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ORIGINAL ARTICLE

Effects of REM sleep restriction during pregnancy on rodent maternal behavior

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Objective: To evaluate the effects of sleep restriction during pregnancy on maternal care and maternal aggression in a rodent model.
Methods: Twenty-three female Wistar rats were assigned to one of two groups: control (n=12) or sleep restriction (n=11) during the entire pregnancy. At the fifth postpartum day, the animals were subjected to the resident-intruder paradigm and to the pup retrieval test.
Results: Sleep restriction during pregnancy had no direct effects on maternal care. Regarding aggressive behavior, defensive aggression was increased by sleep loss, with a lower responsiveness threshold to hostile environmental stimuli. Sleep deprivation during gestation also reduced self-grooming behavior.
Conclusion: Taking increased self-grooming as a behavioral correlate of anxiety in rodents, this study provides evidence that lactating dams were in a condition of reduced anxiety. From an adaptive perspective, this pattern of stress response may function to ensure proper maternal behavior, thereby guaranteeing the survival and viability of the litter. Under a translational perspective, the present article confronts the importance of biological and adaptive features to rodent maternal behavior with the relevance of sociocultural factors to the human mother-infant relationship and to the onset of postpartum depression.

Keywords: Aggression; postpartum; pregnancy; sleep restriction; sleep

Introduction

Maternal behavior is among the most unique and important components of the rodent behavioral repertoire. This behavior is usually observed during a very specific period of the animal's life, i.e., from the end of pregnancy to the time of weaning. Maternal behavior is defined as any action performed by a dam in order to nurture, warm, feed, and protect its litter. It encompasses a set of behavioral parameters that can be grouped into two basic categories: maternal care (behaviors performed by the female towards its litter) and maternal aggression (behaviors performed by the female directed to external factors, objects, or subjects, in order to protect the litter from harm).[1,2]

Rodent maternal behavior represents an evolutionary strategy to adapt the offspring to a given environment and ensure the survival and viability of the litter.[1] A major feature of maternal behavior is its relationship with environmental stress.[3] Under stressful and hostile conditions, dams usually provide less maternal care to the litter, predisposing their pups to greater anxiety, heightened stress responsiveness later in life and, thus, a greater degree of adaptation to a stressful environment. On the other hand, when fostered in more agreeable conditions, dams will engage in higher levels of maternal behavior, generating litters with better coping abilities and less responsiveness to stress when adults. Pups that were exposed to lower levels of maternal behavior during early life also will provide less maternal care to their own litters during adulthood. Conversely, pups exposed to increased maternal care will exhibit more prominent maternal behavior towards their litters.[1,3,4] These characteristics ensure that, as long as environmental conditions remain stable, maternal behavior will be performed in regular patterns along a given lineage.

However, this inherited mode of maternal behavior can be interrupted by environmental alterations occurring before the puerperium, with long-lasting effects on the litter. Pups of high-licking dams (i.e., dams with high levels of maternal behavior), when fostered with low-licking dams, will show less maternal care during adult life. Conversely, pups of low-licking dams, when fostered with high-licking dams, will also display the behavioral profile of their surrogate mothers instead of that of their biological mothers,[3] demonstrating that maternal behavior can be modulated by early-life conditions. Likewise, post-weaning conditions such as enriched or impoverished environments can affect maternal behavior, modulating inherited behavioral patterns.[5] In general, perinatal stress impairs the behavior of the mother during the postpartum period, although the magnitude of the effects depends on the intensity and source of stress.[3,6-13]

One important source of stress during pregnancy is sleep deprivation.[14] In normal human pregnancy, decreased total

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sleep time, sleep efficiency, REM and slow-wave sleep, together with conditions such as greater urinary flow, nocturia, nausea, discomfort from fetal movements, difficulty in assuming usual sleep positions, back pain, and hormonal oscillations, lead to chronic sleep restriction.[14,15] Moreover, additional sleep deprivation, which is commonly observed due to the impositions of modern living, can compound this impact on pregnant women.[16]

Recent studies have argued that the lack of sleep during pregnancy may promote a broad range of impairments in mother-infant relationships, including increased maternal fatigue and postpartum depression.[14,17,18] However, previous preliminary data in animals have demonstrated that these effects may not be observed in certain specific conditions.[18] Thus, further investigation on the direct effects of lack of sleep on maternal behavior is still required. The present study aimed to evaluate the effects of sleep restriction during pregnancy on maternal aggression and maternal care in rodent models.

Methods

Subjects and experimental protocol

Twenty-three female Wistar rats, aged 90 days, were used in this experiment. Animals were provided by the Center for Development of Experimental Models for Medicine and Biology (CEDEME), São Paulo, Brazil. The animals were housed in polypropylene cages (41 × 28 × 140 cm) and placed in monitored rooms with controlled temperature (22±1 °C) and a 12 h:12 h light-dark cycle (lights on at 7 a.m.). After mating and confirmation of pregnancy by vaginal smear, the female rats were allocated into two groups: 1) control (CTRL; n=12) – not subjected to any manipulation during pregnancy; and 2) sleep restriction (SR; n=11) – subjected to sleep restriction during the entire pregnancy (21 days). The animals were housed in groups of four per cage until gestational day 15 (GD15). After GD15, the animals were housed singly to allow dams to perform maternal behavior properly. The day of delivery was defined as postpartum day 0 (PPD0). On the PPD2, the litters were culled to eight pups, to standardize conditions for behavioral observation. Behavioral tests were conducted at PPD5 to assess both maternal aggression and maternal care. PPD5 was chosen because it is located between the peak dates observed for maternal behavior (PPD1-3) and maternal aggression (PPD7-9). The tests used were, respectively, the resident-intruder paradigm[19,20] and the pup retrieval test.[21] The absolute weight of the litters and the mean pup weight (litter weight/number of pups) were assessed at PPD2 and at PPD5, before litter standardization and after behavioral testing, respectively. To minimize pup handling, litters were not weighed on any other days. The dams were weighed at GD1 and GD21 and at PPD2 and PPD5. All animal procedures were performed in accordance with ethical standards, and the experimental protocol was approved by the Universidade Federal de São Paulo (UNIFESP) Research Ethics Committee (protocol 122/10).

Sleep restriction

The SR protocol consisted of subjecting the animals to 18 h of sleep deprivation per day (from 4 p.m. to 10 a.m.) during the entire pregnancy (21 days), using the multiple platforms technique, as previously described.[22] During the remaining 6 h of each day, the animals were returned to their home cages. The multiple platforms technique was conducted in a tiled water tank (110 × 41 × 30 cm), which contained 14 platforms 6.5 cm in diameter and rising 1 cm above the water surface. In this method, the animals are able to behave and move freely throughout the tank while awake. Whenever the animal enters REM sleep, due to the muscle atonia observed in this sleep phase, it falls from the platform or touches its snout to the water, consequently waking. This method promotes complete REM sleep curtailment during the restriction period, a 30% reduction in non-REM sleep, consequent sleep fragmentation, and increased sleep pressure.[22] This protocol was applied to mimic the sleep condition of modern women during pregnancy. Pregnant women sleep during the habitual period (at night), but experience decreased sleep quantity and quality, which results in chronic SR. During the rest of the day, these women exhibit the effects of increased sleep pressure and somnolence. Rats are nocturnal, polyphasic animals and sleep about 12 h per day, mostly during the light period. Thus, in the present model, pregnant rats were also able to sleep during the habitual period (i.e., the light phase), but with reduced sleep quantity (6 h). During the rest of the day, the animals were subjected to SR so as to induce increased sleep pressure, similar to what is seen in human pregnancy.

Resident-intruder paradigm

In this test, an experimentally naïve 60-day-old male rat was introduced into the home cage with the female rat and its litter. Each intruder was used only once, to avoid any behavioral sensitization or modulation due to previous exposure to aggression. The latency, frequency, and duration of behavioral patterns related to maternal aggression (behaviors performed by the dam and directed to the intruder), maternal care (behaviors performed by the dam and directed to the litter), and unspecific behaviors (behaviors not related to maternal behavior or maternal aggression) were quantified in the presence of the intruder male. This test lasted 10 minutes and was conducted during the first third of the dark phase.

The following aggressive parameters were recorded:

- Frontal attack: a measure of offensive aggression, in which the resident animal (the dam) attacks and bites mainly the dorsal region of the intruder.
- Lateral attack: a measure of defensive or responsive aggression, in which the resident animal attacks and bites mainly the snout and face of the intruder.
- Boxing: a measure of defensive aggressiveness, in which both the intruder and the resident animal stand in an upright position and use their forepaws to hit each other.
- Domination (also known as submission, immobilization, pinning, or aggressive posture): a measure of offensive

aggression for the resident and of defensiveness for the intruder. In this case, the intruder lay down on its back, protecting its dorsal region from attacks, while the resident stands upon the intruder, threatening, dominating, and immobilizing it.

The following maternal care parameters were recorded in the presence of the intruder:

- Maternal care: general behaviors performed by the dam and directed to the pups, encompassing licking, grooming, nursing, and kyphosis positions for nurturing.
- Nest building: observed when the dam constructs or repairs the nest the litter is in.

The following unspecific behaviors were recorded:

- Self-grooming: the female grooms its own body.
- Social investigation: the female sniffs the intruder.
- Locomotion: the female moves around the cage, not interacting with the intruder.

Pup retrieval test

Immediately after the end of the resident-intruder paradigm, the dam was removed from the home cage and separated from the litter for 30 minutes. During this period, the nest was deconstructed and the pups were spread throughout the cage. When the female was returned to the cage, the latencies to the following behaviors were quantified: nest building, pup contact, retrieval of the first pup to the nest, retrieval of the last pup, licking/grooming the pups, and nurturing the pups in a kyphotic position. Finally, the time to full maternal behavior (FMB), defined as nest building, retrieval of all pups, and kyphotic position for 3 consecutive minutes, was calculated. This test lasted 30 minutes.

Statistical analysis

Weight measurements (dam weight during pregnancy, postpartum dam weight, litter weight, and mean pup weight) were compared through repeated-measures ANOVA, while variables related to litter description (litter size and male-to-female ratio) were compared through Student's *t* test. Behavioral parameters quantified in both tests were compared by the Mann-Whitney *U* test. Lastly, FMB was classified as "observed" or "not observed" and compared using a chi-square test. Analyses were performed using SPSS version 19. For all cases, $p < 0.05$ was considered significant.

Results

Regarding the weight of the dams during pregnancy, there was no significant group effect, but there were significant effects of time and of the group-time interaction (time [$F_{1,16} = 1{,}114.04$; $p < 0.01$]; group [$F_{1,16} = 3.54$; $p = 0.78$]; interaction [$F_{1,16} = 10.14$; $p < 0.01$]), indicating lower weight gain in dams subjected to SR throughout pregnancy. Considering the weight gain during the postpartum period, sleep-restricted dams exhibited less weight gain after delivery (time [$F_{1,18} = 1.18$; $p = 0.29$]; group [$F_{1,18} = 8.06$; $p = 0.01$]; interaction [$F_{1,18} = 0.61$; $p = 0.44$]). No difference was observed in litter weight (time [$F_{1,21} = 2.29$; $p = 0.17$]; group [$F_{1,21} = 0.13$; $p = 0.72$]; interaction [$F_{1,21} = 0.22$; $p = 0.64$]). For pup weight, an effect of time, but not of group or interaction, was observed (time [$F_{1,21} = 218.02$; $p < 0.01$]; group [$F_{1,21} = 0.15$; $p = 0.70$]; interaction [$F_{1,21} = 0.04$; $p = 0.85$]). Lastly, there were no significant differences in litter size ($p = 0.97$) or male-to-female ratio ($p = 0.89$). Descriptive data for weight measurements and litter characteristics are shown in Table 1.

The resident-intruder paradigm showed significant differences in maternal aggression and self-grooming behavior between the two groups. Significantly lower latency (CTRL: 553.2±155.3 s; SR: 362.7±240.3 s; $p = 0.03$), higher frequency (CTRL: 0.45±1.51 s; SR: 2.20±2.82 s; $p = 0.03$), and greater duration (CTRL: 0.45±1.51 s; SR: 3.40±5.25 s; $p = 0.04$) of boxing behavior were observed in sleep-restricted animals when compared to controls (Figure 1). In addition, the duration of self-grooming was significantly reduced in the SR group when compared to CTRL (CTRL: 121.2±148.0 s; SR: 30.10±20.10 s; $p = 0.02$). No significant results were observed in other maternal, aggressive, or unspecified behaviors during the resident-intruder paradigm (Table 2). The pup retrieval test did not show any significant between-group differences (Table 3). Finally, there was no significant difference between groups in the number of animals that performed FMB ($\chi^2 = 0.12$; $p = 0.72$).

Table 1 Descriptive characteristics of dams and litters in the control and sleep restriction groups

	Control	Sleep restriction	p-value
Dam weight - GD1	231.0±23.63	226.3±25.75	**T < 0.01**; G = 0.78; **I < 0.01**
Dam weight - GD21	357.0±26.67	325.7±20.82	
Dam weight - PPD1	270.4±15.53	254.3±24.47	T = 0.29; **G = 0.01**; I = 0.44
Dam weight - PPD5	281.7±24.00	254.1±19.71	
Litter weight - PPD2	83.00±18.36	86.64±14.46	T = 0.17; G = 0.72; I = 0.64
Litter weight - PPD5	89.04±18.23	90.00±14.30	
Pup weight - PPD2	7.24±0.92	7.52±2.11	**T < 0.01**; G = 0.70; I = 0.85
Pup weight - PPD5	11.20±1.18	11.38±1.73	
Litter size	11.58±2.78	11.55±1.04	0.97
Male-to-female ratio	0.93±0.03	0.95±0.59	0.89

Data presented as mean ± standard deviation. Weight values expressed in grams.
GD = gestational day; G = group effect; I = interaction effect; PPD = postpartum day; SD = standard deviation; T = time effect.
Values in bold indicate statistically significant results.

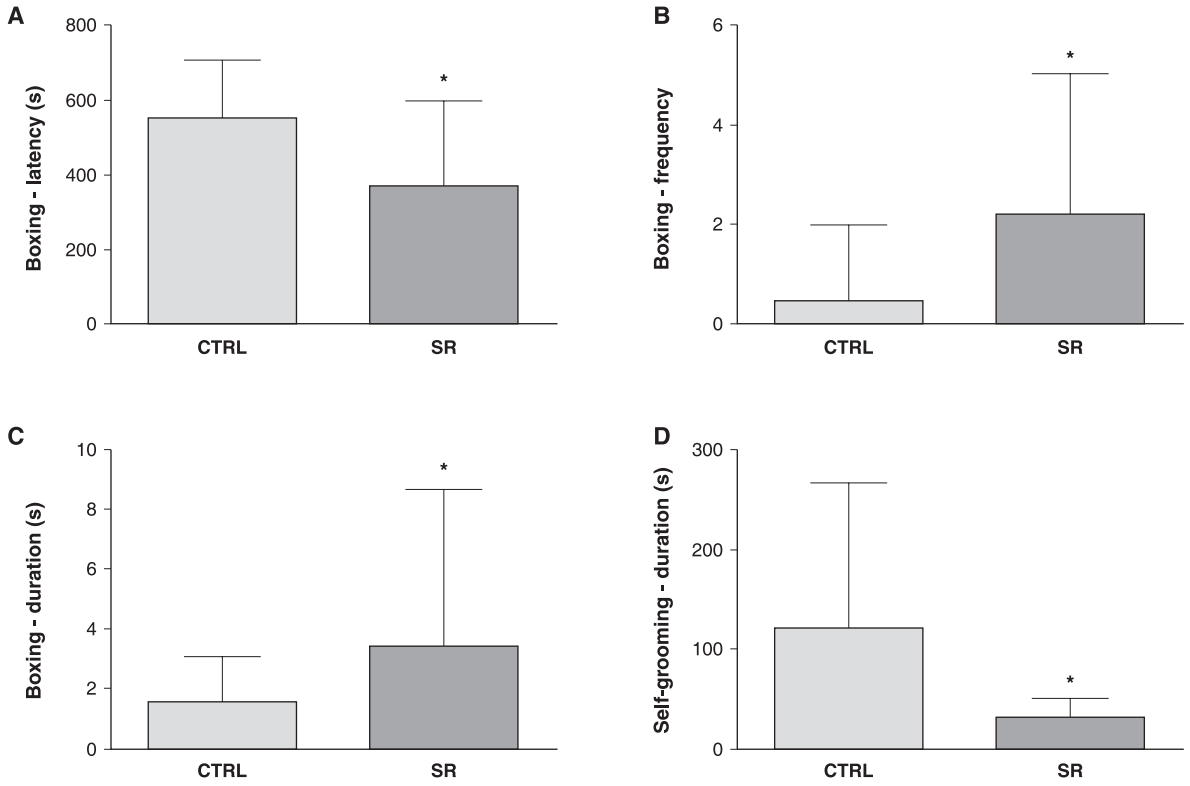

Figure 1 Boxing and self-grooming results, acquired through the resident-intruder paradigm. A) latency for boxing; B) frequency for boxing; C) duration of boxing; D) latency for self-grooming. Data presented as mean ± standard deviation. CTRL = control group; SR = sleep-restricted group. * $p > 0.05$

Discussion

Previous investigations have hypothesized and discussed a possible impairment of mother-infant relationships due to sleep deprivation during pregnancy.[14,17] However, despite these hypothetical predictions and regardless of the well-known impairment of maternal behavior due to gestational stress, a similar previous study failed to detect any effect of sleep loss during pregnancy on maternal care.[18] The present study, which was designed to provide further evidence regarding this relationship, is in accordance with the aforementioned report, as no effects on maternal care were observed. The results presented herein demonstrate that, in female rats, sleep deprivation during pregnancy leads to increased boxing behavior and decreased self-grooming when compared with non-sleep-restricted lactating rats, with maintenance of maternal care levels.

Boxing behavior is considered a measure of defensive aggression.[2] Increased aggressive behavior is a classical consequence of sleep loss, in humans and non-human animals alike,[23,24] and previous ethological studies have described a predominance of defensive activity instead of offensive aggression due to sleep deficits in non-maternal conditions.[25] Thus, the present data demonstrate that increases in defensive aggression due to sleep loss are also observed during lactation. An increase in lateral attack (rather than in boxing) in sleep-deprived dams was observed in a previous report.[18] Although this appears to be a discrepancy between the experiments (lateral attack in the previous report, boxing behavior in the present study), it should be noted that both behaviors belong to the same behavioral scope, i.e., defensive aggression. Hence, both experiments agree that increased defensive behavior is a consequence of SR during pregnancy.

With respect to self-grooming, this is a highly complex behavior,[26] strongly related to stress and anxiety.[26,27] Although not the main behavioral feature of anxiety, increased self-grooming appears as part of the behavioral profile of rodents exposed to an anxiogenic condition.[26] Indeed, self-grooming is widely used as an indirect marker of stress and anxiety in rodents,[28-30] including during lactation.[31] The findings of the present experiment indicate that SR during pregnancy induced an anxiolytic condition, as the duration of self-grooming was lower in sleep-restricted dams than in control females. Similar data have been reported previously,[18] in which latency, frequency, and duration were altered due to sleep deprivation during pregnancy. Thus, at least one grooming-related variable was affected whenever this behavior was measured in the context of sleep deprivation and maternal behavior, indicating that reduced self-grooming is a reliable long-term behavioral effect of SR during pregnancy.

Considering maternal care, assessed both through the pup retrieval test and during the resident-intruder paradigm, no significant between-group differences were observed. We conclude that maternal care remained

Table 2 Between-group comparison of behavioral parameters from the resident-intruder paradigm

	Control		Sleep restriction		
	Mean ± SD	Median	Mean ± SD	Median	p-value
Aggressive parameters					
Frontal attack - latency	358.7±212.5	344	258.3±188.4	210.5	0.30
Frontal attack - frequency	1.45±1.81	1	5.10±5.45	3.5	0.05
Frontal attack - duration	2.82±5.00	1	10.70±12.80	6	0.07
Lateral attack - latency	327.1±182.5	315	200.2±166.6	153.5	0.08
Lateral attack - frequency	2.91±3.21	1	4.20±3.33	4	0.27
Lateral attack - duration	5.73±8.38	2	9.10±12.35	5	0.35
Boxing - latency	553.2±155.3	600	362.7±240.3	400.5	**0.03**
Boxing - frequency	0.45±1.51	0	2.20±2.82	1	**0.03**
Boxing - duration	1.54±5.13	0	3.40±5.25	1.5	**0.04**
Domination - latency	426.1±206.8	600	373.9±242.5	415	0.57
Domination - frequency	0.73±1.91	0	2.30±3.20	1	0.38
Domination - duration	3.18±7.37	0	12.60±15.56	7	0.38
Maternal care parameters					
Nest building - latency	548.1±141.7	600	515.4±179.9	600	0.88
Nest building - frequency	1.09±3.01	0	0.20±0.42	0	0.96
Nest building - duration	6.09±17.71	0	0.60±1.26	0	0.96
Maternal care - latency	437.4±214.0	600	317.7±250.9	209.5	0.31
Maternal care - frequency	2.09±3.62	0	2.40±3.27	1.5	0.71
Maternal care - duration	12.64±27.84	0	18.60±33.60	7	0.43
Unspecific non-parental parameters					
Self-grooming - latency	158.5±128.2	119	233.8±148.2	215.5	0.27
Self-grooming - frequency	6.00±4.19	4	4.30±2.26	3.5	0.39
Self-grooming - duration	121.2±148.0	74	30.10±20.10	27	**0.02**
Social investigation - latency	61.18±178.9	4	8.40±8.97	5.5	0.80
Social investigation - frequency	14.82±7.32	15	14.50±5.97	13.5	0.97
Social investigation - duration	60.73±29.73	61	80.50±40.34	70	0.36
Locomotion - latency	37.73±23.24	37	61.20±106.1	31.5	0.70
Locomotion - frequency	15.18±8.63	13	15.00±5.33	14.50	0.97
Locomotion - duration	30.27±24.47	21	36.30±21.78	28	0.23

Latency and duration values expressed in seconds; frequency values represent the number of times the corresponding behavior was performed.
SD = standard deviation.
Values in bold indicate statistically significant results.

equivalent in both groups, even after the stress caused by sleep loss during pregnancy. Taken together, the present data indicate that SR during pregnancy induced an anxiolytic condition during the postpartum period, as well as an increase in defensive aggressive behavior and maintenance of maternal care levels in both groups.

The relationship between sleep and anxiety has been described as a function of adaptive mechanisms.[32] During the postpartum period, dams usually exhibit a marked stress hyporesponsiveness,[33,34] associated with an accentuated reduction in anxiety-like behavior.[35] These are normal behavioral modulations, which occur in an adaptive sense, to increase the dam's ability to perform maternal behavior properly. This hyporesponsiveness to stress seems to be even more pronounced in face of challenging, disruptive, or hostile conditions.[36] Considering the results obtained in the present experiment, it could be argued that SR potentiated the stress hyporesponsiveness normally observed during the postpartum period. This phenomenon was better observed through the resident-intruder paradigm, in which exposure to an intruder animal constituted a disruptive and hostile stimulus. The observed anxiolysis (manifested mostly by a decrease in self-grooming) was the main outcome, which took place as an effect of the hyporesponsiveness to stress and enabled the dam to both nurture the litter and protect them from any potential harm, even when faced with both chronic and acute stresses (respectively, long-term

Table 3 Between-group comparison of latencies for behavioral parameters from the pup retrieval test

	Control		Sleep restriction		
	Mean ± SD	Median	Mean ± SD	Median	p-value
Pup contact	529.6±615.7	357	146.9±213.9	73	0.09
First pup retrieval	841.8±779.5	1,000	417.5±649.2	73	0.17
Last pup retrieval	1,441±486.4	1,800	944.0±660.3	840	0.08
Nest building	1,357±750.2	1,357	1,052±755.6	1,020	0.41
Licking/grooming	660.7±579.9	383	631.5±535.8	540	0.97
Kyphosis	1,227±604.3	1,431	1,160±567.7	1,160	0.94
Full maternal behavior	1,623±359.3	1,800	1,594±326.9	1,800	0.74

Values expressed in seconds.
SD = standard deviation.

sleep deprivation and the intruder). This anxiolysis would be one among several adaptive mechanisms whereby maternal behavior was modulated and sustained in face of environmental demands and challenges[4] and which is ultimately intended to ensure the survival of the litter. In the present experiment, anxiolysis was a result of sleep deprivation during pregnancy and allowed proper performance of maternal behaviors, encompassing increased maternal aggression and maintenance of maternal care levels.

Considering the maintenance of maternal behavior between groups, some further considerations are warranted. SR is a mild intervention when compared to total sleep deprivation. The SR protocol was chosen because it was considered the best method to simulate the sleep deficit observed in pregnant women, whereas other methods would lack such translational coherence. Even so, one could hypothesize that, if more aggressive methods of sleep curtailment were applied (such as total sleep deprivation), deficits in maternal behavior would be seen. This supposition becomes plausible because other sources of stress have already been shown to negatively affect maternal behavior,[6,9,37] suggesting that effects on maternal behavior are a function of the source and intensity of the stressor. Thus, there might be a threshold for stress up to which the dam can cope. In the present case, SR produced levels of stress for which adaptive mechanisms may have been able to compensate. Moreover, based on the present findings, we cannot ascertain whether the results were due to a specific effect of SR or to sleep loss acting as a generic stressful condition. In any event, sleep deprivation is virtually inseparable from stress and may itself be a stressor. Therefore, it may be advisable to considerer the present results as a consequence of the sleep deprivation-stress dyad. Further experiments using corticosterone replacement or adrenalectomized animals may be useful to provide additional data on this issue. Lastly, it should be noted that the pup retrieval test was performed after the resident-intruder paradigm. Thus, rather than an exclusive effect of SR during pregnancy, the maintenance of maternal care would be better interpreted if taken as an effect of SR combined with an acute hostile environment.

Additionally, interesting discussions can be raised from comparisons of the present study with similar previous investigations. To the best of our knowledge, four other experiments addressing the effects of lack of sleep on maternal behavior have been published,[18,38-40] all with some methodological differences when compared to the present experiment. Pires et al.,[18] in the only previous experiment to encompass maternal aggression among the measures of maternal behavior, observed similar results of reduced anxiety, increased aggressive behavior, and maintenance of maternal behavior. Pardo et al.[40] also observed maintenance of maternal behavior following a similar protocol of REM sleep restriction conducted from gestational days 12 to 20. Radhakrishnan et al.[39] also observed no significant effect of sleep deprivation on maternal behavior, but with a protocol that consisted of total SR through the gentle handling method (as opposed to the above-listed studies, which used REM sleep restriction through platform methods) during the last third of pregnancy. Conversely, Gulia et al.[38] were the only authors to observe impairment of maternal behavior following sleep deprivation, employing a protocol composed of REM sleep restriction during the last third of pregnancy. Of note, Gulia et al. employed the single platform method, instead of the modified multiple platform method used in previous experiments. Comparison of these studies shows that most of the variation between them is attributable to methodological issues, such as duration of sleep manipulation (whole pregnancy vs. last third), type of sleep deprivation (REM sleep restriction vs. total SR), and method of sleep deprivation (single or multiple platform methods, gentle handling). This reinforces our suspicion that the results acquired so far may be due to the stress intrinsically related to sleep deprivation and that there may a threshold of stress up to which the dam can cope in order to provide sufficient amounts of maternal behavior. Thus, certain methods may not be so stressful as to affect maternal behavior,[39] while others may exceed the stress threshold the dam is able to cope with and overcome. Gulia et al.[38] were the only investigators to employ experimental conditions that led to an impairment in maternal behavior, but the change of higher pup retrieval times in sleep-deprived dams was observed only on postpartum days 1 to 3, with no long-term or sustained effects. This is an interesting observation, as it highlights a possible short-term effect of lack of sleep during pregnancy, which would be a combined result of both sleep deprivation and maternal fatigue. This condition resembles the ''postpartum blues'' commonly observed during the first days after delivery in humans, rather than postpartum depression, which is more often an object of research. Taking all these comparisons into consideration, we conclude that sleep deprivation does not lead to a decrease in maternal behavior throughout the lactation period, but its short-term effects – specifically, the changes observed during the very first days of lactation – should not be neglected.

It bears noting that the present interpretation of the data, based mostly on behavioral adaptive mechanisms, is not in complete accordance with the hypothesis that SR during pregnancy would result in impaired mother-infant relationships. Nevertheless, the prior hypothesis remains plausible. Adaptive mechanisms are evolutionarily selected functions that are very important to animal behavior. However, in human maternal behavior, a great impact of sociocultural factors on maternity and on the mother-infant relationship can be noted, regardless of adaptive mechanisms, which may attenuate their effects. In other words, in human beings, societal, cultural, and environmental factors could be stronger than the protective adaptive mechanisms that are responsible for the maintenance of maternal behavior in response to stress. Thus, such factors would make an important contribution to the onset of postpartum depression, postpartum blues, or any other deficits in the human mother-infant relationship. Additional studies in humans are warranted to fully elucidate the factors at work and their respective importance.

Overall, the present study demonstrates that aggressive behavior, mainly defensive aggression, is increased by

sleep loss, evincing a lower threshold of responsiveness to hostile environmental stimuli. In addition, SR during gestation reduces self-grooming behavior. Taken as a behavioral correlate of anxiety in rodents, this behavior suggests that lactating dams were in an anxiolytic condition. Lastly, SR during pregnancy has no effects on maternal behavior. From an adaptive perspective, this pattern of stress response may ensure that maternal care and maternal aggression will be performed properly, ultimately guaranteeing the survival and viability of the litter.

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Disclosure

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