EVIDENCE FOR THE EXISTENCE OF MOTHERING STYLES IN GUINEA PIGS (CAVIA APEREA F. PORCELLUS)

by

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Summary

Mothering styles are generally assumed to exist, in particular in the case of primates. However, an experimental procedure to ensure this assumption has been lacking and, moreover, mothering style was always defined *post hoc*. The short inter-birth interval and the possibility to cross-foster make the guinea pig a suitable species that has an advantage over primates for this type of study.

The maternal behaviour of ten subjects was registered during mothering of four subsequent litters. To challenge a possible consistency of maternal behaviour two variables were manipulated: parentage (own young or adopted young) and the condition of the mothers (pregnant or non-pregnant).

The concordances found suggest that behavioural parameters necessary to characterize a mothering style in guinea pigs should contain either locomotor, affiliative or aggressive behaviour. Other behavioural parameters were not found adequate for characterizing mothering styles.

As significant concordances of maternal behaviour were found, in spite of the challenges offered, we conclude that guinea-pig mothers consistently differ from each other and hence that 'mothering styles' exist in guinea pigs.

Introduction

Within one species different strategies of maternal behaviour can be observed under natural conditions. A particularly good example of that is the feral goat. After parturation, female feral goats either remained in the vicinity of their neonate during lying out or left the neonate alone while they foraged with the herd (O'Brien, 1984).

If individual differences in maternal behaviour, such as mentioned above, are consistent over several lactational periods then they are referred to as mothering style (Altmann, 1980; Berman, 1990a; Maestripieri, 1993). It is not always clear, however, whether consistency of the mother-young relationship is meant or exclusively unprovoked maternal behaviour (Berman, 1990b).

It is generally supposed that mothering style influences behaviour of the offspring, not only shortly after weaning but even during adulthood (see *e.g.* Hinde & Spencer-Booth, 1968; Wachs & Grün, 1982). For animals some evidence has been provided for this supposed influence of mothering style on the later behaviour of the offspring. For respectively yellow baboons and rhesus macaques Altmann (1980) and Berman (1990a) considered the likeness of mothers and daughters with regard to the 'rejective behaviour towards their offspring' to be due to experiences of the daughters with the behaviour of their mothers during youth. Furthermore, Altmann (1980) reported that young of '*laissez-faire*' mothers leave their mothers at an earlier age for a great distance than young of 'restrictive' mothers. Consistent with this finding Fairbanks & McGuire (1988) showed that vervet monkey young of 'restrictive' mothers took longer to enter a novel environment and showed less interest in events occurring outside their enclosure than young of '*laissez-faire*' mothers. Of Bonnet-macaques it is noted by Andrews & Rosenblum (1991, 1993) that the more time a mother spends foraging, the less initiative the young takes to leave the mother. For chimpanzees it has been shown that more sociable mothers had young that spent less time in social play than young of less sociable mothers (Hemelrijk & Kogel, 1989). Wilsson (1984) reported that the more aggressive German shepherd bitches treated their pups, the less likely the pups were to initiate contact with a passive person.

However, none of these studies could exclude that maternal behaviour is being directed by the young. For instance Simpson (1985) suggested

the restrictive behaviour of the mother as being partly a reaction to the explorative nature of the young. Consistency in maternal behaviour could therefore result from succeeding young sharing part of their genes. Fairbanks & McGuire (1988) however argued against a purely genetic view that it is not sufficient to explain the degree of flexibility in maternal protectiveness they observed when young were threatened. However, the validity of arguments like this has never been put to the test by an experimental approach.

To enable an experimental approach in the future the goal of this study was to find out whether consistencies exist in maternal behaviour over succeeding litters. We adopt the definition of mothering style in terms of consistencies of individual differences in maternal behaviour (Altmann, 1980; Berman, 1990a; Maestripieri, 1993) and define mothering styles as *the occurrence of consistency over a number of periods of maternal care with regard to relative differences between mothers for parameters of maternal behaviour* . Our experimental subject was the guinea pig of which the maternal behaviour has been described extensively (Kunkel & Kunkel, 1964; Rood, 1972; Porter *et al.*, 1973; Berryman & Fullerton, 1976; König, 1985; Hennessy & Jenkins, 1994). The relatively short inter-birth-interval of guinea pigs (10 weeks) allows to observe several litters of one mother within a reasonably short span of time. Furthermore, guinea pigs readily accept and nurse strange young. These aspects make this species more suitable for an experimental approach than primates.

The maternal behaviour of a number of subjects was registered during mothering of four subsequent litters. To challenge a possible consistency of maternal behaviour two variables have been manipulated: 'parentage' (own or adopted young) and the reproductive state of the mother (pregnant or non-pregnant). 'Parentage' was chosen to enable genetic differences between young of succeeding litters to interfere with the maternal behaviour. It also allows us to conclude whether there is a dependency between the genetic 'make up' of the young and the maternal behaviour.

The reproductive state of the mother was manipulated with the intention to increase the chance on earlier weaning as a result of an intensified parent-offspring conflict (Trivers, 1974). This is likely to occur when a mother becomes pregnant whilst still giving milk to a previous litter. Pregnancy and lactation are both physiologically 'expensive' (Blaxter, 1971; Martin, 1984) which has consequences for the fitness of the mother (*e.g.* Clutton-Brock *et al.*, 1989). An example of this can be seen in bison (*Bison bison*) of which

pregnant mothers show a decrease in nursing time compared to non-pregnant mothers (Green *et al.*, 1993).

Methods

Animals and housing

Ten female guinea-pigs ranging in age from 3 to 18 months at the start of the experiment were used as subjects. All animals were laboratory raised from an outbred colony. Seven subjects were nulliparous at the start of the experiment.

During synchronization of their oestrus cycle and during pregnancy the subjects were housed in groups of 4-5 females in mesh cages ($1 \times 0.8 \times 0.7$ m). Only when impregnation was needed females were separated and housed with a male in a Macrolon cage ($0.36 \times 0.58 \times 0.2$ m). Females always had the same male for a partner and did not share their male with other subjects during the whole experiment. We had no indication that males had a direct influence on the maternal behaviour. At least three days before the expected delivery subjects were separately housed in a steel observation cage ($1.3 \times 0.4 \times 0.4$ m) with a Plexiglas front. Males were left with the females until 24 hours after delivery in case a post-partum conception was needed.

All cages had wood chips for bedding. Pelletized food (Complete Cavy diet, Hope farms B.V., Woerden, The Netherlands) and water were present *ad libitum*. Hay and apple were regularly presented in a standard way; presentations were timed in such a manner that this did not interfere with video registrations. Room temperature was 19-22 degrees Celsius. Lights were on from 0.30 A.M. until 0.30 P.M. During the dark-period red lights enabled video-registration.

Design and procedures

To be able to conclude whether maternal behaviour was consistent the maternal behaviour of the subjects was observed during the mothering of four subsequent litters. To avoid likeness of young of subsequent litters to be responsible for consistencies in maternal behaviour the young of litters 1 and 4 were cross-fostered (see Table 1).

To enable cross-fostering of the young shortly after birth the oestrus cycle of the mothers was synchronized by means of a silastic implant filled with progesterone (length 35 mm, radius 4 mm, thickness 0.5 mm, produced by Silastic Rubber B.V. Hilversum, The Netherlands). Synchronization was performed before the first and the third litter.

TABLE 1. *Experimental design: Interferences to challenge consistency of maternal behaviour*

	First litter	Second litter	Third litter	Fourth litter
Reproductive state of the mother	pregnant	non pregnant	pregnant	non pregnant
Parentage	adopted pups	own pups	own pups	adopted pups

Further, an extra physiological burden was imposed during the mothering of the first and the third litter. This was achieved by post-partum conceptions after the first and the third delivery (see Table 1). (A post-partum oestrus is a normal phenomenon in guinea pigs and not specifically induced by the experimenters for this experiment.) The pregnancy resulting from a post-partum conception is an extra physiological burden to the mother as this means she is pregnant and lactating at the same time.

Ultimately 36 hours after birth littersize was standardized to three pups. By sometimes waiting 36 hours a larger number of pups of litters with more than three young could be used for cross-fostering. So by this procedure young that were cross-fostered differed maximally 36 hours in age. As guinea pigs have two teats standardizing littersize at three pups enlarges the chance to observe rejective behaviour of the mothers. Also total amount of time spent on mothering increases when there are more pups than teats (König, 1985).

Except for one mother, which had only male pups in the second and fourth litter, in every litter both sexes were present. The sex ratios amounted to 15:15 for the first three litters. For the fourth litter the sex ratio was 16:14.

On days 3, 5, 7, 10, 14, 17, 21 and 24 after delivery (day 0) 90 minutes video registrations were made. Registrations started 30 minutes after onset of the dark-period and were made by red light. A pilot study had shown that between 30 and 120 minutes after onset of the dark period usually at least one suckling bout could be observed.

The behaviour of the mother was registered by continuous sampling from the video. The locations of mother and pups were sampled every minute.

Parameters

Maternal behaviours

1 Admit ventrum contact: a pup is positioned in such a way that its snout contacts mother's ventrum longer than 10 seconds and milk can be drunk (see *e.g.* Schiml & Hennessy, 1990) (frequency).
2 Refuse ventrum contact: a pup tries to contact mother's ventrum but is not allowed so longer than 10 seconds (frequency).
3 Grooming and sniffing the pups' fur (frequency).
4 Anogenital licking of the pup (frequency).
5 Nose-nose contact (between mother and pup; frequency).
6 Aggression: summation of the parameters pushing, boxing and causing flight (frequency).
7 Leave, mother leaves pup(s) (frequency).
8 Approach, mother approaches pup(s) (frequency).
9 Lead, mother walks without changing distance between mother and pups (frequency).
10 Walking distance of mother (m).
11 Duration of admitting ventrum contact (1).
12 Duration of anogenital licking (4).
13 Ratio of ventrum contact: $1/(1 + 2)$.
14 Lead *vs* walking ratio: $9/(7 + 8 + 9)$.

Descriptive data about maternal behaviour, which we chose not to repeat here, can be found in several previous studies (Kunkel & Kunkel, 1964; Rood, 1972; Harper, 1976; König, 1985; Hennessy & Jenkins, 1994).

Data preparation and statistics

As maternal behaviour changes between delivery and weaning the observational data were divided into two periods: period I (day 3 up to and including day 10) and period II (day 14 up to and including day 24). The caesura has been put between day 10 and day 14 as from day 10 on sex differences start to appear in the behaviour of the pups in relation to testosterone levels in the blood (Hornschuh & Sachser, 1995). This procedure effectively reduced variance.

To check for systematic differences in maternal behaviour between subsequent litters for each parameter the mean scores over the observation days of period I and of period II were tested with a MANOVA with a repeated measurements design.

To comply with our definition of mothering styles as the occurrence of consistency over a number of periods of maternal care with regard to relative differences between mothers for parameters of maternal behaviour, Kendall's Coefficient of Concordance was used. For each parameter the same mean scores as mentioned above were used to test for a concordance of the differences between mothers over subsequent litters. If a significant concordance can be shown for differences in the behaviour between a number of mothers over several periods of maternal care this implies the existence of differences in mothering style between individual mothers which are consistent in time. After all a significant concordance can only occur if mothers differ from each other. In case that the concordance is not significant this does not mean there can be no consistency of maternal behaviour in time. Such consistency however would not imply the existence of mothering styles as mothers would not be differing from each other.

To avoid an inflated risk of type I error due to the large number of dependent variables that were being tested, which were also partly correlated, we adjusted alpha. Parameters were divided into four classes based on pragmatic grounds reflecting relationships between parameters: (a) frequencies of affiliative behaviour, (b) frequency of aggressive behaviour, (c) frequencies of locomotive behaviour and (d) other types of parameters (duration + distance). All classes were allowed a total alpha risk of 0.05. This means that the alpha risk for individual parameters was 0.01 within classes (a) and (d), 0.05 within class (b) and 0.016 within class (c).

Results

Comparison of subsequent litters

No differences were found between the behaviour of the mothers during parenting subsequent litters. Just for one single parameter a difference between behaviour of the subsequent litters was found: lead *vs* walking ratio (15) in period I ($F_{3,7} = 14.54$; $p = 0.002$). Given the number of parameters tested, this single result can not be considered sufficient evidence for an effect of the challenges. Therefore we have to conclude that none of the challenges we offered to the consistency of the maternal behaviour had a significant impact. Also age of the mothers and/or their parity can not be shown to have a significant impact.

Of all the other parameters only one reached the conventional 0.05 alpha level thereby indicating a trend: leave (8) in period I ($F_{3,7} = 6.07$ $p = 0.02$).

Consistency of maternal behaviour

In Table 2 the p-values of Kendall's Coefficient of Concordance are presented for both Period I and Period II and with the corresponding adjusted significancies. For a considerable number of parameters it was shown that mothers differed consistently from each other over four litters.

Of the parameters reflecting affiliative behaviour mothers differed consistently from each other over four litters for the parameters grooming (3) in both period I and II, and admit ventrum contact (1) and duration of ventrum contact (11) in period II.

Aggression (6) as well as most parameters reflecting locomotion (7, 8, 9, 10) were shown to differ consistently in both period I and II.

TABLE 2. *p-values of Kendall's Coefficient of Concordance*

	Behavioural parameters	Class	p-values	
			period I day 3-10	period II day 14-24
1	Admit ventrum contact	a	0.06	*0.01**
2	Refuse ventrum contact	a	0.65	0.96
3	Grooming	a	*0.01**	*0.01**
4	Anogenital licking	a	0.16	*0.03*
5	Nose-nose contact	a	*0.04*	*0.05*
6	Aggression	b	*0.03**	*0.02***
7	Leave pups	c	*0.01**	*0.02*
8	Approach pups	c	*0.01**	*0.01**
9	Lead pups	c	*0.01**	*0.00**
10	Walking distance	d	*0.00**	*0.03*
11	Duration ventrum contact (1)	d	*0.04*	*0.01**
12	Duration anogenital licking (4)	d	0.34	0.09
13	Ventrum contact ratio: 1/(1 + 2)	d	0.20	*0.02*
14	Lead ratio: 9/(7 + 8 + 9)	d	0.13	*0.05*

In italics significancies according to conventional alpha of 0.05 are given. An '*' marks adjusted significancies.

Discussion

In this study we tried to validate the existence of mothering styles. We defined mothering styles as the occurrence of consistency over a number of periods of maternal care with regard to relative differences between mothers for parameters of maternal behaviour. As significant concordances were found we conclude that guinea-pig mothers consistently differ from each other with respect to maternal behaviour and hence that 'mothering styles' exist in guinea pigs.

The parameters that were found to be concordant can pragmatically be divided into three groups, affiliative behaviour, aggression and locomotor behaviour. Each of these three groups can be expected to influence later behaviour of the pups. Affiliative behaviour like grooming and admit ventrum contact are likely to strengthen the bond between mother and young. A positive social relation between mother and young, in which the mother serves as a 'secure base', positively influences later explorative behaviour of the young (*e.g.* Bowlby, 1969; Ainsworth *et al.*, 1978).

Likewise aggression is expected to have an opposite effect: decreasing the quality of the social relation and thus negatively influencing later explorative behaviour of the young (*e.g.* Bowlby, 1969; Ainsworth *et al.*, 1978).

Locomotor behaviour of the mother strongly effects the time the mother is in contact with the young as well as the distance between mother and young. We saw for instance that some mothers consistently ate in short bouts, therefore leaving (and approaching) their young very often, whereas other mothers left their young only a few times (but longer) to eat or drink. This particularly holds in period I during which the young spent more time in the nest than in period II. Leaving the young is no longer found to be significant in period II probably because the young more often left the mother. In the case that Bonnet macaque mothers were forced to leave their young behind to go foraging, the time spent foraging was negatively correlated with the young's initiative the to leave the mother (Andrews & Rosenblum, 1991, 1993). Locomotor behaviour of guinea pig mothers also results in the mother being absent. This might influence later explorative behaviour of the young as far as leaving the mother is prerequisite for exploration.

Our conclusion that mothering styles exist in guinea pigs is strengthened by the fact that consistencies of differences between mothers were found in spite of challenges: beforehand parentage and the reproductive state of the

mother were varied. Possible effects of these challenges were examined by comparing the absolute differences between mothering of subsequent litters. The absence of effects of parentage (own or adopted young) excludes that the consistency of maternal behaviour can be attributed exclusively to the consistency of behaviour of the young as a result of their genetic likeness. This means also that the assumption of Fairbanks & McGuire (1988) — that a purely genetic view cannot explain consistency of maternal behaviour — cannot be contradicted. The absence of effects of the reproductive state of the mothers (pregnant or non-pregnant) shows that there is no change in weaning age. Also the increasing age and experience of the mothers in raising young did not influence maternal behaviour significantly nor did the age difference between the mothers at the start of the experiment.

Sofar all studies have used a *post-hoc* definition of mothering style when examining correlations between maternal behaviour and later behaviour of the young (*e.g.* Altmann, 1980; Wilsson, 1984; Simpson, 1985; Fairbanks & McGuire, 1988; Hemelrijk & Kogel, 1989; Berman, 1990a; Andrews & Rosenblum, 1991; Maestripieri, 1993). One of the focus points of criticism on this kind of studies has been the use of *post-hoc* definitions (*e.g.* Lamb, 1987). The present study shows that the underlying assumption of previous reports — that mothering styles exist — is probably correct, at least where guinea pigs are concerned. Our findings further enable the experimental study of the relation between mothering styles and later explorative behaviour of offspring.

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