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ORIGINAL ARTICLE

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Is maternal behavior correlated with later explorative behavior of young guinea pigs (*Cavia aperea f. porcellus*)?

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Abstract The results of previous studies, mostly involving primates, have shown a correlation between mothering styles and later explorative behavior of the young. On the basis of our previous study on the existence of mothering styles in guinea pigs we conclude that three main components of maternal behavior are useful for these kinds of studies: locomotion, affiliative behavior, and aggressive behavior. In the present study we examined the extent to which these components were correlated with later explorative behavior of guinea-pig pups. The later explorative behavior of 48 pups from 16 mothers was measured after weaning in a series of tests designed to highlight different aspects of exploration. The results indicate that maternal behavior does not have a predominant correlation with later explorative behavior of the pups. Correlations were not found between the affiliative and aggressive behavior of the mothers and the later explorative behavior of the pups. Mothers scoring high on locomotion had pups that showed more explorative behavior than did the pups of mothers scoring low on locomotion. This correlation, however, was not linear and was significant for only one parameter.

Key words Explorative behavior · Mothering behavior · Guinea pig

Introduction

It is generally assumed that maternal behavior plays a marked role in the development of explorative behavior by offspring. Mothering style is supposed to influence the behavior of the young even into adulthood (e.g., Hinde and Spencer-Booth 1968; Wachs and Grün 1982). The mother is considered crucial to the development of explorative behavior because she is considered the secure base from which all explorative escapades of the young start, and her control over these escapades is assumed to shape the eventual explorative behavior of the young (Ainsworth et al. 1978; Bowlby 1969).

For instance, Wilsson (1984) has reported a negative correlation between aggression displayed by German shepherd bitches toward their pups and the explorative behavior of their pups toward a passive person and the occurrence of violent behavior later in life. Andrews and Rosenblum (1991, 1993) provided Bonnet macaques with variable foraging possibilities by installing, e.g., an apparatus to keep the mother occupied with her hands and a wire-mesh partition to prevent the young from following her mother to the foraging site. They reported in both experiments that the more time the mother spent foraging, the less initiative the young showed to explore beyond the zone of contact with the mother. Among yellow baboons, "laissez-faire" mothers have young that wander a greater distance from their mothers at an earlier age than do the young of "restrictive" mothers (Altmann 1980). Fairbanks and McGuire (1988) found in vervets that under seminatural conditions the young of "restrictive" mothers took longer to enter a novel environment and showed less interest in events occurring outside their enclosure than did the young of "laissez-faire" mothers. In a later study in which maternal protectiveness was well controlled the same authors found an identical effect of maternal protectiveness (Fairbanks and McGuire 1993). In apparent contrast, Simpson (1985) reported results obtained with rhesus macaques; the young of "restrictive" mothers showed more initiative to explore a cage where the mother could not follow them than did the young of "laissez-faire" mothers.

The discrepancy between the findings reported by Fairbanks and McGuire and those obtained by Simpson could be attributable to differences between the species

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and the environments from which they originate but could also be due to differences in methodology (Fairbanks and McGuire 1988). Another problem is that in both studies the explorative behavior of the young was measured with the mother present in such a way that she could influence her offspring's behavior.

In the present study an eventual influence of the behavior of the mother during the test was excluded by individual testing of the explorative behavior of the young after weaning. For assessment of several aspects of exploration, three test situations were used: a novel object, an empty home cage, and a novel cage. In a previous study we had found that for the characterization of mothering styles in guinea pigs, three behavioral categories could be used: locomotion, aggression, and affiliative behavior (Albers et al. 1999). The aim of the present study was to find out whether these maternal behaviors correlated with the explorative behavior of the young.

Material and methods

Animals and housing

A total of 16 adult female guinea pigs ranging in age from 3 to 18 months and their 48 pups were used as subjects. The litter size varied between 2 and 4 pups (see Table 1); 27 pups were male and 21 were female. Four litters consisted of pups of only one sex. All animals were laboratory-reared from an outbred colony.

At least 3 days before the expected delivery each female was separately housed in a steel observation cage (1.3×0.4×0.4 m) with a Plexiglass front. Litters stayed with their mothers for 24 days, after which the mother was removed and an identical cage was connected to the observation cage to form a home cage consisting of two compartments connected by a small passage. The two compartments allowed the individual testing of exploration within the familiarity of the home cage. When a subject is put into a novel cage, escape responses may prevail over the urge to explore (Russell 1983). During testing the subject was in the test compartment and its littermates were in the other compartment (see Fig. 1).

All cages had wood chips for bedding. Pelleted food (Complete Cavy diet, Hope Farms B.V., Woerden, The Netherlands) and water were provided ad libitum in the compartment opposite the one used for testing. The ambient temperature was 19–22°C. Lights were kept on from 7:00 a.m. until 7:00 p.m.

Classification of mothers

On days 3, 5, 7, 10, 14, 17, 21 and 24 after delivery (day 0), 90-min video recordings of maternal behavior were made. Record-

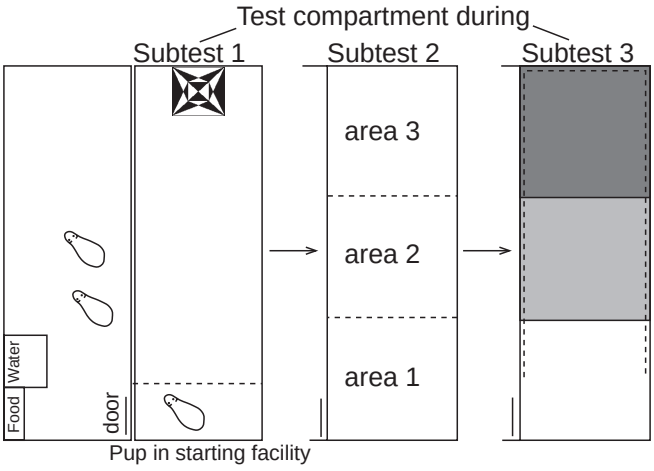

Fig. 1 Schematic overview of the test procedure. *To the left* a complete home cage is shown whose right half has been arranged for subtest 1. During testing the connecting door between the two compartments was closed. A transparent sliding door was placed *at the dotted line* to create a start facility (the start facility in subtest 2 and subtest 3 was identical to the start facility in subtest 1). *At the back* a novel object is present. The test compartment is virtually divided into three areas as shown in the subtest 2 arrangement: an empty compartment. In subtest 3, beyond the starting door a novel environment is created inside the test compartment. Hardboard walls are placed *along the dotted lines*; areas 2 and 3 contain a hardboard floor, which in area 2 is covered with a thin layer of woodchips

Table 1 Classification of the mothers for three factors according to quartile borders (*1* A score in the first quartile, border included; *2* a score in the intermediate quartiles; 3 a score in the fourth quartile, border included)

		Factors of maternal behavior:			
		Locomotion	Aggression	Allogrooming	
		24.6	1.3	1.5	Median (frequency/90 min)
		3.3–56.9	0–3.3	0.3–4.3	Range
		11.5–27.5	0.4–2.0	1.0–2.7	Quartiles
Mother 1	(3 pups)	1	3	2	
Mother 2	(3 pups)	1	3	2	
Mother 3	(4 pups)	1	2	1	
Mother 4	(2 pups)	3	1	2	
Mother 5	(3 pups)	3	3	1	
Mother 6	(2 pups)	1	1	3	
Mother 7	(3 pups)	1	1	2	
Mother 8	(4 pups)	2	2	2	
Mother 9	(4 pups)	2	1	2	
Mother 10	(2 pups)	2	2	3	
Mother 11	(3 pups)	3	1	1	
Mother 12	(2 pups)	2	2	3	
Mother 13	(4 pups)	3	1	2	
Mother 14	(3 pups)	3	3	3	
Mother 15	(3 pups)	3	3	2	
Mother 16	(3 pups)	2	2	1	

ings started at 30 min after the onset of the dark period and were made by red light. A pilot study had shown that at between 30 and 120 min after the onset of the dark period, usually at least one suckling bout could be observed. The behavior of the mother was registered by continuous sampling from the video. On the basis of these findings, mothers were classified for the factors locomotion, aggression, and allogrooming.

For each mother the average values noted for the frequency of locomotion (in approaching, leaving, and leading the pups), aggression (aggressive actions directed toward the pups), and allogrooming (grooming of the pups) were used as classifiers. The mothers were divided into the following three groups using the quartile borders: scoring within the first quartile, scoring within the second or third quartile, and scoring within the fourth quartile (see Table 1).

Exploration test

Pups were tested individually in a series of three subtests highlighting different aspects of explorative behavior. All subtests were undertaken in the test compartment, which was half of the home cage in which the pups had been housed from the age of 24 days onward. The front part of the test compartment consisted of a 22-cm-long start cage giving access to the rear part (108 cm) via a transpartent sliding door. The first subtest presented the pup with a novel object (a wooden black-and-white pyramid) at the back of the test compartment. This subtest was taken at the age of 28 days and was meant to measure the exploration of a novel object within a familiar environment.

In the third subtest, taken at the age of 30 days, the subject was confronted with a novel environment. The novel environment consisted of hardboard walls and a hardboard floor that were installed within the test compartment. The walls were painted brown with white stripes: the floor was brown, and its front half was strewn with wood chips (like the front 43 cm of the test compartment; see Fig. 1).

Test procedure

Prior to testing, the test compartment was prepared as follows: the connection dividing the home cage into two compartments was closed, with all pups being in the compartment opposite the test compartment; the transpartent door of the start cage was inserted; the test compartment was furnished according to the subtest that was about to be performed; the subject was put into the start cage; and after 3 min the Plexiglass door was removed, allowing access to the entire test compartment for 16 min. Scoring of behavioral parameters was done by a combination of one-zero-sampling and all-occurrences-sampling (Altmann 1973).

Parameters

The following parameters were scored:

1. Location (state)* (see parameter 14). For scoring of locations the cage was virtually divided into 12 squares (20×22 cm). Being in a certain square was treated as a state. Eventual areas as presented in Results as well as distances were derived from these states. States of location were treated independently of the states of behavior (stretched attention and freezing).
2. Stretched attention (state).
3. Freezing (state).
4. Grooming (event scored one-zero with a refractory period of 30 s: ESOZ30).
5. Sniffing at the wall (ESOZ30).
6. Sniffing at the floor (ESOZ30).
7. Sniffing at the novel object*, (ESOZ30).
8. Sniffing at the border of the novel room*, (ESOZ30).
9. Walking slowly, (event, walking without leaving the present location within 3 s).
10. Walking normally (event, walking involving crossing into an adjacent location within 3 s).
11. Walking fast (event, whereby crossing of more than one adjacent location within 3 s).
12. Walking distance.
13. Maximal distance from the starting position.
14. Latencies of the first occurrence of all parameters marked with an asterisk.

Data preparation and statistical analysis

Three possible classifications of maternal behavior were tested for their explanatory value with regard to pup behavior. For this purpose, pups were divided into the following three experimental groups for each of the three maternal factors: group 1, pups of mothers scoring low (within the first quartile); group 2, pups of mothers scoring intermediately; and group 3, pups of mothers scoring high (within the fourth quartile).

Differences between these three groups of pups were analyzed using the Kruskal-Wallis test followed by the Mann-Whitney U-test (MWU-t) as a post-hoc procedure (with alpha adjusted to 0.025 for significance). Bonferroni correction was used to control the potential inflation of a type I error; however, as this would leave nonsignificant all results but one (see Results, Table 2), we presented alpha values as if no Bonferroni correction had been used. The effect of Bonferroni correction is covered below in Discussion.

Results

Of the parameters shown in Fig. 2, the duration of presence in area 3, the latency of reaching area 3, and the maximal distance from the starting position clearly suggest that in subtests 1 and 3, all pups were presented with an approach-avoidance conflict. This effect was strongest in subtest 3, as most of the pups clearly hesitated to enter the novel environment. Statistical comparisons between the behavioral-parameter values recorded for subtest 2 and those noted for subtests 1 and 3 did not lead to any conclusion about differences between the experimental groups and are therefore not presented in this report.

Subtest 1 (novel object) and subtest 2 (empty test compartment) did not discriminate between the experimental groups. A correlation seemed to exist between the locomotion of the mother and the explorative behavior of the pups, but only in subtest 3 (the novel environment). However, post-hoc testing showed that even if this finding were significant after Bonferroni correction, there would be no straightforward correlation. Most of the significant differences were found between pups from mothers scoring intermediately and those from mothers scoring high on locomotion (group 2 and group 3) instead of between the extremes (group 1 and group 3).

Pups from mothers that scored high on locomotion walked longer distances (MWU-t, group 3>group 2, n=15, 15, P<0.005), walked normally more often (MWU-t, group 3>group 2, n=15, 15, P<0.025; group 3>group 1, n=15, 18, P<0.025), and walked slowly less often (MWU-t, group 3<group 1, n=15, 18, P<0.001; group 2<group 1, n=15, 18, P<0.005).

Table 2 Significance of pup behavior in an exploration test in relation to the maternal behavior they experienced. Any number represents significance (Kruskall-Wallis test) of pup behavioral elements in relation to the maternal behavior they experienced (*df*=2). All empty cells are nonsignificant. Significance means there was a correlation between maternal behavior and the later behavior of the pups. The results of post-hoc tests are mentioned in Results

Behavioral elements	Mothers classified on								
	Locomotion			Allogrooming			Aggression		
	Subtest 1	Subtest 2	Subtest 3	Subtest 1	Subtest 2	Subtest 3	Subtest 1	Subtest 2	Subtest 3
Duration in area 3			0.0054		0.0126				
Duration in area 2									
Duration in area 1					0.0038				
Latency of arrival in area 3			0.0486						
Latency of arrival in area 2				0.0116		0.0341			
Grooming (frequency)	0.0179								
Latency of starting to groom									
Walking slowly (frequency)		0.0001[a]	0.0073						
Walking normally (frequency)			0.0082				0.0188		0.0484
Walking fast (frequency)									
Walking distance			0.0161						
Maximal distance from start position			0.0342						
Sniffing floor (frequency)									0.0258
Sniffing wall (frequency)			0.0072					0.0429	
Freeze (duration)									
Stretched attention (duration)									
Contact with novel object (frequency)	0.0191								
Sniffing novel object (frequency)									
Sniffing border novel room (area 2, freq.)									
Sniffing border novel floor (area 3, freq.)									
Latency of sniffing border novel room									
Latency of sniffing border novel floor									

[a] The only correlation that would remain significant after Bonferroni correction

Pups of mothers that scored high on locomotion also went farther into the novel environment (MWU-t, group 3>group 2, n=15, 15, P<0.025). They had a shorter latency of arrival in area 3 (MWU-t, group 3<group 2, n=15, 15, P<0.025) and spent more time there (MWU-t, group 3>group 2, n=15,15, p<0.005). Furthermore they sniffed more often at the walls of the cage (MWU-t, group 3>group 2, n=15, 15, P<0.005; see Fig. 2).

No correlation was found between aggressive behavior of the mother toward the pups and the later explorative behavior of the pups. The few recorded instances of significance (see Table 2) are not convincing (even without Bonferroni correction), given the large number of pup-behavioral elements that were tested, and do not justify further post-hoc testing. The same conclusion holds when the level of maternal allogrooming is compared with the later explorative behavior of the pups.

Discussion

The explorative behavior of young guinea pigs is not predominantly correlated with the maternal behavior they have experienced in their youth. There seems to be a correlation between maternal locomotion and the explorative behavior of the pups in subtest 3, the novel environment, where 7 of 20 parameters are significant if no Bonferroni correction is used. Also, 1 of 16 parameters in subtest 2 remains significant after Bonferroni correction.

Mothers with a high score for locomotion had pups that scored higher in subtest 3 on locomotion-related parameters of explorative behavior but also sniffed more often at the walls of the cage. However, post-hoc testing showed that the main differences occurred between pups from high-scoring mothers and pups from intermediately scoring mothers, not between pups from high-scoring mothers and pups from low-scoring mothers. Thus, not only does the significance not hold up to Bonferroni correction, but the correlation between maternal locomotion and the explorative behavior of the pups is not straightforward and seems to depend solely on a difference between the pups from mothers scoring high on locomotion and the other pups.

Due to our use of three subtests in which different aspects of explorative behavior were highlighted, we are confident that the findings did not result from limited observations. Visual inspection of the data reveals an evi-

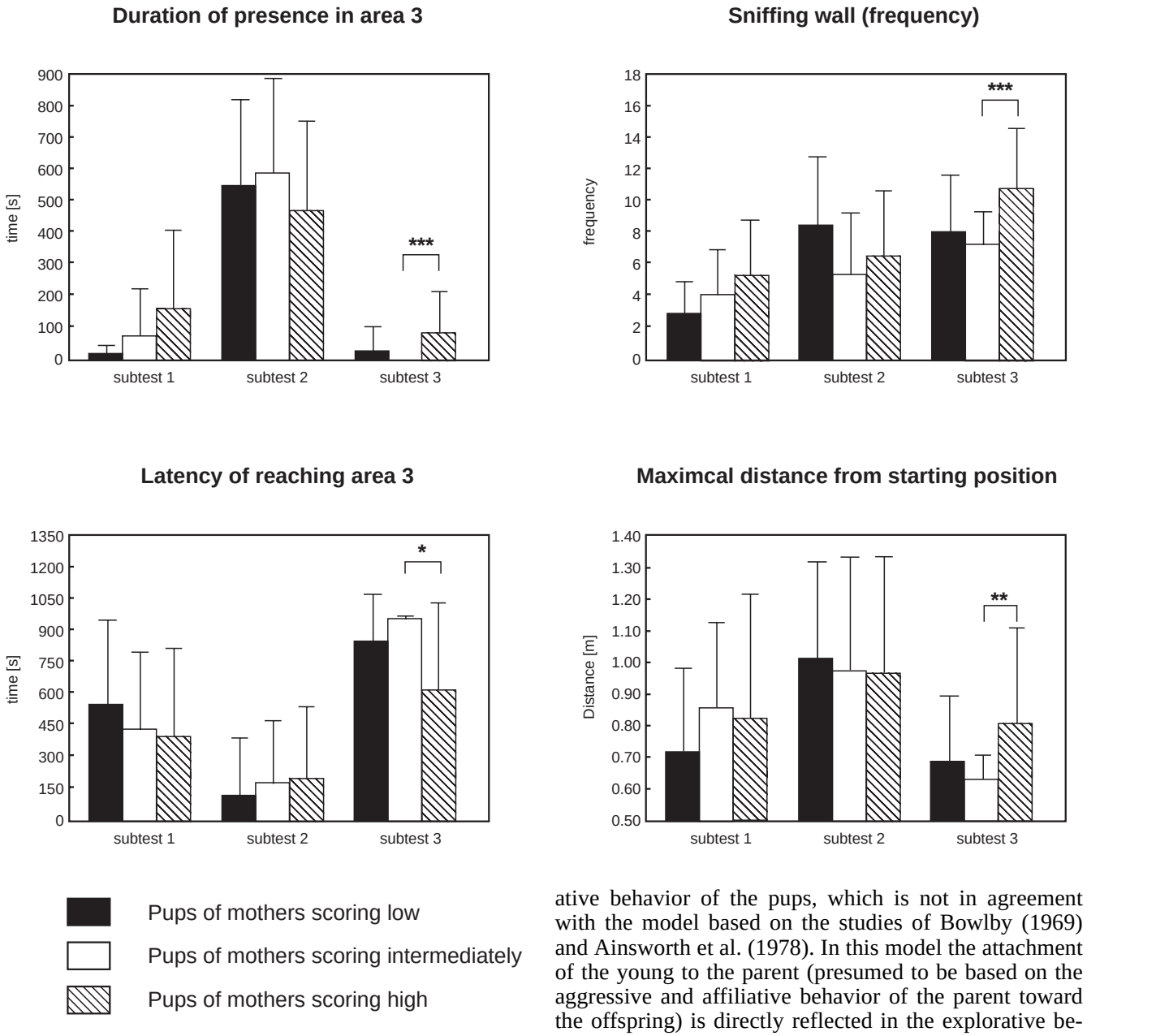

Fig. 2 Pup behavior in relation to maternal locomotion

dent approach-avoidance conflict in subtests 1 and 3 as well as a consistent difference between the mean values and the extremes that is sufficient for the exclusion of a skewed distribution of the variance.

Most previous studies that have reported a correlation between maternal behavior and the later explorative behavior of offspring have not defined their mothering styles according to parameters of locomotion. Definitions such as “restrictive mothers” and “laissez-faire mothers” (e.g., Fairbanks and McGuire 1988, 1993; Simpson 1985) are complex and include aspects of both aggressive and affiliative behavior. However, in the present study, maternal grooming and maternal aggression toward the pups did not correlate with the later explorative behavior of the pups, which is not in agreement with the model based on the studies of Bowlby (1969) and Ainsworth et al. (1978). In this model the attachment of the young to the parent (presumed to be based on the aggressive and affiliative behavior of the parent toward the offspring) is directly reflected in the explorative behavior of the young (Ainsworth and Wittig 1969; Bowlby 1969). Though widely accepted, this model does not lack for dispute.

Criticism has focused on the observation that in studies based on this model, maternal behavior and explorative behavior of the young have not been measured independently (e.g., Lamb 1987). For instance, in the studies of Fairbanks and McGuire (1988) and Simpson (1985), both of which found a correlation between maternal restrictiveness and the explorative behavior of offspring, albeit in opposite directions, the explorative behavior of the young was determined in the presence of the mothers. Thus, the mother could have influenced the behavior of the young during the test. In a later experiment conducted by Fairbanks and McGuire (1993), which was nicely controlled with regard to the determination of differences between mothers, the exploration

test of the young was actually done in the presence of the entire group of animals, including other young subjects; this makes the interpretation even more difficult, as these offspring should not have been treated as statistically independent subjects.

This criticism does not hold for the present study. Maternal behavior was measured independently from the explorative behavior of the young. The factors of maternal behavior that were used were based on previous research in which we ascertained which parameters of maternal behavior were suitable for the characterization of individual mothers; these characters were shown to be both stable over several subsequent litters and independent of the congenital behavior of the young (Albers et al. 1999). Individual testing of the pups excludes the direct influence of the mother on the subjects during testing.

Like previous studies on the effects of mothering styles, our experiment does not allow conclusions to be drawn about the mechanism behind the correlation between maternal behavior and the explorative behavior of the young. Neither genetic origin nor maternal behavior during the lactation period can be ruled out as causative factors. The finding in guinea pigs that the locomotor activity of the mother does correlate to some extent with the later explorative behavior of the young, whereas affiliative or aggressive behavior by the mother does not, might reflect the relative importance of locomotor behavior for this species. Guinea pigs have no defensive capability whatsoever and depend solely on flight for survival from predators. Exploration of the home range is important for successful avoidance of predation (Russell 1983). Mothers that walk around a lot might in this way prime their young to explore more than do mothers that walk less.

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