with all their infants were classified as having poor maternal behavior. The remaining monkeys were classified as having inconsistent maternal behavior.

Primiparous monkeys were classified into 2 groups (good and poor), based on their maternal behavior.

Effects of parity on maternal behavior. To determine whether adequacy of maternal behavior improves with increasing parity, we compared the proportion of 'adequate care' cases at each number of deliveries. As shown in Figure 1, adequacy of maternal behavior appears to improve after giving birth at least twice. However, this analysis may not reflect the natural tendency for improvement of maternal behavior, as monkeys showing inadequate maternal behavior may have been preferentially been excluded from the breeding colony as a means of colony management. Therefore, in a second analysis, we evaluated dams that gave inadequate maternal care to their first offspring based on the adequacy of mothering toward the second offspring. The monkeys that did not improve their maternal behavior at the second delivery were classified again, this time according to their maternal adequacy toward the third offspring. Data from the inconsistent group were excluded from this analysis. We then calculated the improvement ratio (IR) for each delivery number as $N_a / (N_a + N_i)$, where N_a is the number of monkeys that improved their maternal behavior and N_i is the number of monkeys that continued inadequate maternal behavior. If all monkeys that showed inadequate mothering toward the previous offspring improved, the value of IR was 1. Conversely, if none improved, the value of IR was 0.

Relationship of the maternal behavior of the mother to that of the daughter. A total of 340 pairs of mothers and daughters among the monkeys were included in the study. Because the subjects in the present study consisted of the monkeys belonging to various generations, some subjects were represented both as mother and as daughter. When a monkey had several daughters who experienced delivery, the dam was paired with each daughter. In other words, the number of times that a monkey was represented as mother was the same as the number of her daughters who had experience of delivery. Two analyses were conducted using the data from these pairs..

First, to investigate similarity of maternal behavior between mother and daughter, we calculated the ratio of the number of observations of adequate maternal behavior to the total number of deliveries for each monkey. We defined this value as individual adequacy (IA). We then examined the correlation of IA between daughter and mother by Spearman rank correlation coefficient.
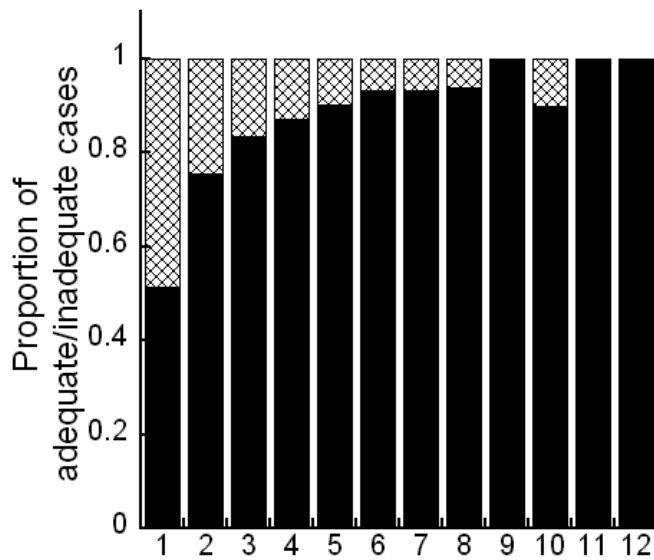
Figure 1. Apparent improvement of maternal behavior with childbirth. We classified each case by the number of deliveries and calculated the ratio of adequate to inadequate maternal behavior. Because there was a possibility that monkeys that showed inadequate behavior were excluded preferentially from the breeding colony, we conducted another analysis (see Figures 2 and 3).

Table 1. Distribution of monkeys, arranged by the consistency of adequacy of maternal behavior

Parity	No. of subjects				Total
	Good	Improved	Poor	Inconsistent	
1	79	na	108	na	187
2	77	30	44	2	153
3	56	58	29	6	149
4	67	34	17	5	123
5	56	24	11	3	94
6	43	22	0	7	72
7	32	15	2	5	54
8	20	11	3	1	35
9	12	7	0	0	19
10	5	2	0	1	8
11	0	1	0	0	1
12	1	0	0	0	1
Primiparous	79	na	108	na	187
Multiparous	369	204	106	30	709
Total	448	204	214	30	896

na, not applicable

Second, to investigate whether the quality of maternal care received in infancy influenced the maternal behavior of the daughter, we divided the daughters into 2 groups according to the quality of maternal care they received (adequate and inadequate). We then compared the IA value and the consistency in adequacy of maternal behavior in the 2 groups of daughters by t test.

Effects of sex of the infant on maternal behavior. We divided all cases by the sex of the infant. We then calculated the incidence of adequate and inadequate maternal behavior in each group and compared them by χ^2 test.

All statistical analyses were performed using StatView statistical software (version 5.0; SAS Institute, Inc., Cary, NC).

Results

Consistency in adequacy of maternal behavior. Of 3266 normal deliveries, 2459 (75.3%) were associated with adequate maternal behavior, and the remaining 807 (24.7%) were categorized as having inadequate maternal care. The severity and continuity of inadequate maternal behavior differed. As soon as inadequate behavior was observed by an animal technician, the infant was separated from the mother for treatment as needed. In 390 of the 807 (48.3%) cases with inadequate maternal behavior, the physical condition of the infant was good, and the dam showed signs of accepting her infant; therefore, the infant was returned to his or her biological mother and was reared by her until their separation. However, if the mother continued displaying inadequate behavior or if the physical condition of the infant was impaired, the infant was reared by artificial nursing (266 of the 807 cases, 33.0%) or by foster mothers (151 cases, 18.7%).

The results of classifying monkeys by the consistency in adequacy of maternal behavior are shown in Table 1. Of primiparous monkeys (n = 187), 42.2% were categorized as having good maternal behavior, and 57.8% were categorized as having poor maternal behavior. Of multiparous monkeys (n = 709), 52.0% were categorized as good; most of the remaining monkeys had

maternal behavior that improved with subsequent births (28.8%) or that remained poor regardless of parity (15.0%). Only 4.2% of the multiparous monkeys were classified as having inconsistent maternal behavior regardless of parity.

In the improved group, the number (mean ± SD) of times that dams continued to show inadequate behavior from the first delivery was 1.5 ± 0.9, with 4.5 ± 2.1 deliveries. The total number of normal deliveries which dams in this group experienced was 909. In 614 of these cases, their maternal behaviors were determined as adequate. In the other 295 cases, the maternal behaviors were determined as inadequate. In the inconsistent group, the mean number of deliveries was 5.1 ± 1.9, and the total number of normal deliveries was 152. In 84 of these cases, maternal behavior of the dams was determined as adequate. In the other 68 cases, the maternal behavior was determined as inadequate.

Effects of parity on maternal behavior. As shown in Figures 2 and 3, the incidence of adequate maternal behavior at the first delivery was 51.7%. The highest IR was observed at the second delivery. After that, the value of IR was low but nonvanishing (Figure 3). However, only a few dams required more than deliveries to develop adequate maternal behavior (Figure 2).

Relationship of the maternal behavior of a mother to that of her daughter. The correlation between the IA of mothers and daughters was not statistically significant (Figure 4; Spearman's rank correlation coefficient, n = 340 pairs, $P > 0.1$). Furthermore, the IA value of the daughters that received adequate maternal care in infancy was not significantly different from that of the daughters that received inadequate care in infancy (t test, t(338) = –0.1, $P > 0.10$; IA of daughters that received adequate care, 0.5 ± 0.4; IA of daughters that received inadequate care, 0.5 ± 0.4). Moreover, consistency in adequacy of maternal behavior did not differ between the 2 groups of daughters (Figure 5).

Effect of sex of the infant on maternal behavior. In total, 1709 infants were male and 1557 were female. For 75.0% (1282) of the male infants and 75.6% (1177) of the female, mothers showed adequate maternal behavior. The quality of maternal care the infants received did not differ according to their sex (χ^2 test, $P > 0.1$).
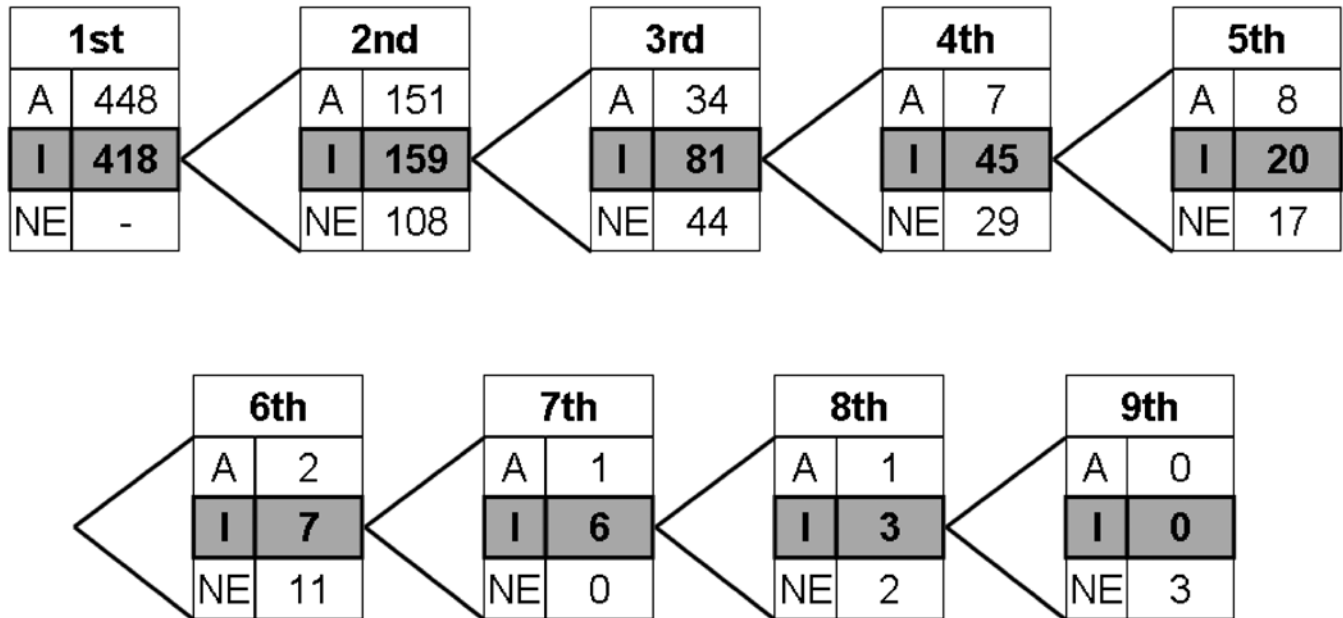
Figure 2. Schema for calculation of improvement ratio (IR) for each delivery number. The ordinal number at the top of each box is the number of deliveries. Inside each box is the number of subjects in each category: A, monkeys that showed *adequate* maternal behavior at delivery; I, monkeys that showed *inadequate* maternal behavior at delivery; NE, monkeys that *did not experience* that number of deliveries. The total number of monkeys at each delivery number is equal to the number of monkeys categorized as I at the previous delivery number. Because the number of monkeys belonging to I became 0 at the ninth delivery, we stopped the analysis at that step.

Discussion

One of the most important questions we asked is whether monkeys in our breeding colony show inadequate maternal behavior at a higher rate than do group-reared or free-ranging monkeys. The incidence of inadequate maternal behavior in the TPRC was 24.7% (807 of 3266 cases). However, our assessment of inadequacy is quite strict: a dam defined as having inadequate maternal performance as soon as she displays a single suboptimal rearing behavior. Moreover, this classification is never revised, even if the dam improves her maternal behavior by the time of protocol-defined separation from her infant. In approximately half (390 of 807) of the cases defined as having inadequate maternal behavior, the dam showed the suboptimal behavior only transiently and then reared her infant successfully without any intervention until the separation. Therefore, we consider the actual percentage of inadequate maternal behavior to be 12.8% (417 of 3266 cases).

In 1 study, the incidence of inadequate maternal behavior in group-reared monkeys was 1.9% to 12.2%.[13] However, the authors stated that the actual incidence might be higher because they counted only severe cases of neglect and abuse. We are aware that not all infant deaths are the result of inadequate maternal care, and for comparison, infant mortality in a free-ranging troop was 6.7% to 16.2%.[9,10,18] Compared with these data, the incidence of inadequate maternal behavior in the TPRC is not unreasonably high.

However, our results do not suggest that the social experience of dams has no effect on their maternal behavior. In our study, the incidence of adequate maternal behavior by individually reared monkeys at the first delivery was 51.7%. In a 1981 study,[21] among 6 long-tailed macaques that received peer-rearing with 6 to 7 age-mates until sexual maturation, all but 1 showed normal maternal care to the first offspring. In a 1989 study of 10 long-tailed macaques reared in different social conditions,[11] 1 group consisted of monkeys that were born and reared in family groups until the first delivery. Another group consisted of monkeys that were born in family groups but were reared with 6 to 7 age-mates. All monkeys in both groups showed adequate maternal behavior. In other studies,[1,20] most of the monkeys that had limited social experience could not rear their first infants, but these authors observed only 4 to 8 monkeys. Of 50 rhesus monkeys that were reared without mothers, 34 (68.0%) abused or neglected their first infants.[19]

The monkeys that showed increased incidence of adequate maternal behavior[11,21] than that in the current study received peer-rearing for a longer time and with more age-mates than did those in the TPRC. In contrast, those that showed poorer rearing skills[1,19,20] were reared in a poorer social environment than those in the TPRC. These results suggest that the duration and complexity of social rearing affect maternal behavior at the first delivery.

As already mentioned, about half the monkeys in our study showed inadequate mothering at their first delivery, but about half of those monkeys improved their maternal behavior by their second delivery. Moreover, few monkeys showed inconsistent maternal behavior overall (Table 1). Overall, about 75% of the monkeys we studied had developed adequate maternal behavior by the time of their second delivery. These results suggest that the maternal behavior can be improved through the delivery experience. Regardless of whether the monkeys are captive or wild, many investigators have suggested that previous deliveries help the dam learn how to treat her infant and contribute to the overall improvement of infant survival rates.[6,9,10,13-15] Even monkeys that received no maternal care in infancy were able to improve their maternal behavior with repetition of delivery.[7,19]

We identified no factors other than parity that affected maternal behavior. Previous studies in group-living monkeys suggested that infant abuse, not neglect, tended to be observed only in particular matrilines.[12,13] We cannot know all the details regarding inadequate maternal behavior at the TPRC in the past, because the breeding records were designed to record

Figure 3. Improvement ratio (IR) for each delivery number. The open circle indicates the incidence of adequate maternal behavior at the first delivery for all subjects (n = 896). The closed circles indicate the IR. We calculated the IR for each delivery number by the formula $N_a / (N_a + N_i)$, where N_a is the number of monkeys that improved their maternal behavior, and N_i is the number of monkeys that continued inadequate maternal behavior. The actual values of N_a and N_i for each delivery number are shown in Figure 2.
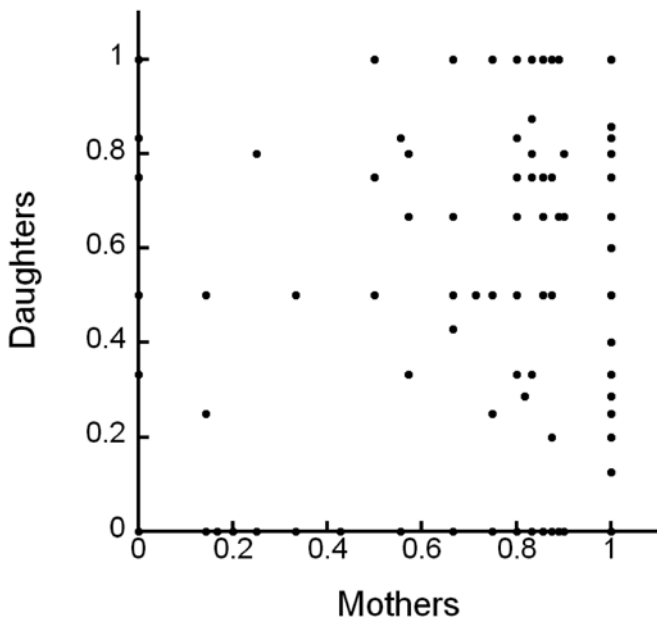

Figure 4. Correlation of individual adequacy (IA) between mothers and daughters (n = 340 pairs). Because some dots overlapped, the number of dots in the figure is less than the number of the pairs. There was no significant relationship between the IA of mothers and that of daughters.

maternal behavior only as adequate or inadequate. Perhaps we found no correlation in the adequacy of maternal behavior between mothers and daughters because of a limited choice of categories. We would need to examine the medical history for each infant until mother–infant separation to determine why maternal behavior was judged inadequate (for example, if the dam physically abused her infant). Moreover, although infant
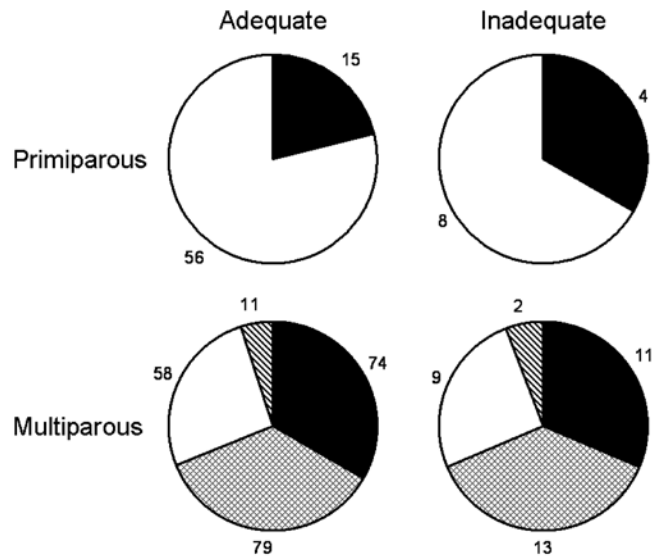

Figure 5. Relationship of maternal behavior of the mothers to that of their daughters. We divided the daughters into 4 groups according to the quality of maternal care they received (adequate or inadequate) and parity (primiparous or multiparous). Numbers show the number of subjects in each group. Black, good; cross-hatched, improved; white, poor; striped, inconsistent.

behavior between the sexes is quite different,[3,16] we did not find any effects of the infant's sex on maternal behavior. Supporting our finding, another study reported that sex of the infant was not a risk factor for abuse or neglect.[15]

Few previous reports about maternal behavior in long-tailed macaques are available; to our knowledge, there are only 2 observational experiments that compared maternal behavior in different rearing conditions.[11,17] Although another article[21] contains statistical data on maternal behavior in captive and peer-reared long-tailed macaques, only 6 subjects were assessed at their first delivery only. Most of the other studies we cite involve other *Macaca* species, and interspecies differences might not be negligible. Considering that long-tailed macaques are used in experiments as widely as other species, more information about their maternal behavior is needed.

Although the incidence of inadequate maternal behavior in the TPRC is not unreasonably high, we are apprehensive about the future. The maternal behavior of peer-reared or isolation-reared monkeys may differ from that of mother-reared monkeys,[4] and differences in maternal behavior may exist between laboratory-born and wild-born monkeys in the TPRC.[17] The differences might increase in each subsequent generation, as could the incidence of inadequate maternal behavior. Indeed, in the current study, the proportion of daughters in the group with good maternal behavior was lower than that overall and the ratio of the daughters in the group with poor maternal behavior was higher than that overall (Table 1 and Figure 5). Directly comparing the adequacy of maternal behavior between generations is difficult because the mean number of deliveries of each generation appears to differ. However, we need to determine whether the incidence of inadequate maternal behavior is likely to increase in future generations. Moreover, the SPF level required differs by experiment, and whether the level of social experience for each subgroup of monkeys can be changed depending on the purpose of the proposed research will be important to determine. Perhaps, for example, extension of the pair-rearing period[2] will decrease incidence of abnormal behavior in our monkeys. Further, modification of the cages may

make it possible to avoid disturbing the physical contact among the monkeys living in the adjoining cages.[5] For TPRC—and other facilities—to continue supplying high-quality monkeys, such possibilities need to be considered.

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