Bulletin of the Psychonomic Society
1987, 25 (2), 133-135

The effect of pup presence and intruder behavior on maternal aggression in rats

KEVIN J. FLANNELLY
University of Hawaii, Honolulu, Hawaii

and

ERNEST D. KEMBLE
University of Minnesota, Morris, Morris, Minnesota

Maternal aggression was not affected by a brief (1 min) interval of pup separation and was not dependent upon the behavior of male intruders. Dams' latency to attack increased significantly within 4 h of pup removal. Duration of offense was decreased by 8 h of separation and all aggression was abolished after 24 h of separation. The results demonstrate that the short-term maintenance of maternal aggression does not depend on pup stimulation or the behavior of male intruders. Maternal aggression decreases systematically, however, when pups are absent for longer intervals.

Previous research clearly demonstrates a time-dependent reduction of maternal aggression in rats (Erskine, Barfield, & Goldman, 1978, 1980; Ferreira & Hansen, 1986) and mice (Gandelman, 1972; Paul, Gronek, & Politch, 1980) when pups are separated from the dam. The time course of this effect remains unclear, however, because only a few separation intervals have been used and no studies have examined the effect of removing the pups for more than 5 h. And although pup removal of a few minutes or less does not disrupt maternal aggression in mice, the effect of such manipulation has not been investigated in rats. The major purpose of these experiments was to investigate the effects of dam-pup separations of 1 min, 4 h, 8 h, and 24 h. A secondary purpose of Experiment 1 was to confirm previous reports that maternal aggression is unrelated to the behavior of intruding males (Erskine, Denenberg, & Goldman, 1978; Paul et al., 1980).

GENERAL METHOD

Animals

The subjects were 36 female Long-Evans rats, 85-115 days old. Seventy-two males of the same strain were used as intruders for aggression tests. These males were 60-80 days old and weighed 205-275 g at the time of testing. After being mated for 1 week with stud males, subjects were housed individually in 38×32×18 cm plastic pan cages with pine shavings for bedding. The stud males were not used as intruders. Each intruder was used only once and was considerably smaller than the female with which it was tested.

Test Procedure

Each subject was given two tests of aggression against an unfamiliar male intruder placed into the dam's home cage. Each test was a maximum of 10 min in length, beginning with the placement of the intruder in the corner of the cage farthest from the nest. Latency to attack (first bite or other aggressive act) by the female was recorded with a stopwatch. Total duration of all offensive behaviors (offensive sideways, offensive upright, and full aggressive posture) and number of bites (Flannelly, Kemble, Blanchard, & Blanchard, 1986) were recorded for 1 min once the female attacked. The short test interval and the small size of the intruder were utilized to ensure attack by the dam and to limit the possibility of retaliatory attack by the male, which might otherwise have affected the offensive behavior of the female on the second test (K. J. Flannelly & L. Flannelly, 1985; K. J. Flannelly, L. Flannelly, & Lore, 1986; Takahashi & Lore, 1982). The initial test was given on the afternoon of the day of parturition.

Please address reprint requests to Kevin J. Flannelly, 445 Kaiolu St., Apt. 206, Honolulu, HI 96815.

EXPERIMENT 1

Experiment 1 was designed to confirm previous reports that maternal aggression is not altered by short-term dam-pup separation (Gandelman, 1972; Paul et al., 1980) and is unrelated to the behavior of male intruders (Erskine, Denenberg, & Goldman, 1978; Paul et al., 1980). This was accomplished by testing lactating females for aggression with and without their pups present during intruder presentation and by assessing the behavior of intruders prior to maternal attack when the pups were present during the test.

Method

The 12 subjects were given two aggression tests separated by a 1-h interval. For one test, the dam and pups were left undisturbed and a male intruder was placed into the home cage. For the other test, the pups were removed within 1 min of the presentation of the intruder. Each female was tested in both conditions, with order of conditions counterbalanced across the subjects. In addition to maternal aggression, several of the intruder's behaviors were recorded in the pups-present condition. These were latency to cross into the half of the cage containing the nest, latency to contact any pup (including sniffing or simply walking over it), and latency to bite pups.

Results

Ten of the 12 subjects attacked male intruders when their pups were present, and 9 of these 10 also attacked

when their pups were absent. Mean latency to attack for dams in the pups-absent condition (mean = 162.0 sec, *SE* = 79.8) was not reliably greater than that of dams tested with their pups (mean = 129.9 sec, *SE* = 67.6). Females tested without their pups also exhibited levels of offense (mean = 17.9 sec, *SE* = 4.2) comparable to those shown by dams with their pups (mean = 20.8 sec, *SE* = 5.2), and bit intruders just as often. Mean number of bites by females with and without their pups was 2.1 and 2.3, respectively. Dependent *t* tests revealed no significant difference in mean group performance between conditions on any measure (*ps* > .10).

No significant correlation [$r(11) = 0.06$] was found between subjects' latency to attack and the latency of intruders to cross into the nest half of the cage in the pups-present condition. Mean latency to enter the nest half of the cage was 402.3 sec (*SE* = 84.3), whereas mean offense/bite latency for females in this condition was 126.9 sec. Although 5 males were attacked after approaching the nest, 5 others that did not approach the nest were also attacked. Of 3 males that actually entered the nest, 2 were attacked and 1 was not. No intruder injured any of the pups.

EXPERIMENT 2

The results of Experiment 1 are consistent with earlier reports indicating that the initiation of attack by the dam is not precipitated by the behavior of the intruder toward her pups (Erskine, Denenberg, & Goldman, 1978; Paul et al., 1980). Our results also extend earlier findings with mice that short-term separation of dams and pups does not attenuate maternal attack (Paul et al., 1980; Svare, 1977). Other work with domestic rats (Erskine, Barfield, & Goldman, 1978, 1980; Ferreira & Hansen, 1986) and mice (Svare, 1977, 1979), however, has shown that maternal aggression does decline after the removal of pups for several hours. The time course of this effect was the focus of Experiment 2.

Method

Twenty-four females served as subjects. After an initial aggression test with their pups present, dams were randomly assigned to four posttest conditions for retesting: (1) 4 h after removal of their pups, (2) 8 h after pup removal, (3) 24 h after pup removal, or (4) 24 h after the initial test but with pups present throughout this interval. Pups were removed immediately after the initial test in Conditions 1-3.

Results

The results of Experiment 2 are presented in Table 1. Because of between-group variability in pretest scores, statistical analyses were based on within-group comparisons. Dependent *t* tests conducted on the pretest/posttest difference scores revealed a significant posttest increase in latency to attack within 4 h of pup removal ($p < .05$). The apparent increase in latency for dams whose pups were present during the 24-h interval between tests was produced by a single subject that failed to attack on the posttest.

Although there was no reliable change in duration of offense when pups were absent for 4 h, offense decreased significantly by 8 h ($p < .05$) and was completely abolished by 24 h (Wilcoxon matched pairs test, $p < .05$). A significant reduction in number of bites was observed only when pups were absent for 24 h (Wilcoxon, $p < .05$). There were no significant pretest/posttest changes on any measure when pups remained with the dams for 24 h (*ps* > .10).

DISCUSSION

The results of Experiment 1 clearly show that pup presence is not essential for the initiation of maternal attack. This is consistent with previous studies on *M. musculus* that reported high levels of attack against intruders when females were tested shortly after removal of their litters (Paul et al., 1980; Svare, 1977). Here, too, aggression after brief separations was both quick and intense. Also consistent with previous findings, initiation of attack by dams was not precipitated by the behavior of intruders toward the pups (Erskine, Denenberg, & Goldman, 1978; Paul et al., 1980). Thus, the present findings support the view that dams do not directly defend their young in response to a threat posed by an intruder, even though their aggression may serve to protect the pups from harm (Paul et al., 1980). Like intermale aggression (K. J. Flannelly & Blanchard, 1982; K. J. Flannelly & Thor, 1976), maternal aggression is probably elicited by olfac-

Table 1
Mean Maternal Aggression and Standard Error of the Mean Against Intruding Males by Primiparous Long-Evans Rats Before Removal of Their Pups (Pre) and at Various Times After Pup Removal (Post)

		4 h After Pup Removal		8 h After Pup Removal		24 h After Pup Removal		24 h With Pups	
Measure		Mean	*SEM*	Mean	*SEM*	Mean	*SEM*	Mean	*SEM*
Latency to Attack (sec)	Pre	15.3	3.2	37.2	16.3	51.5	19.3	85.5	14.8
	Post	339.7	119.6*	317.8	96.8*	600.0	0.0*	147.8	91.4
Duration of Offense (sec)	Pre	35.8	4.9	28.6	6.4	26.3	3.9	31.5	9.3
	Post	18.5	10.3	11.8	7.7*	0.0	0.0*	13.6	6.6
Number of Bites	Pre	2.5	0.4	2.7	0.7	4.1	1.6	2.2	0.5
	Post	1.5	0.8	1.3	0.5	0.0	0.0*	2.3	0.7

*Significant difference between pre- and posttest scores, $p < .05$.

tory cues of the intruder, rather than by the intruder's behavior (Ferreira & Hansen, 1986). It is thought that both types of fighting are triggered when an attacker detects that an intruder's odor differs from its own, or that of its home site or territory (Adams, 1976; Lynds, 1976; Mink & Adams, 1981; Paul et al., 1980).

Despite substantial within-group variability in Experiment 2, it is clear that maternal attack showed a general decline during the first 4-8 h after pup removal and was completely obliterated after 24 h of separation. Because females whose pups were with them for 24 h showed no reduction in aggression, it is apparent that the decreased aggression observed in other groups was due to the pups' absence rather than to time alone. Such controls have not been used in previous studies of pup removal.

A recent study of maternal aggression in rats (Ferreira & Hansen, 1986) corroborates research on mice (Svare, 1977, 1979) in which it has been found that the dam's aggressive potential can be sustained for several hours by olfactory cues from the pups, even when physical contact with them is prevented. Various mechanisms must therefore exist to ensure the maintenance of the dam's aggressiveness. The present study reveals, however, that in the absence of such cues the female quickly resumes a nonbelligerent attitude toward strange males. Thus, in the event of pup loss, females would quickly resume mating.

REFERENCES

Adams, D. B. (1976). The relation of scent-marking, olfactory investigation, and specific postures in the isolation-induced fighting of rats. *Behaviour*, **56**, 286-297.

Erskine, M. S., Barfield, R. J., & Goldman, B. D. (1978). Intraspecific fighting during late pregnancy and lactation in rats and effects of litter removal. *Behavioral Biology*, **23**, 206-218.

Erskine, M. S., Barfield, R. J., & Goldman, B. D. (1980). Postpartum aggression in rats: I. Effects of hypophysectomy. *Journal of Comparative Psychology*, **94**, 484-494.

Erskine, M. S., Denenberg, V. H., & Goldman, B. D. (1978). Aggression in the lactating female rat: Effects of intruder age and test arena. *Behavioral Biology*, **23**, 52-66.

Ferreira, A., & Hansen, S. (1986). Sensory control of maternal aggression in *Rattus norvegicus*. *Journal of Comparative Psychology*, **100**, 173-177.

Flannelly, K. J., & Blanchard, R. J. (1982). Decreased aggressive and social responsiveness of chronically anosmic male rats. *Bulletin of the Psychonomic Society*, **19**, 173-176.

Flannelly, K. J., & Flannelly, L. (1985). Opponents' size influences maternal aggression. *Psychological Reports*, **57**, 883-886.

Flannelly, K. J., Flannelly, L., & Lore, R. K. (1986). Postpartum aggression against intruding male conspecifics by Sprague-Dawley rats. *Behavioural Processes*, **13**, 279-286.

Flannelly, K. J., Kemble, E. D., Blanchard, R. J., & Blanchard, D. C. (1986). Effects of septal-forebrain lesions on maternal aggression and maternal care. *Behavioral & Neural Biology*, **45**, 17-30.

Flannelly, K. J., & Thor, D. H. (1976). Territorial behavior of laboratory rats under conditions of peripheral anosmia. *Animal Learning & Behavior*, **4**, 337-340.

Gandelman, R. (1972). Mice: Postpartum aggression elicited by the presence of an intruder. *Hormones & Behavior*, **3**, 23-28.

Lynds, P. G. (1976). Olfactory control of aggression in lactating female house mice. *Physiology & Behavior*, **17**, 157-159.

Mink, J. W., & Adams, D. B. (1981). Why offense is reduced when rats are tested in a strange cage. *Physiology & Behavior*, **26**, 567-573.

Paul, L., Gronek, J., & Politch, J. (1980). Maternal aggression in mice: Protection of the young is a by-product of attacks at the home site. *Aggressive Behavior*, **6**, 19-29.

Svare, B. (1977). Maternal aggression in mice: Influence of the young. *Biobehavioral Reviews*, **1**, 151-164.

Svare, B. (1979). Maternal aggression in mice: The nonspecific nature of exteroceptive maintenance by young. *Aggressive Behavior*, **5**, 417-424.

Takahashi, L. K., & Lore, R. K. (1982). Intermale and maternal aggression in adult rats tested at different ages. *Physiology & Behavior*, **29**, 1013-1018.

(Manuscript received for publication October 11, 1986.)