

**The Regulation of Infanticide and Parental Behavior:
Implications for Reproductive Success in Male Mice**

Frederick S. vom Saal and Lynn S. Howard

The Regulation of Infanticide and Parental Behavior: Implications for Reproductive Success in Male Mice

Abstract. *Infanticide has been proposed to be a pathological response to overcrowding or other forms of environmental stress and thus a maladaptive behavior. However, in male house mice this behavior is predictable and is modulated by learning. Committing infanticide can increase a male's reproductive success and in some situations may therefore be an adaptive behavior.*

Infanticide, the killing of young, occurs in many species, including humans (1). Experiments with rodents on the effects of overcrowding on social behavior led to the hypothesis that infanticide is a response to a breakdown in social structure and, as such, is a pathological or nonadaptive behavior (2). Recently, it was suggested that in some circumstances an animal may benefit from committing infanticide (3). Infanticide is thus considered to have evolved in response to positive selective pressure and to be predictable and adaptive. Hrdy (3) classified infanticide in terms of the manner in which an animal might benefit from killing infants. Our experiments concern one category of infanticide—that relating to sexual competition between males.

It has been suggested that a male that commits infanticide can increase his reproductive success at the expense of competitors by killing a competitor's offspring and then mating with the mother. This sexual-competition hypothesis is

based on Darwin's concept of sexual selection and involves three assumptions: (i) that there exist mechanisms to assess paternity so that males are unlikely to kill their own offspring, (ii) that the killing of a female's young results in her ovulating and mating with the infanticidal male sooner than she could have had her young not been killed (ovulation being inhibited in a lactating female), and (iii) that the behavior is mediated at least in part by genotype and thus heritable. If these criteria are met, then once the genotype for infanticide appears, it should rapidly increase in frequency in a population, since males with the infanticidal genotype should produce more offspring than males with the noninfanticidal genotype (3). Our experiments were designed to test the sexual-competition hypothesis.

There is evidence that only the one dominant male mouse in a breeding group mates and produces young (4). Since dominance status appears to be a

major factor in determining the reproductive success of a male mouse, the relation of dominance status to the behavior of male mice toward newborn young was examined. Studies have revealed that mating experience reduces the proportion of male mice that commit infanticide (5). Thus, the possibility that mating experience per se might serve as a mechanism for parental recognition and inhibit male mice from committing infanticide only during the time that they would be in contact with their own young (3 to 8 weeks after mating) was also examined.

Male mice (CF1) that were sexually naive were paired, and males that had mated with two females 2 weeks earlier were also paired (6). Members of a pair were placed together for 1 hour each day for 7 days. Dominance was assessed by observing males fighting during the last day of pairing and by examining each animal's rate of urine marking the next day. Dominant male mice deposit hundreds of urine marks, but subordinate males excrete urine in a few large pools (7). Only animals that could be clearly classified as dominant or submissive in terms of both aggressiveness and urine marking were examined for infanticide on the day after urine marking. For the test two newborn mice (sired by other males) were placed in the corner of a male's cage for 30 minutes. A preliminary study had demonstrated that neither the sex nor the age of the young influences the tendency of male mice to commit infanticide (8). Three behaviors were recorded when the young were removed from a male's cage: (i) infanticide—one or both of the young were severely wounded or killed; (ii) parental behavior—one or both of the young were found in the nest with the male hovering over them; and (iii) ignored—neither newborn mouse was wounded or in the nest, and both young were cold (9). Most sexually naive dominant males committed infanticide, and most sexually experienced dominant males exhibited parental behavior. Subordinate males, regardless of mating experience, tended to behave parentally (Table 1).

The test for infanticide was conducted 3 weeks after some of the dominant males had mated because the length of pregnancy in house mice is 19 to 21 days. To determine whether the inhibition of infanticide, which had been observed 3 weeks after mating in the dominant, sexually experienced males, was temporary, the dominant males ($N = 33$) were retested 3 months after they had mated with two females (9 weeks after the initial test for infanticide). On the retest,

88 percent of the sexually experienced dominant males committed infanticide, and 12 percent exhibited parental behavior, whereas on the initial test, 15 percent of these males had committed infanticide, and 76 percent had exhibited parental behavior (Table 1). These findings demonstrate that infanticide is inhibited and parental behavior is facilitated 3 weeks after mating (when a female would deliver the male's offspring). But, between 3 weeks and 3 months after mating, this effect is lost. Since only about 45 percent of CFI males without fighting or mating experience commit infanticide with this testing procedure (8, 10), fighting and achieving dominance appear to facilitate the tendency of male mice to have a long-term facilitating effect on infanticide. Mating experience inhibits infanticide only during the time that a male would be likely to kill its own offspring.

Nonpregnant female mice ovulate every 4 to 5 days (11). With the exception of a period of postpartum estrus the night after parturition, lactation inhibits ovulation in mice (12). Also, implantation of the embryos is usually delayed by about a week in nursing CFI females that are inseminated during postpartum estrus. [The length of the delay and thus the duration of pregnancy is influenced by the number of nursing young (13).] Thus, males that commit infanticide and mate with a nursing female should produce their young at a faster rate than noninfanticidal males. This possibility was examined by placing a sexually naïve male mouse ($N = 40$) in a cage with a female that had delivered a litter within the previous 15 hours (14). There was a statistically significant difference in the length of time before the female delivered the intruder male's offspring depending on whether the male killed all of the female's young [mean \pm standard error of the mean: infanticidal males ($N = 22$), 22.1 ± 0.9 days; noninfanticidal males ($N = 10$), 29.8 ± 1.9 days, $t(30) = 6.3$, $P < .001$]. For cases ($N = 8$) in which one to three offspring of the first litter survived, the mean length of time for the next litter to be produced was 25.5 ± 2.8 days. None of the 40 males tested killed the offspring that they sired. A sexually naïve male mouse that kills a female's nursing young thus produces its own offspring sooner than does a noninfanticidal male.

This experiment was also conducted with 20 male mice that had mated with two females 3 weeks before being placed into a cage with a female that had delivered a litter within the previous 15 hours. The nursing females had all been insemi-

Table 1. Behavior of 90-day-old dominant and subordinate male mice that had either mated with two females or were sexually naïve toward two newborn mice that were placed in the male's cage for 30 minutes. Significantly more sexually naïve than sexually experienced dominant males exhibited infanticide, while significantly more sexually experienced than sexually naïve dominant males exhibited parental behavior ($\chi^2 = 31.4$, d.f. = 2, $P < .001$). Significantly more dominant than subordinate sexually naïve males exhibited infanticide ($\chi^2 = 19.9$, d.f. = 2, $P < .001$). The sexually experienced dominant, sexually experienced subordinate, and sexually naïve subordinate males did not differ significantly in their behavior (χ^2 , $P > .1$).

Behavior	Dominant				Subordinate			
	Sexually naïve		Sexually experienced		Sexually naïve		Sexually experienced	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Infanticide	28	82	5	15	5	23	7	28
Parental	4	12	25	76	9	41	15	60
Ignored	2	6	3	9	8	36	3	12

nated by other colony males, and their litters had been reduced to eight young. None of the sexually experienced males appeared to kill any of the nursing young: only six of 160 young (4 percent) were not alive at weaning; this percentage of loss is observed even when a male is not present. The mean number of days before the birth of the offspring sired by these 20 males was 28.3 ± 2.0 days. Thus mating experience, rather than recognition of the female with which a male had mated, inhibits infanticide in male mice 3 weeks after mating.

In many environments mice form small breeding groups called demes that typically consist of one dominant male, which may produce 95 percent of the offspring in a deme, a few subordinate males that do not reproduce, and a number of adult females with nursing young (4, 15). The tendency to commit infanticide is inhibited in subordinate male mice, suggesting that they are not a threat to the offspring produced by the dominant male as long as the dominant male is alive. All subordinate males used in our studies mated when placed with sexually receptive females. Subordinate males thus provide a reserve of reproductively competent males. When the dominant male in a deme dies, the subordinate males will fight until one becomes dominant (15). Since the new dominant male will probably not have mated, achieving dominance will increase the likelihood that this male will kill the nursing offspring of the previous dominant male. When a female's nursing young are killed, the length of time for the female to produce young sired by the new dominant male will be reduced. This satisfies the requirement of the sexual-competition hypothesis for an infanticidal male to produce his own offspring at a faster rate than a noninfanticidal male.

Once a new dominant male begins

mating its tendency to commit infanticide is inhibited and parental behavior is facilitated during the time that a female would be nursing this male's offspring. The sexual-competition hypothesis states that for infanticide to be an adaptive trait there must be a mechanism for assessing paternity to ensure that a male will not kill his own offspring. Since only one dominant male mouse in a deme produces offspring, it appears that having mated 3 weeks before coming in contact with newborn young is sufficient to ensure that the dominant male will not kill its own offspring.

The third assumption of the sexual-competition hypothesis is that infanticide is a heritable trait. It is presumed, therefore, that variation in the tendency of male mice to exhibit infanticide or parental behavior toward nursing young reflects variation in genotype. However, infanticide is just one of a host of traits (for example, aggression, urine marking, and sexual behavior) that require the presence of circulating gonadal steroids to be exhibited in adulthood and that are modulated by gonadal steroid concentrations during early life; these behaviors are also modified by experience (10, 16). The process by which selection operates on behaviors that are modulated by both gonadal hormones and experience, and are therefore thought to be polygenic (17), is unclear. But our findings are consistent with the hypothesis that infanticide is a predictable and adaptive behavior in male mice, since in some situations, infanticide can increase a male's reproductive success.

FREDERICK S. VOM SAAL

*Division of Biological Sciences
and Department of Psychology,
University of Missouri, Columbia 65211*

LYNN S. HOWARD

*College of Veterinary Medicine,
University of Missouri*

References and Notes

1. M. Dickerman, *Annu. Rev. Ecol. Syst.* **6**, 107 (1975); B. Montag and T. Montag, *Minn. Med.* **62**, 368 (1979).
2. J. Calhoun, *Sci. Am.* **206**, 139 (February 1962); R. Curtin and P. Dolhinow, *Am. Sci.* **66**, 468 (1978).
3. R. Trivers, in *Sexual Selection and the Descent of Man*, B. Campbell, Ed. (Aldine, Chicago, 1972), p. 136; S. Hrdy, *Ethol. Sociobiol.* **1**, 13 (1979).
4. J. DeFries and G. McLearn, *Evol. Biol.* **5**, 279 (1972).
5. J. Labov, *Behav. Ecol. Sociobiol.* **6**, 297 (1980); F. vom Saal, paper presented at a meeting of the International Society of Developmental Psychobiology, Cincinnati, November 1980.
6. All CF1 male mice used in the studies were housed separately in plastic mouse cages when 35 days old and tested when 70 to 90 days old.
7. Males that had been paired were placed on either side of a wiremesh partition in a box (30 by 30 by 15 cm) for 1 hour. Whatman 2 filter paper was used as the substrate, and when it is placed under a black light fluorescent bulb (GE F15T8-BLB), the individual urine marks can be counted [C. Desjardins, J. A. Maruniak, F. H. Bronson, *Science* **182**, 939 (1973)].
8. Two newborn male or female mice were placed in a cage with a sexually naive male ($N = 15$ males per group). The results were (i) female pups: infanticide, 44 percent; parental toward, 19 percent; and ignored, 37 percent; (ii) male pups: infanticide, 44 percent; parental toward, 25 percent; and ignored, 31 percent (χ^2 test, $P > .1$). Other sexually naive males ($N = 30$ per group) were tested for their response to newborn or 7-day-old mice by the same procedure. The results were (i) newborn mice: infanticide, 50 percent; parental toward, 23 percent; and ignored, 27 percent; (ii) 7-day-old mice: infanticide, 43 percent; parental toward, 50 percent; and ignored, 7 percent ($P > .1$).
9. A male mouse virtually never exhibits infanticide toward one newborn mouse and parental behavior toward the other when two young are placed into the male's cage.
10. F. vom Saal, *J. Reprod. Fertil.* **62**, 633 (1981); in *Hormones and Aggressive Behavior*, B. Svare, Ed. (Plenum, New York, in press).
11. _____, S. Pryor, F. Bronson, *J. Reprod. Fertil.* **62**, 33 (1981).
12. M. Smith, *Fed. Proc. Fed. Am. Soc. Exp. Biol.* **39**, 2571 (1980).
13. F. vom Saal, unpublished observations; S. Mantelenakis and M. Ketchell, *J. Reprod. Fertil.* **12**, 391 (1966).
14. Each pregnant female was housed in a cage (30 by 30 by 15 cm) divided in two by a wooden partition. Three hours after a litter was delivered, a male was placed into the empty area for 30 minutes, after which the barrier was removed. Males were thus placed with females before the time of postpartum estrus. The number of days from the introduction of the male to the delivery of the next litter was recorded, and the original young that survived were weaned at this time or when they were 30 days old. The number of young in the new litter that survived to 5 days of age was counted to assess the possibility that some young had been killed.
15. J. Reimer and M. Petras, *J. Mammal.* **48**, 88 (1967); W. Lidicker, *J. Anim. Ecol.* **45**, 677 (1976).
16. J. Maruniak, C. Desjardins, F. Bronson, *Am. J. Physiol.* **233**, E-495 (1977).
17. R. Lande, *Evolution* **34**, 292 (1980); S. Maxon, in *The Biology of Aggression*, P. Brain and D. Benton, Eds. (Sijthoff & Noordhoff, Alphen aan den Rijn, Netherlands, 1981), p. 69.
18. We thank S. Blaffer-Hrdy and J. A. Maruniak for their suggestions during the preparation of this manuscript and J. Broich for her excellent technical assistance. Supported by NIMH grant MH35079 and by University of Missouri Institutional Biomedical Research Support grant RR 07053 from the National Institutes of Health.

9 October 1981; revised 8 December 1981