Belg. J. Zool. — Volume 120 (1990) — issue 1 — pages 51-65 — Brussels 1990

(Manuscrit reçu le 8 juin 1988)

ACCELERATION OF THE WEANING PROCESS OF YOUNGER RHESUS MONKEY INFANTS BEFORE THE ANNUAL MATING SEASON STARTS

by

RÉGINE VERCAUTEREN DRUBBEL

Address of the laboratory where the observations have been realized :
MRC Unit on the Development and Integration of Behaviour (Cambridge University)
High Street, Madingley, Cambridge CB 8AA (England)

Present address : Laboratoire de biologie animale et cellulaire CP 160
Université Libre de Bruxelles
Avenue F. D. Roosevelt 50, B-1050 Bruxelles (Belgium)

SUMMARY

Part of the weaning process of young captive rhesus monkeys (*Macaca mulatta*) was studied during the weeks preceding the onset of the annual mating season of autumn-winter. The delay in the emancipation of the youngest infant and this of the infants of subordinate mothers was most conspicuous in the beginning of the study period. Even though the maximal age difference between the infants was relatively large, only slight differences between their degrees of independence remained at the end of the study period. The results suggest that the mothers accelerate the emancipation of their late infants as the following mating season approaches. This catching up phenomenon could have an adaptive value for the mothers.

Key-words : primatology, *Macaca mulatta,* weaning.

INTRODUCTION

The relationship between a rhesus monkey (*Macaca mulatta*) mother and her infant changes markedly in the weeks and months following birth (in captivity : DIENSKE and METZ, 1977 ; SIMPSON *et al.,* 1986 ; on Cayo Santiago : BERMAN, 1980 ; in India and Nepal : JOHNSON and SOUTHWICK, 1984). It was possible to build up a picture of this relationship by analysing the type, the quality and the pattern of interactions that take place between them (HINDE, 1976). A certain consistency in the gradual nature of the development of the mother-infant relationship does appear (HINDE and SPENCER-BOOTH, 1967). Nevertheless it became clear that various factors may induce differences in mother-infant relationships (SIMPSON and HOWE, 1980). Some of them result from the individual properties of the mothers

and infants themselves. For example : the sex of the infant, the status and seniority of the mother in the colony, the number of infants the mother had before and the characteristics of infant or mother (BERMAN, 1980 ; HINDE and HERRMANN, 1977 ; HOOLEY and SIMPSON, 1981 ; TARTABINI and SIMPSON, 1986 ; STEVENSON-HINDE and SIMPSON, 1981 ; SEAY, 1971 ; WHITE and HINDE, 1975). Other differences are determined by social factors as the group composition, the presence of playmates or of other females coveting the infant (DE JONGE *et al.*, 1981 ; SIMPSON and HOWE, 1986 ; SPENCER-BOOTH, 1968). Of course these factors may interact in a complicated way. In this study, we analysed the influence of the dominant versus subordinate status of the mother on the development of rhesus mother-infant interaction. During the weaning period the developing organism must make the major transition from a state of complete dependence on parental care to one of independence. The concept of weaning is of central importance in the study of behavioural development. However it is still a term with many shades of meaning (MARTIN. 1984). It may sometimes retain its narrow reference to nutritional self-sufficiency from mother's milk and self-sufficiency that is imposed rather than voluntary (ALTMANN, 1980). In this restricted sense it refers to a relatively brief preriod during mammalian ontogeny. However, in a broad sense the word weaning covers the whole process of loosening the mother-infant bond, resulting in an independent adult existence (COLLINGE, 1987). This constitutes a major transformation which may span an extensive period in ontogeny (GALEF, 1981). Here, we use the term weaning in a broad sense and chose to study an area of this last aspect, expressed in some weaning-related behaviour of both mothers and infants. We think it is also important to regard weaning as part of the whole reproductive strategy and not only as an isolated process of ontogeny. Rhesus monkeys, as many other primates, are considered as seasonally polyoestrous as conception occurs only in particular seasons during which females cycle again, if they do not conceive at once (RICHARD, 1985). In practice, seasonal acyclicity may often be difficult to distinguish from postpartum amenorrhea, but the two have quite different implications for the interbirth interval. For example, after the death of their suckling infant non-seasonal primates exhibiting a postpartum amenorrhea begin to cycle again shortly after the infant's death (as for *Presbitys entellus* : see HRDY, 1980, or for *Papio cynocephalus* : see ALTMANN, 1980). Females that are seasonally polyoestrous do not resume their cycle before the next mating season. In the long run it is the timing of gestation and lactation, not the sexual cycle as such, that is important for reproductive success. In seasonally breeding primates the interbirth interval depends on the number of months in the year during which a female can cycle and conceive.

The present study bears on a colony that has one mating season per year, lasting from autumn through winter, like the wild rhesus monkeys of North India (LINDBURG, 1971).

MATERIAL AND METHODS

Material

Eight mother-infant pairs, living in four social groups were studied. Six infants were females, two males. At the beginning of the study the youngest infant was 7 weeks, the oldest 18 weeks (Fig. 1). Each group consisted of five to eight individuals including two mothers with their infants.

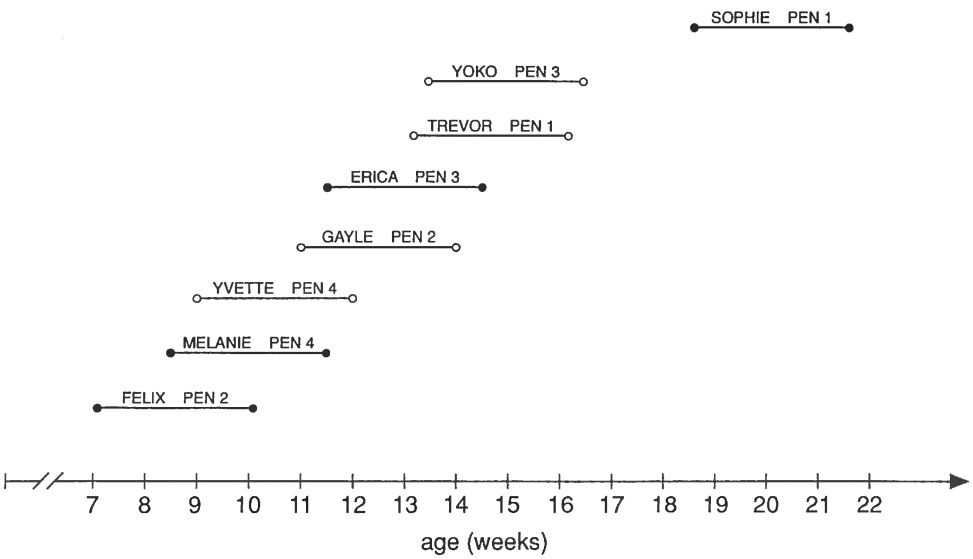

Fig. 1. — The ages of the infants during the observation period.

Infants of		
● dominant mother :	pen	○ subordinate mother :
Sophie °06.04.82	1	Trevor °13.05.82
Felix °27.06.82	2	Gayle °31.05.82
Erica °27.05.82	3	Yoko °13.05.82
Melanie °16.06.82	4	Yvette °12.06.82

The composition of the groups did not change during the study period. Each of them inhabited an outdoor pen (floor : 8 × 3 m, height : 4 m) communicating with an indoor room (floor : 2.5 × 1.5 m, height : 2 m). Indoor temperatures were kept above 13°C. Members of one group could hear, see and smell those of the other groups, but could not make physical contact. Every morning, monkey pellets, peanuts and sunflower seeds were distributed on the floor. The monkeys immediately started to eat and stopped spontaneously after a while, thus leaving a certain amount of food available during the whole day until the next morning. At the beginning of the afternoon a supplement of fresh fruit and vegetables was added. This was completely consumed in the next two hours. Further details of the history and management of the colony are given by ANDERSON and SIMPSON, (1979).

Many different ethologists used to make observations on the colony, almost daily, for many years.

Method

All observations were made from an inside room with one window to the monkeys' inside room and one window to their outer part. The monkeys were accustomed to observers, who behaved as neutrally as possible. A microphone transmitted the sounds from the cage to the observation room.

Quantitative data on mother and infant were separately collected on checksheets in a way that allowed continuous and sequential notes and also a two minutes scan method (HINDE, 1973). At any time, during the observation session, any situation or change of situation was recorded in respect to four classes of distance : on nipple, all mother-infant contact except infant on nipple, without contact but within arm's reach (within 60 cm) and at a distance greater than 60 cm. Any change from one class of distance to the other was recorded as either approach or leaving by mother or/and infant. Every two minutes a mark was written down in order to use those sequential and uninterrupted notes also as an instantaneous scan method with a two minutes interval. In addition, the following interactions were also noted whenever they occured :

Mother-infant interactions :

Mother rejects her infant (R) : occasions on which the mother hits the infant (including pulling, grabbing and biting), passively prevents or breaks contact within 5 s of the infant making contact with or taking the nipple. A mother passively prevents access to her nipple by putting her arm up as the infant's mouth approaches her chest and/or by pulling her nipples up and/or by twisting her torso away (SIMPSON and Howe, 1986).

Mother restrains her infant (r) : occasions when the mother holds the infant tightly as it tries to move or squirm away, or when she pulls an infant that has already broken contact, closer to herself again.

Mother-mother interactions :

Attacking, threatening, chasing and *supplanting* directed by mother A at mother B, and *avoiding, fear-grinning* and *presenting* (in non-grooming context) directed by mother B at mother A, were regarded as evidence for dominance of mother A over mother B (SIMPSON and HOWE, 1986). In every group one mother was regarded as dominant if the above described interactions always occured in the same direction. For this study we used the observations made between august 12th and september 6th, 1982. Most of these were done between 12 a.m. and 1.30 p.m. or between 4 and 7 p.m., while mother and infant were not sleeping nor involved in an eating session. The two mother-infant pairs of the same social group were each observed on the same day during 62 to 107 min. The principle was to change from group

every day. Therefore, every four days the two mother-infant pairs of the same group were reobserved. Only a few times this rythm could not be respected due to external circumstances. But the time interval between two following sessions was always comprised between a minimum of three and a maximum of five days, as shown on the graphs (Figs. 2 to 6).

From an other study we made on the social context of this four groups, it became obvious that group 4 showed a particular terrorizing adult male. He often bit the members of his group in a context that could not predict his agression. This influenced the agonistic, grooming and play interactions of all members of the group. Therefore, the results of group 4 are sometimes considered separately.

RESULTS

Six relative frequencies were used to analyze the data. Two were measures of mother-infant proximity. Three of the other measures concerned relative roles of mother and infant in determining the mother infant proximity as described by HINDE and SPENCER-BOOTH (1967) and HINDE (1974).

1. Percentages of mother-infant contacts (Fig. 2)

The number of instantaneous observations, made at a two minutes' interval on the same day, when a mother was in contact with her infant (N*c*) as proportion of the total (N*t*) watched, is expressed in :

$$Nc \times 100 / Nt$$

This measure is inspired from the index described by HINDE and SPENCER-BOOTH (1967), but we used a scan method rather than a one-zero sampling. The decreasing percentages of contacts reflect the increasing independence of the infant.

In the beginning of the study, the highest percentages of contacts in groups 1, 2 and 3 occured for all subordinate mothers and the dominant mother of the youngest infant. At the end the situation looked quite different as the higher percentages decreased faster. Consequently, the differences between the means of the dominant mothers and the subordinate ones seem to diminish with time. The status of the mother and even the age of the infant would act less and less upon their independence as time went on. It looked as if the degrees of independence of the offspring tended to level out. This suggests a « catching up » phenomenon. This is most strongly supported by the fact that, at their infant's 14 weeks, the subordinate mother-infant pair of pen 1 (1 SMI) and 3 SMI rate higher than 2 SMI and the dominant mother-infant pair of pen 3 (3 DMI), but then they do their « catching up » in the next 2-3 weeks. Moreover, the fact that the ranges of the observations, at 13-14 weeks, for 1 SMI and 3 SMI hardly overlap with those for 2 SMI and 3 DMI is important because it suggests that the differences are not merely due to sampling error in the observations. The infant of the subordinate mother of group 4 would be the only exception. Hence, at this stage her independence would remain

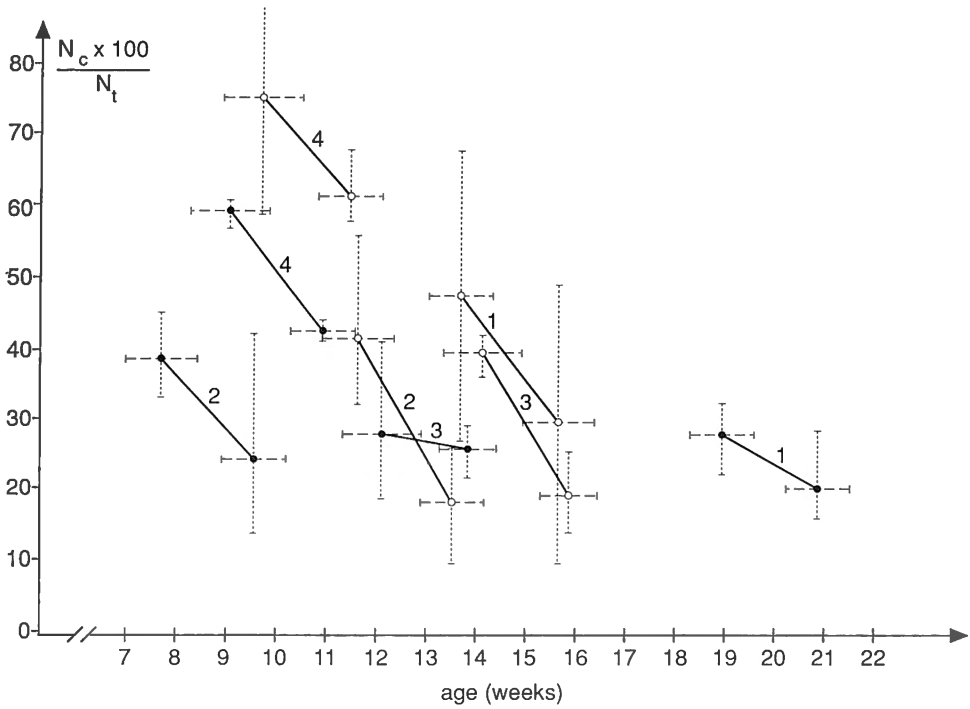

Fig. 2. — Proportion of time in contact : number of two minutes' observations during which the infant was in contact with the mother as proportion of the total number of observations. The means of the index and the extreme values (limits of vertical dotted lines) are put in the middle of each observation period represented by the horizontal dotted line. The mean of the first three and that of the last three observation sessions are joined by a plain line. They are plotted according to the age of the infant in the middle of the period including the three sessions.

- ● Infant with dominant mother,
- ○ Infant with subordinate mother

more related to its mother's rank. Nevertheless two short observation sessions (of 22 and 33 minutes during the same two observation periods of three weeks) of the subordinate mother-infant pair of group 4, made in the « absence » of the dominant male (*i.e.* while he was sitting in the other part of the cage or sleeping) showed much lower percentages of contacts (57 % and 55 %) than those on the graphs (76 % and 62 %).

2. **Relative frequency of rejections** (Fig. 3)

This measure was given by the ratio of the number of times the infant attempted to get on its mother and was rejected (R) to the total number of contacts, either

on the infant's initiative (MK*i*), or on the mother's (MK*m*) and of the infant's unsuccessful attempts to contact (R), *i.e.* :

$$R \times 100 / MKi + MKm + R$$

Since the frequency with which the infant gains contact on the mother's initiative (MK*m*) decreases rapidly over the first weeks of life, the relative frequency of rejections during the study period approximates to the failure rate of the infant's attempts (HINDE, 1974).

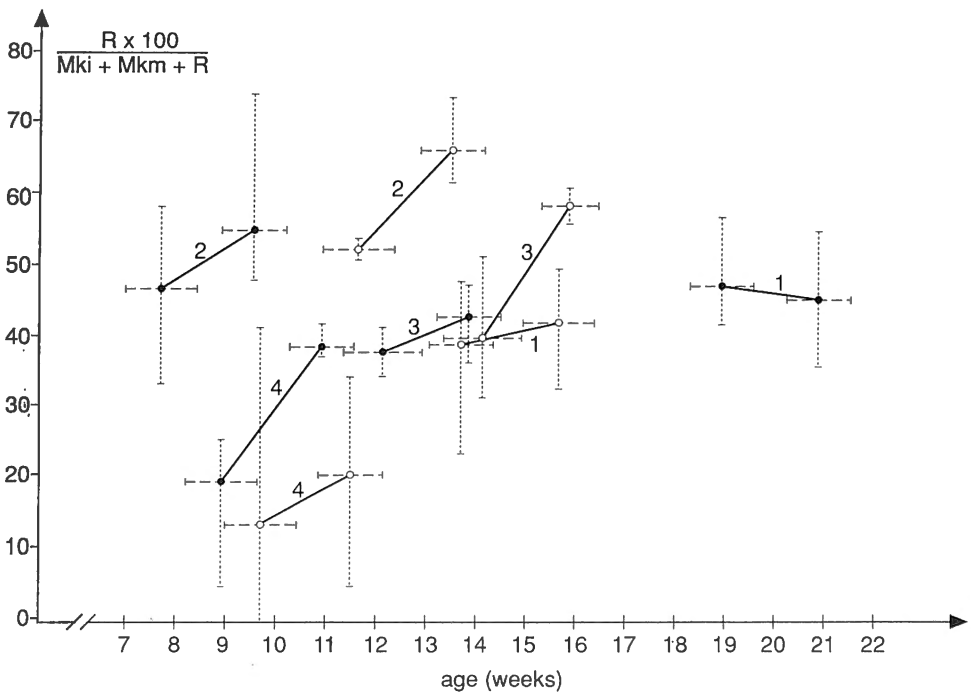

Fig. 3. — Relative frequency of rejections : ratio of the number of occasions on which the infant attempted to gain contact and was rejected by the mother (R) to the number of occasions on which it made contact on the mother's initiative (M*km*), made contact on its own initiative (M*ki*) or attempted unsuccessfully to gain contact (R). The means of the index and the extreme values (limits of vertical dotted lines) are put in the middle of each observation period represented by the horizontal dotted line. The mean of the first three and that of the last three observation sessions are joined by a plain line. They are plotted according to the age of the infant in the middle of the period including the three sessions.

- ● Infant with dominant mother,
- ○ Infant with subordinate mother

All mothers increased their relative frequency of rejections except the dominant mother of the oldest offspring, who tended to decrease it.

Those measures remained lower for the mothers of group 4, especially for the subordinate mother. Nevertheless, as for the preceding index, her relative frequencies of rejections were higher in the « absence » of the dominant male (36 and 41 % instead of the 13 and 20 % on the graphs).

3. Infant's role in making mother-infant contact (Fig. 4)

This index is the difference between the percentage of contacts (on nipple or other) made on infant's initiative and the percentage of contacts broken by the infant, *i.e.* :

$$(MKi \times 100 / MKi + MKm) - (BKi \times 100 / BKi + BKm)$$

abbreviated to % MK*i* − % BK*i* (HINDE, 1974 and HINDE and ATKINSON, 1970).

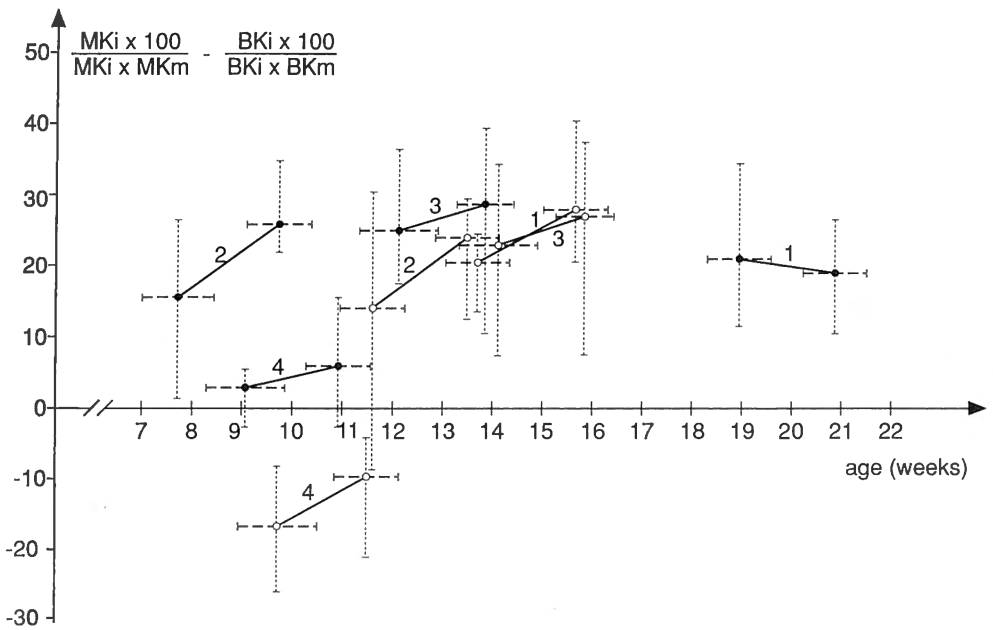

Fig. 4. — Infant's role in seeking contact : number of contacts made on the infant's initiative, as a percentage of the total number made by mother and infant, minus number of contacts broken off by the infant, as percentage of the total number broken. The means of the index and the extreme values (limits of vertical dotted lines) are put in the middle of each observation period represented by the horizontal dotted line. The mean of the first three and that of the last three observation sessions are joined by a plain line. They are plotted according to the age of the infant in the middle of the period including the three sessions.

- ● Infant with dominant mother,
- ○ Infant with subordinate mother

If the infant were responsible for all makes and no breaks this index would have a value of + 100 %, and if the mother were responsible for all makes and no breaks it would be − 100 %. A positive value means that the infant is primarily responsible for the contacts.

From Fig. 4 it is obvious that all infants, except one, were more responsible than their mothers for seeking contacts. As for the frequencies of rejections, the infant's role increased with time, except for the oldest infant where it rather decreased.

In group 4, it is the subordinate mother who is primarily responsible for seeking contacts. But here too, as in the previous measures, the results were markedly different and even positive in the « absence » of the adult male (+ 8 and + 14 % instead of − 15 and − 19 % on the graphs). On these occasions the subordinate mother was not seeking infant's contact more than mothers in other groups.

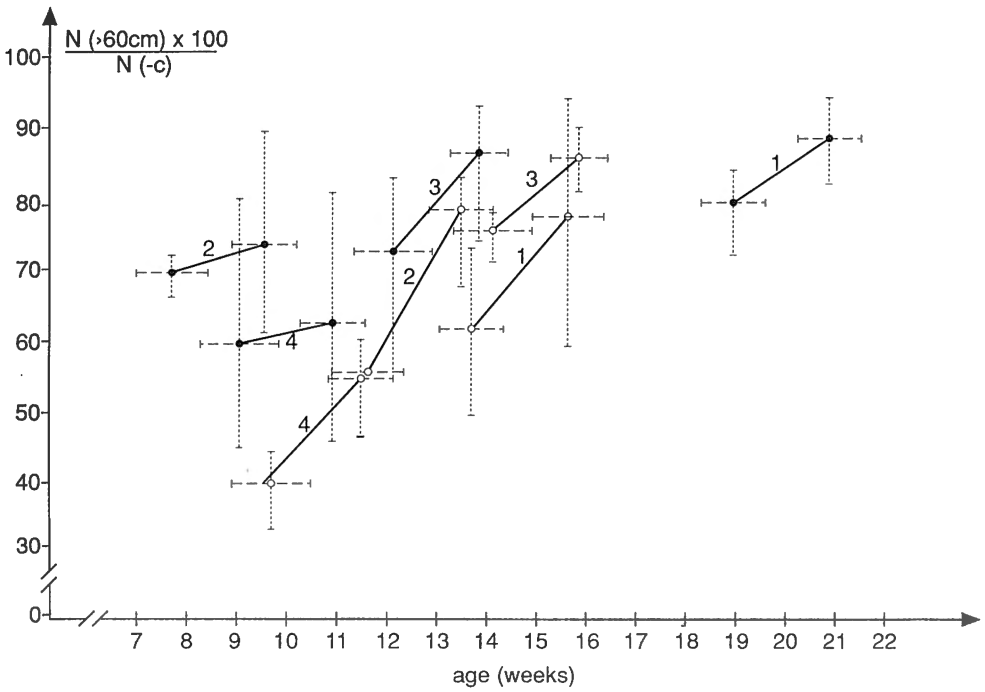

Fig. 5. — Proportion of time out of arm's reach of mother : number of two minutes' observations during which the infant was more than 60 cm from the mother (N > *60 cm*) as proportion of the number for which it was off her (N − *c*). The means of the index and the extreme values (limits of vertical dotted lines) are put in the middle of each observation period represented by the horizontal dotted line. The mean of the first three and that of the last three observation sessions are joined by a plain line. They are plotted according to the age of the infant in the middle of the period including the three sessions.

- ● Infant with dominant mother,
- ○ Infant with subordinate mother

4. The proportion of time spent at a distance of more than 60 cm (Fig. 5)

This measure resulted from the number of instantaneous observations made at a two minutes' interval on the same day, when the infant was at more than 60 cm from its mother as a proportion of the total number when it was off her, *i.e.* :

$$N(> 60\ cm) \times 100 / N(-c) \quad N(-c) = Nt - Nc$$

The distance of 60 cm was chosen because it is considered as the limit of a rhesus mother's arm reach.

This index is inspired from that described by HINDE and SPENCER-BOOTH (1967), but we used a scan method rather than a one-zero sampling.

The increasing proportion of time the infant spent at a distance of more than 60 cm also shows some kind of increasing independence of the infant. The values of the younger offspring of the subordinate mother of groups 1, 2 and 4 who at first spent least time at a distance, increased the fastest. The degrees of independence of the infants of groups 1, 2 and 3 seemed to level out with time. The same could be said for the babies of group 4. In the last group the status of the mother kept acting most upon the emancipation of the offspring. From the beginning to the end of the observation period the infant of the subordinate mother remained markedly more dependent.

5. Infant's role in seeking proximity less than 60 cm (Fig. 6)

The infant's role in proximity was assessed by counting the number of approaches (the distance decreases from > 60 cm to < 60 cm) and leavings (the distance increases from < 60 cm to > 60 cm), and by calculating the difference between the percentage of approaches due to the infant's movement (AP*i*) and the percentage of leavings due to the infant's movement (L*i*), *i.e.* :

$$(APi \times 100 / APi + APm) - (Li \times 100 / Li + Lm)$$

A positive result would indicate that the maintaining of proximity is mostly due to the mother and a negative result that it is mostly due to the infant (HINDE and ATKINSON, 1970 ; HINDE, 1974).

All measures were positive except in the beginning for the infant of the subordinate mother of group 4. This sustains the fact that almost all infants were mostly responsible for seeking the proximity of the mother. The subordinate mother of group 4 was the only mother, who was primarily responsible for seeking proximity and this solely at the beginning of the observation period. As time went on, she drastically decreased her responsibility and at the end the baby became even more responsible than herself.

6. Restraints by the mother

The last measure is the percentage of restraints by the mother. It is defined as the ratio of the number of times the mother restrained (r) her infant to the total

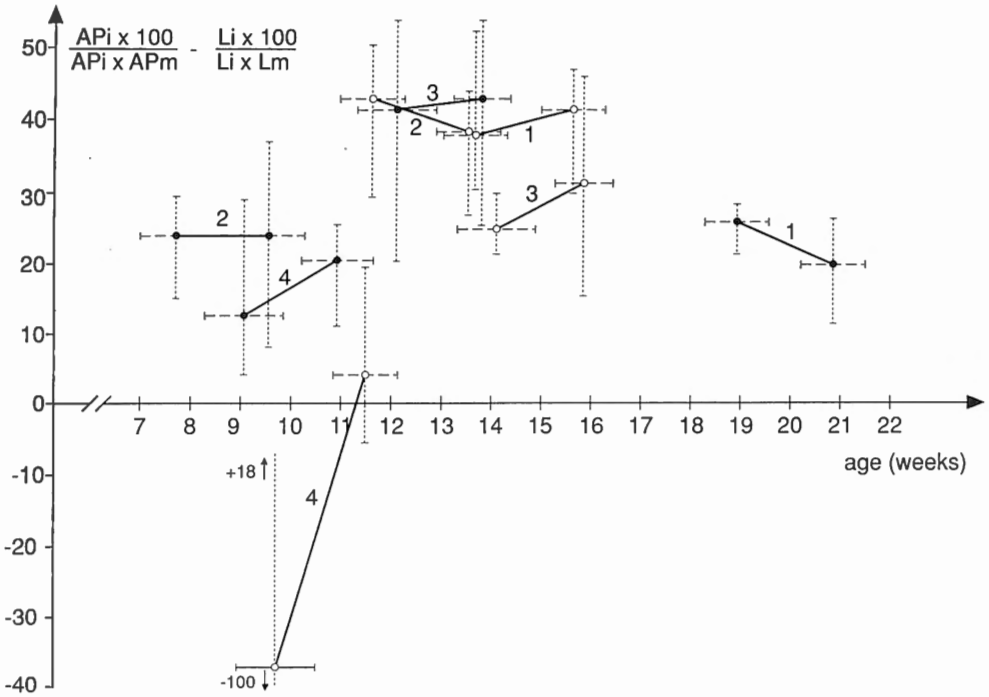

Fig. 6. — Infant's role in seeking proximity : number of approaches made by the infant, as percentage of the total number made by the mother and the infant, minus the number of leavings made by the infant, as percentage of the total number made. The means of the index and the extreme values (limits of vertical dotted lines) are put in the middle of each observation period represented by the horizontal dotted line. The mean of the first three and that of the last three observation sessions are joined by a plain line. They are plotted according to the age of the infant in the middle of the period including the three sessions.

- ● Infant with dominant mother,
- ○ Infant with subordinate mother

number of times the mother broke contact and the infant's either successful or unsuccessful attempts to break contact, *i.e.* :

$$r \times 100 / BKi + BKm + r$$

All mothers restrained extremely rarely, except the subordinate mother of group 4. Of all dominant mothers of groups 1, 2 and 3 only two restrained their infant (once each). The subordinate mothers of the same groups scored a mean of 10 times in absolute value (*i.e.* 1 %) in the beginning and restrained only twice at the end.

In group 4, the dominant mother restrained 4 times in the beginning and only once at the end. While the subordinate mother of this group, counted 24 % of restrainings in the beginning and 19 % at the end. As for other measures, the situation was markedly different in the « absence » of the adult male, when she restrained only once in 64 attempts by her infant to leave her.

Although the values of this index were too low to be considered alone, they confirm the general trend of the other results, *i.e.* the active involvement of the subordinate mother of group 4 which delayed the emancipation of her infant.

Temporal evolution of the measures

The age-changes in the mother-infant interactions could depend on changes in the infant's behaviour, changes in the mother's behaviour, or both (HINDE, 1974). If the proportion of time in contact (Fig. 2) decreases with increasing percentages of rejections (Fig. 3) and increasing infant's role in contact (Fig. 4), the emancipation of the infant must be primarily due to changes with the mother. This was the case for each mother-infant pair, except the one with the oldest infant (group 1). Here the correlation is positive and the emancipation could be primarily due to changes with the infant.

The situation is different, if we consider the proportion of time at a distance of more than 60 cm (Fig. 5). The changes in the infant's role in maintaining proximity was only clear for the subordinate mother-infant pair of group 4. For this pair we can tell that, as both indices increased with time, the mother is primarily responsible for this kind of increasing independence too.

In sum, for most pairs, the mother's changes were primarily responsible for the decreasing proportion of time in contact, but when contact was broken, changes in mother and infant had a similar role in the increasing proportion of time spent beyond arm's reach. This could be due to the fact that the mother's most important point is to get free from « too much contact » with her infant. Once the contact is broken, she may concede a bigger part of initiative to the infant to augment its proportion of time out of arm's reach.

DISCUSSION

In four captive groups of rhesus monkeys, part of the weaning process of eight infants was observed in detail during the last weeks preceding the onset of the annual mating season. Several factors seem to influence the rate of increasing independence of the infants. The results suggest that this independence may be delayed in three circumstances. First, the younger age of the infant, as described by DIENSKE and METZ (1977) and HINDE (1974). Second, the lower status of the mother, consistent with SIMPSON and HOWE (1986). Finally, the particular social context of the presence of a feared adult male. SIMPSON and HOWE (1986) observed that the mothers, submitted to higher rates of aggression from other adults, played a more important role in maintaining proximity with their 8-week-old infants.

Furthermore, two particular points appear in our observations, most obviously in groups 1, 2 and 3. On the one hand, the differences between the dominant and the subordinate mothers were more noticeable at the beginning than at the end of the study. On the other hand, even the expected differences between the degrees of independence in relation to the infants' ages only, became surprisingly smaller at

the end of the study. This is an amazing finding if one expects a gradual development of the mother-infant relationship only in function of the infants' age. Facts tend to give evidence of a « catching up » phenomenon : the emancipation going faster for offspring that, in the beginning, are more dependent of their mother. As the correlations between the indices suggest, this catching up phenomenon would be primarily due to the behaviour of the mother, who would fasten the emancipation of her « late » infant. This is not in contradiction with TRIVERS' argument (1974) that the infant must be selected to elicit more parental investment than the parent is selected to provide. Another major factor, different from infants' age, could interfere. At the approach of the annual mating season, the emancipation of the « late » infants would be accelerated (in regard of the more precocious infants) and reach an optimal degree at the onset of the mating season. In terms of inclusive fitness, this could have an adaptive value for the mother : too much contact between mother and infant could make it difficult for the mother to invest in her sexual activities with males or a delay in the infants' weaning could delay the mother in resuming her sexual cycles. SIMPSON *et al.* (1981) observed that mothers proving quicker to conceive their next infants tend to reject them more often.

This emphasizes that there are many factors that may influence the reproductive strategy and that these likely interact in a complex fashion. It could be worthwhile to reconsider the evolution of mother-infant relationship, in seasonally polyoestrous species, by gathering the observations of infants grouped in age-classes relative to the onset of the following mating season, as well as pooled in the usual age-classes only in function of their birth date. This could give some insight in the question : is the rate of emancipation of young seasonally polyoestrus primates, a function of the proximity to the following mating season ?

ACKNOWLEDGMENTS

We are particularly grateful to Mr. Michaël Simpson for his extensive and thoughtful comments on an earlier draft. For helpful discussions and hospitality in his laboratory we wish to acknowledge Mr. Robert Hinde. We are greatly indebted to Mr. Raymond Rasmont, for the help in realizing this study and his extent comments on the manuscript. For his pertinent criticisms, we like to thank Mr. Jacques Pasteels. We are especially touched by the apposite remarks of Miss Jacqueline Naisse, who sadly left us during the elaboration of this manuscript. Many thanks to Jean Loui De Ridder for drawing the figures.

REFERENCES

ALTMANN, J. (1980), *Baboon Mothers and Infants*. Harvard University Press, Cambridge, Massachusetts, XIV + 242 pp.

ANDERSON, D. M. and M. J. SIMPSON (1979), « Breeding performance of a captive colony of rhesus monkeys, *Macaca mulatta* ». *Laboratory Animals*, **13**, 275-281.

BERMAN, C. M. (1980), « Mother-infant relationships among free-ranging rhesus monkeys on Cayo Santiago : a comparison with captive pairs ». *Anim. Behav.*, **28,** 860-873

COLLINGE, N. E. (1987), « Weaning variability in Semi-Free-Ranging Japanese Macaques (*Macaca fuscata*). *Folia primatol.*, **48,** 137-150.

DIENSKE, H. and H. A. METZ (1977), « Mother-infant body contact in macaques : a time interval analysis ». *Biol. Behav.*, **2,** 3-27.

DE JONGE, G., H. DIENSKE, E. A. VAN LUXEMBURG and L. RIBBENS (1981), « How rhesus monkey infants budget their time between mothers and peers ». *Anim. Behav.*, **29,** 598-609.

GALEF, B. G. (1981), « The ecology of weaning : parasitism and the achievement of independence by altricial mammals ». In : *Parental care in Mammals,* D. J. Gubernick and P. H. Klopfer ed., Plenum Press, New York, 211-241.

HINDE, R. A. (1973), « On the design of check-sheets ». *Primates,* **14** (4), 393-406.

HINDE, R. A. (1974), *Biological Bases of Human Social Behaviour.* McGraw-Hill, New York, XV + 462 pp.

HINDE, R. A. (1976), « Interactions, relationships and social structure ». *Man* (Lond.), **11,** 1-17.

HINDE, R. A. and S. ATKINSON (1970), « Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in monkeys ». *Anim. Behav.*, **18,** 169-176.

HINDE, R. A. and J. HERRMANN (1977), « Frequencies, durations, derived measures and their correlations in studying dyadic and triadic relationships ». In : *Studies in Mother-Infant Interaction.* H. R. Schaffer, Academic Press, London, 19-46 pp.

HINDE, R. A. and Y. SPENCER-BOOTH (1967), « The behaviour of socially living rhesus monkeys in their first two and a half years ». *Anim. Behav.*, **15,** 169-196.

HOOLEY, J. and M. J. SIMPSON (1981), « A comparison of primiparous and multiparous mother-infants dyads in *Macaca mulatta* ». *Primates,* **255** (3), 379-392.

HRDY, S. (1980), *The langurs of Abu.* Harvard University Press, Cambridge, Massachussets, XVIII + 361 pp.

JOHNSON, R. L. and C. H. SOUTHWICK (1984), « Structural diversity and mother-infant relations among rhesus monkeys in India and Nepal ». *Folia primatol.*, **43,** 189-248.

LINDBURG, D. (1971), « The rhesus monkeys in North India : an ecological and behavioural study ». In : *Primate Behavior. Developments in Field and Laboratory Research II,* Rosenblum ed., Academic Press, New York, 1-6.

MARTIN, P. (1984), « The meaning of weaning ». *Anim. Behav.*, **32,** 1257-1259.

RICHARD, A. (1985), « Primates in nature ». Freeman and Cie, U.S.A., X + 558 pp.

SEAY, B. (1971), « Maternal behaviour in primiparous and multiparous monkeys ». *Folia Primatol.*, **4,** 146-168.

SIMPSON, M. and S. HOWE (1980), « The interpretation of individual differences in rhesus monkey infants ». *Behaviour,* **72,** 3-4.

SIMPSON, M. and S. HOWE (1986), « Group and matriline differences in the behaviour of rhesus monkey infants ». *Anim. Behav.*, **34,** 444-459.

SIMPSON, M. J. A., A. E. SIMPSON, J. HOOLEY and M. ZUNZ (1981), « Infant-related influences on birth intervals in rhesus monkeys ». *Nature,* Lond., **290,** 49-51.

SIMPSON, M. J. A., A. E. SIMPSON and S. HOWE (1986), « Changes in the rhesus mother-infant relationship through the first four months of life ». *Anim. Behav.*, **34,** 1528-1539.

SPENCER-BOOTH, Y. (1968), « The behaviour of group companions towards rhesus monkey infants ». *Anim. Behav.*, **16,** 541-557.

STEVENSON-HINDE, J. and M. SIMPSON (1981), « Mothers' characteristics, interactions and infants' characteristics ». *Child development*, **52,** 1246-1254.

TARTABINI, A. and M. J. A. SIMPSON (1986), « Maternal rejection and infant social behaviour in small groups of rhesus monkeys : the use of confidence intervals in arguments from individual cases ». In : *Ontogeny, Cognition and Social Behaviour of Primates.* G. J. Else and P. C. Lee ed., Cambridge University Press, Cambridge, 239-249 pp.

TRIVERS, R. L. (1974), « Parent-offspring conflict ». *Am. Zool.*, **14,** 249-264.

WHITE, L. E. and R. A. HINDE (1975), « Some factors affecting Mother-Infant relations in rhesus monkeys ». *Anim. Behav.*, **23,** 527-542.