Infanticide by Virgin CF-1 and Wild Male House Mice (*Mus musculus*): Effects of Age, Prolonged Isolation, and Testing Procedure

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The frequency of infanticide by juvenile, young-adult, and adult male house mice (*Mus musculus*) was compared in CF-1 albino mice and the F_1–F_4 male offspring of wild mice trapped in Missouri. When tested in their home cages for their behavior toward a single 2-day-old pup after being individually housed for 5 days, juvenile CF-1 and wild males were equally likely to exhibit infanticide (about 35%). But, adult wild males were significantly more likely to exhibit infanticide (about 90%) than were adult CF-1 males (about 45%). We propose that differences in exposure to testosterone during fetal life may contribute to the difference in the incidence of infanticide between CF-1 and wild males. Prolonged isolation (45 days) significantly reduced the proportion of wild male mice that exhibited infanticide when the males were tested in their home cages, but not when the males were tested by being placed into the cage of lactating females and their 2-day-old young. Virtually all adult wild males exhibited infanticide when they were tested in their home cages (with either a 2-day-old or 7-day-old pup) or when they were placed into the cages of lactating wild female mice and their 2-day-old young. But, when adult wild males were placed with lactating wild females on Day 7 postpartum, the females attacked the males and most males were prevented from exhibiting infanticide.

In house mice (*Mus musculus*) that have been bred for generations in the laboratory, between 30 and 80% of sexually naive, adult males spontaneously exhibit infanticide (kill preweanling young), depending on the stock examined (Svare & Mann, 1981; vom Saal, 1983a). In contrast, virtually all wild male house mice (that are the offspring of animals trapped in the field) exhibit infanticide when tested in the laboratory (Jakubowski & Terkel, 1982; McCarthy & vom Saal, 1986).

The regulation of infanticide in mice is extremely complex; there is evidence for genetic, hormonal, experiential and environmental influences on this behavior. It has

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also been proposed that infanticide might play a role in population dynamics in mice (vom Saal & Howard, 1982; Brooks, 1984; vom Saal, 1985; McCarthy & vom Saal, 1985, 1986). The fact that most research on infanticide in mice has been conducted with stocks of mice that have been reared for many generations in the laboratory has thus been of concern, since determining the relevance of the findings from these studies to natural populations of mice requires that experiments be conducted with wild mice that have not been subjected to generations of selective breeding.

In the current study the ontogeny of infanticide was examined in both CF-1 male mice and the F_1–F_4 male offspring of animals wild-trapped in a field near Columbia, Missouri. In addition, the effects of utilizing different testing procedures, different housing conditions, and different aged young as stimulus animals on infanticidal behavior in male mice were examined.

General Methods

Animals and Housing

Wild house mice (*Mus musculus*) were trapped using Sherman livē traps in an abandoned building in a field on the Charles W. Green Experimental and Research Wildlife Management Area located in Boone County, Missouri. Approximately 100 mice were originally trapped (roughly 40 males and 60 females) and were then bred (1 male and 1 female per cage) in a closed colony in which no brother–sister matings were allowed. The F_1–F_4 offspring of the wild mice were utilized in the present experiments. These animals are referred to as wild-type mice since they do not represent a random sampling of wild mice (about 20% of the pairs of wild-trapped mice did not produce young when mated in the laboratory). The litters were weaned at 23 days of age and then housed in same-sex groups until 5 days prior to testing.

CF-1 albino house mice were also examined for their behavior toward young. A breeding stock of CF-1 mice was purchased from Charles River Farms (Wilmington, MA) in 1979 and have been randomly bred in a closed colony since that time. These animals were raised and tested utilizing the same procedures described for the wild mice.

All animals were housed in rooms maintained at 23 ± 1°C on a 12:12 light:dark cycle with lights on at 0600 hours. Animals were housed in polyethylene cages (18 x 29 x 13 cm) with pine shavings. Purina lab chow and water were available ad libitum.

Testing Procedure

Two separate testing procedures were utilized in the present studies: (1) either a 2-day-old mouse pup was placed into the cage of an individually-housed test animal or (2) the test animal was placed into the cage of a lactating female of the same stock and her litter. All animals to be tested were housed individually for 5 days prior to the test, and all test animals were naive (i.e., they had no previous experience with pups) unless specifically indicated.

In the first testing procedure, one pup was quietly placed into a corner of the cage (not near the nest) of a singly housed male, and the animals were left undisturbed for 30 min. If the male was found in the nest hovering over the pup and the pup was warm, the behavior was recorded as "parent," if the pup had been killed, the behavior was recorded as "infanticide," and if the pup was cold but unharmed, the behavior was recorded as "untouched." In all of the experiments in which this testing procedure was

used, Chi Square analyses were conducted comparing groups of males in terms of the frequencies of these three behaviors.

It has been observed that neither the sex nor the age (1–20 days old) of the pups influence the frequency of infanticide in virgin male mice from domestic stocks when tested in their home cages (vom Saal & Howard, 1982; vom Saal, 1985; Svare, Mann, Kinsley, & Broida, in press). It has also been observed that isolated male mice from domestic stocks do not behave differently toward pups of different strains (Svare & Mann, 1981), and wild male mice trapped in Israel do not behave differently toward wild or domestic-stock mouse pups (Jakubowski & Terkel, 1982). Thus, with the exception of Experiment IV-A, both CF-1 and wild-type males were tested in their home cages for their behavior toward a 2-day-old CF-1 mouse pup.

The second testing procedure involved the test male being placed into the cage of a lactating female and her litter. Only wild-type males were tested using this procedure, and they were placed with wild-type females and their pups. If after 14 hr the pups were found dead, the behavior of the test male was recorded as "infanticidal." If the pups were found alive, the behavior of the test male was recorded as "noninfanticidal." Chi Square analyses were conducted on the proportion of animals that were infanticidal vs noninfanticidal.

The litter sizes were not standardized to avoid having to remove the lactating females from their cages (since this procedure results in about 25% of wild-type females exhibiting infanticide when they are returned to the cage after 2 hr; McCarthy & vom Saal, 1985, but no litter that contained fewer than 4 pups was utilized. Even though some wild-type females exhibit infanticide when they are removed from their cages for 2 hr, lactating wild-type females do not exhibit infanticide when their cages are handled while they remain inside (unpublished observation). In addition, we have reported elsewhere that when wild-type males were placed into the cages of lactating wild-type females 3 weeks after mating, none of the pups were killed, since mating inhibits infanticide in male mice (vom Saal, 1985; McCarthy & vom Saal, 1986). This finding is important since it reveals that placing a male into the cage of a lactating female does not induce infanticidal behavior in the female.

In all of the experiments except Experiment IV-A, infanticidal males always killed the entire litter of a female rather than just a few pups. When the entire litter of a lactating female was killed by a test male, a single infanticidal event was considered to have occurred. It would be inappropriate to consider the death of each pup in a litter as an independent act of infanticide, and the Chi Square Test can only be performed on data that are independent of each other. The use of the entire litter as a single unit is therefore the appropriate procedure for statistical analyses, and, in addition, it is appropriate in terms of the reproductive consequences to the male of exhibiting infanticide: only if the entire litter is killed can the male then quickly mate with the female and produce his own young (which has been proposed to be one of the ultimate causes of infanticide in male mice), since a lactating female mouse is inhibited from ovulating and mating with an infanticidal male subsequent to the brief period of postpartum estrus (for theoretical discussion and experiments addressing this question see: Hrdy, 1979; vom Saal & Howard, 1982; vom Saal, 1985; McCarthy & vom Saal, 1986).

There have been concerns among researchers of infanticide that while testing males by placing a single pup into their cages is preferable in terms of the number of pups that are used, the procedure is certainly not one which in any way approximates what might happen outside of a laboratory setting. This is not to suggest that the second testing procedure is "naturalistic" from an ecological point of view, but it seems likely that in the wild, male mice would encounter unfamiliar females and their litters in environments

other than the males' home territory. Since the 2 testing procedures differ in a number of ways: handling of the males, novelty of the testing environment, number of pups encountered, presence of a female, when the two testing procedures lead to different results (as has occurred; McCarthy and vom Saal, 1986), determining the basis for the difference would require other experiments.

Results

Experiment I

Infanticide by Adult Males

In this experiment the proportion of adult CF-1 and wild-type males exhibiting infanticide was compared. In addition, the effects of 2 different procedures for testing the behavior of male mice toward young previously examined in CF-1 males (vom Saal & Howard, 1982) was evaluated in wild-type males.

(A). Infanticide by adult wild-type and CF-1 males tested in their home cages. Sixty adult, virgin, wild-type males, between 90 and 120 days old, were tested for infanticide by placing a pup into each male's home cage, and 87% of the males exhibited infanticide (see Fig. 1). A large sample of wild-type males was utilized since this experiment also served as a pretest for males that were utilized in subsequent experiments in which prior experience exhibiting infanticide was required (see: McCarthy and vom Saal, 1986). Twenty-five adult, virgin, CF-1 males, between 90-120 days of age, were also tested utilizing the same procedure and 44% exhibited infanticide (see Table 1). Adult, virgin, wild-type males are thus significantly more likely to exhibit infanticide than are adult, virgin, CF-1 males [$\chi^2(2) = 16.8$, $p < .001$].

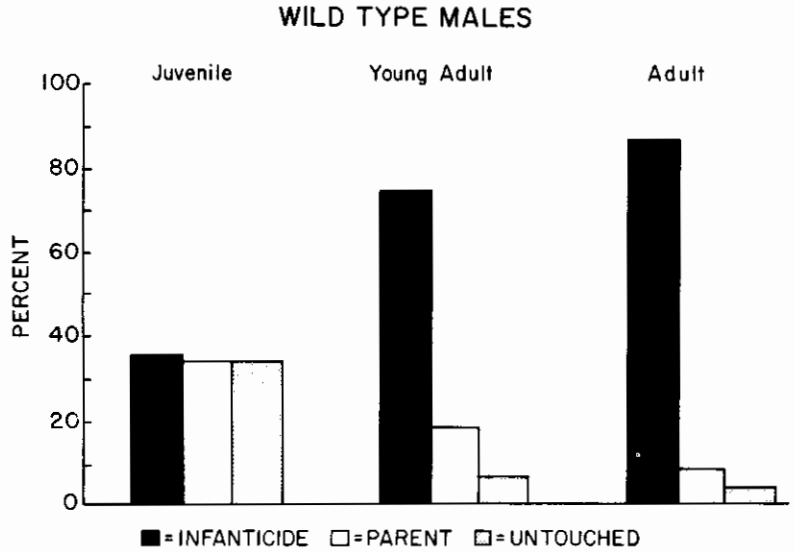

Fig. 1. Behavior of juvenile (40–45 day old; $n = 12$), young adult (55 – 60 days old; $n = 12$), and adult (90–120 days old; $n = 60$) wild-type male mice toward a single 2-day-old CF-1 mouse pup that was placed into each male's home cage for 30 min. One of three behaviors was recorded: Infanticide = the pup was killed, Parent = the pup was in the male's nest with the male hovering over it, or Unhandled = the pup was cold and not in the nest.

(B). Infanticide by adult wild-type males when placed into the cage of a lactating female. In the previous experiment all of the males were tested while in their home cages. In this experiment we examined the behavior of wild-type males toward young when the males were each placed into the cage of a lactating wild-type female and her 2-day-old young. Sixteen adult, virgin, wild-type males, between 90 and 120 days old, were tested for infanticide, and in 15 cases (94%) the entire litter was killed. During the time that the males were being placed into the females' cages, no fighting was observed, and when the males were removed from the cages, no evidence of wounding of the males or females was observed, suggesting that no fighting had occurred. Given the assumption that the males rather than the lactating females killed the young (see General Methods), there is no significant difference in the frequency of infanticide by virgin, wild-type males when tested in their home cages (see Experiment I-A) or when placed with lactating females and their 2-day-old young (χ^2; $p > .1$). This same experiment had previously been conducted with CF-1 male mice that were placed into the cages of lactating females and their 1-day-old young, and 55% of the males ($N = 40$) were observed to immediately exhibit infanticide (vom Saal & Howard, 1982). This previously observed frequency of infanticide in CF-1 males (55%) is similar to that for CF-1 males in Experiment I-A that were tested in their home cages (44%).

Experiment II

Ontogeny of Infanticide in Male Mice

Approximately 90% of adult, virgin, wild-type male mice exhibit infanticide, while about 45% of adult, virgin, CF-1 male mice exhibit infanticide. The purpose of this experiment was to determine if the age of onset of infanticidal behavior was different in CF-1 and wild-type male mice. All of the males in this experiment were tested for infanticide by having one CF-1 pup placed into their home cages for 30 min.

(A). Infanticide by young-adult wild-type and CF-1 males. Twelve young-adult, virgin, wild-type males, between 55 and 60 days old, were tested for their behavior toward a single 2-day-old CF-1 pup, and 75% of the males exhibited infanticide (see Fig. 1). The behavior of these young-adult wild-type males toward pups is thus not significantly different from that of the 90–120-day-old wild-type males that were tested in Experiment I-A (χ^2; $p > .1$).

Young-adult, virgin, CF-1 males, between 55 and 60 days old, were also tested for infanticide. Of the 52 males tested, 8% exhibited infanticide, 90% behaved parentally, and 2% left the pup untouched. Therefore, this group of young-adult CF-1 males was significantly less likely to exhibit infanticide than similarly aged wild-type males [$\chi^2(2) = 35.0$, $p < .001$] and also significantly less likely to exhibit infanticide than were the 90–120-day-old CF-1 males tested in Experiment I-A [44% exhibited infanticide; $\chi^2(2) = 22.4$, $p < .001$]. However, the finding that only 8% of young-adult CF-1 males exhibited infanticide does not agree with a prior experiment using the same testing procedure in which 29% of 60-day-old CF-1 males were observed to exhibit infanticide (vom Saal, 1985). In this previous study the males were isolated for a longer period of time prior to testing than were the males in this experiment, but based on the results of Experiment III (see below), prolonged isolation would be expected to have decreased rather than increased the incidence of infanticide. We therefore replicated this experiment with 96 60-day-old CF-1 males, and 31% exhibited infanticide, 38% behaved parentally, and 31% left the pup untouched. These frequencies of behavior toward young in young-adult CF-1 males are not significantly different from the frequencies observed in adult CF-1 males in Experiment I-A (see Table 1). When these same young-adult, CF-1 males

TABLE 1. The Percent of Juvenile (40–45 Days Old), Young-Adult (55–60 Days Old, and Adult (90–120 days old) CF-1 Male Mice That Either Exhibited Infanticide, Exhibited Parental Behavior, or that Left a Single 2-Day-Old Pup Untouched when the Pup Was Placed into a Male's Cage for 30 min.

	Juvenile	Young-Adult	Adult
Infanticide	36	31	44
Parent	32	38	40
Untouched	32	31	16
	$N = 31$	$N = 96$	$N = 25$

were tested at 80 days of age, 43% exhibited infanticide, 47% behaved parentally and 10% left the pup untouched (McNemar's test for the significance of changes, young-adult vs adult; $p > .1$). The reason that a large number of males were tested in this experiment was that they were being pretested for their behavior toward young prior to being examined in other pharmacological studies of infanticide. The frequency of infanticide in these 60-day-old CF-1 males is thus virtually identical to that reported previously (29%) by vom Saal (1985), and the basis for the low incidence of infanticide (8%) and high incidence of parental behavior (90%) in the first group of young-adult, CF-1 males described above in unknown.

(B). Infanticide by juvenile, wild-type and CF-1 males. A comparison of the behavior toward young of wild-type and CF-1 juvenile males (between 40 and 45 days old) was also made. Twelve wild-type males were tested, and 34% exhibited infanticide (see Fig. 1). Juvenile wild-type males are thus significantly less likely to exhibit infanticide than are adult wild-type males [$\chi^2(2) = 23.0$, $p < .001$], but the juvenile and young-adult wild type males did not differ significantly in their behavior [$\chi^2(2) = 4.4$, $p > .1$]. Thirty-one juvenile CF-1 males were also tested, and 36% exhibited infanticide. Thus, juvenile, young-adult and adult CF-1 males did not differ significantly in their behavior toward young (χ^2; $p > .1$; see Table 1). In addition, there was no significant difference in behavior toward young between juvenile wild-type and juvenile CF-1 males (χ^2; $p > .1$).

Experiment III

Influence of a Prolonged Period of Isolation on Infanticide by Wild-Type Males

It has been observed that long periods of postpubertal isolation inhibit infanticide and enhance parental behavior by C57 male mice if the males are tested by placing a single pup into their home cages (Ghiraldi & Svare, in press), but not if the males are placed into the cage of a lactating female and her litter (Brooks & Schwarzkopf, 1983). In contrast, vom Saal (1983a, 1985) concluded that long periods of isolation did not influence the proportion of CF-1 male mice that exhibited infanticide when the males were tested in their home cages. The objectives of this experiment were: (1) to determine whether a prolonged period of isolation would influence the proportion of wild-type male mice that exhibited infanticide, and (2) to determine whether any effect of a prolonged period of isolation might depend on the testing procedure used.

(A). Males tested in their home cages. Wild-type males were housed individually at 65 days of age and then tested for infanticide 45 days later by placing a single CF-1 pup into the cage of each male. The males were only handled once during the period of

isolation in order to change the bedding in their cages. Eleven males were tested, and 36% exhibited infanticide (see Fig. 2). The frequency of infanticide for wild-type males that were isolated for 45 days is thus significantly different from that of similarly-aged, adult wild-type males that were isolated for only 5 days prior to testing in Experiment I-A [87% exhibited infanticide; $\chi^2(2) = 19.5$, $p < .001$].

(B). Males placed with females and their 2-day-old young. In order to determine if the testing procedure would influence the isolation-induced inhibition of infanticide, virgin wild-type males were housed individually when 65 days old and tested for infanticide 60 days later by being placed into the cage of a lactating female and her 2-day-old young. A 60-day period of isolation was used to increase the likelihood of there being an effect of isolation, given that Brooks and Schwarzkopf (1983) did not find an effect of isolation on the behavior of male mice toward young using this testing procedure. Twelve males were tested, and in 11 cases (92%) the entire litter was killed (see Fig. 2). Given the assumption that it was the male rather than the female that exhibited infanticide, this frequency of infanticide is significantly different from that for the wild-type males isolated for 45 days in the above experiment [$\chi^2(1) = 5.5$, $p < .01$], but is not significantly different from the behaviors exhibited by virgin wild-type males that were tested in the same manner but isolated for only 5 days in Experiment I-B (94% exhibited infanticide; χ^2; $p > .1$). Therefore, it appears that the testing procedure has a significant effect on whether wild-type males will exhibit infanticide after prolonged isolation.

Experiment IV

The Behavior of Wild-Type Males toward 7-Day-Old Pups

In domestic stocks of mice postpartum aggression is first observed on the third day postpartum, is most intense about 7 days postpartum, and then declines thereafter (Svare,

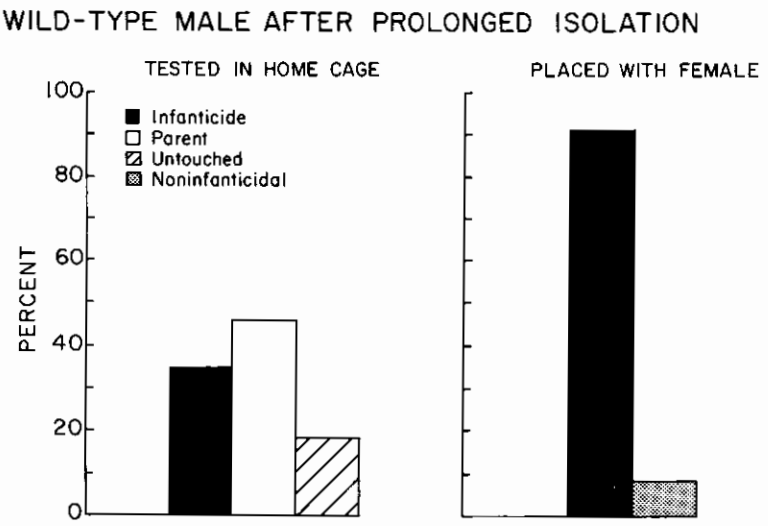

Fig. 2. The behavior of sexually naive wild-type male mice toward young after a prolonged period of isolation. Males were tested in their home cages ($n = 11$) for their behavior toward a single 2-day-old CF-1 mouse pup during a 30-min test. The males were classified as to whether they exhibited infanticide, parental behavior or left the pup unhandled. Thirteen other wild-type male mice were tested by being placed into the cages of lactating wild-type females and their 2-day-old young. These males were left with the lactating females for 14 hr and then classified as infanticidal or noninfanticidal based on whether the litters were alive.

1981). In the experiments reported here, as well as other experiments in which we have examined the behavior of wild-type female mice (McCarthy & vom Saal, in press, a; McCarthy, Bare, & vom Saal, in press; unpublished observations), we have observed that lactating wild-type females do not attack intruders placed into their cages on Day 2 postpartum, but do exhibit aggression on Day 3 postpartum. In this experiment we examined the possibility that lactating female mice might be able to prevent males from killing their litters by placing wild-type males into the cages of lactating wild-type females and their 7-day-old young. In addition, wild-type males were also tested in their home cages with one 7-day-old wild-type mouse pup.

(A). Wild-type males tested in their home cages with a 7-day-old pup. Nine 150-day-old wild-type males were tested for their behavior toward a single 7-day-old wild-type mouse pup that was placed into each male's cage for 30 min. Of the 9 males, 78% exhibited infanticide, 11% exhibited parental behavior, and 11% left the pup untouched. The proportion of wild-type males that exhibited infanticide in this study is thus not significantly different than the proportion of wild-type males that exhibited infanticide when tested in their home cages with a 2-day-old CF-1 pup.

(B). Wild-type males placed with lactating females and their 7-day-old young. Nine wild-type males (90 days old) were each placed into the cage of a lactating wild-type female and her 7-day-old young (there were between 4 and 6 pups per litter). In this experiment the animals were observed for the first 30 min after the males were introduced into the females' cages. The objective was to determine whether the females were able to protect their young from being killed by the males. The males were left in the females' cages for 14 hr, after which they were removed, and the surviving pups as well as the adults were examined for evidence of wounding.

Three of the males (33%) were observed exhibiting infanticide, and in these three cases the entire litters were killed; the mothers of these pups exhibited tail-rattling (a behavior that typically occurs prior to an attack in mice) but did not attack the males during the 30-min observation period. In one other case 2 pups from a litter of 5 were found dead at the end of the 14-hr test period, but the male was also dead (the female had been observed attacking the male). This male was not counted in the infanticidal category since the entire litter was not killed (see General Methods). In the remaining 5 cases (56%) none of the pups were killed or wounded, but 3 of these males were wounded (not killed) by the female. It thus appears that postpartum aggression by a lactating female plays a role in determining whether or not a male house mouse can successfully exhibit infanticide, since 4 of the males were observed being attacked by the female, and these males were not successful in killing the litter. The proportion of wild-type males that appeared to successfully kill the entire litter (which would be necessary for the female to rapidly ovulate) in this study (33%) was less than the proportion of males that exhibited infanticide when they were tested for their behavior toward 7-day-old young in their home cages (78%), although the difference did not exceed the .05 level for statistical significance [infanticidal vs noninfanticidal; $\chi^2(1) = 3.6$; $p = .058$]. But, significantly more litters were killed when males were placed into the cages of lactating females on the second day after parturition (94%; Experiment I-B) than when males were placed into the cages of lactating females on the seventh day after parturition [33%; $\chi^2(1) = 10.6$, $p < .01$].

Discussion

In Experiment III we observed that prolonged isolation resulted in a significant inhibition of infanticide in wild-type male mice when they were tested in their home cages but not when they were placed into the cages of lactating females and their litters.

It is unclear at this time exactly what the mechanism mediating this inhibition might be. But, considerable research has been conducted concerning the physiological changes associated with isolation that lead to an increase in intermale aggression and sexual behavior in male mice (Garattini, Giacalone, & Valzelli, 1969; Valzelli, 1969; Welch & Welch, 1969; Brain, Nowell & Wouters, 1971; Brain, 1975; deCatanzaro & Gorzalka, 1979; Brain & Benton, 1983).

An important issue illustrated by the above finding is that the testing procedure utilized can influence an animal's tendency to exhibit infanticide. Different testing procedures have also previously been found to produce conflicting results concerning the regulation of infanticide in wild-type male mice. Specifically, when tested 3 weeks after mating (at the time that their own young would be born), wild-type male mice were inhibited from exhibiting infanticide when placed into the cage of a lactating female and her litter (1 out of 30 males exhibited infanticide), but not when tested in their home cages (about 90% of the males exhibited infanticide; McCarthy and vom Saal, 1986). In contrast to the different results obtained with these 2 testing procedures when wild-type males were examined, CF-1 male mice were inhibited from exhibiting infanticide beginning about 2 weeks after mating regardless of the testing procedure utilized (vom Saal & Howard, 1982; vom Saal, 1985).

The strategies adopted by females to protect themselves against the costly loss of a litter due to infanticide by an intruder male are also of interest. During the first night after parturition, female mice exhibit postpartum estrus. This allows for the reinsemination of a female immediately after parturition and a second delivery at the time when the first litter is weaned (see: vom Saal & Howard, 1982; Rosenblatt & Siegel, 1983). Postpartum aggression in laboratory stocks of mice does not begin until the 3rd day postpartum (Svare, 1981). We have not observed any evidence of aggression by lactating wild-type females toward male intruders on Day 2 postpartum, but wild-type females have been observed to exhibit aggression toward intruder males on Day 3 postpartum (present results as well as unpublished observations). Prior to the onset of postpartum aggression, the litter of a female mouse is particularly vulnerable to infanticide. Apparently, the reproductive advantage of immediate reinsemination outweighs the potential risk of losing a litter due to infanticide.

The fact that the aggressive state of the female does play a role in determining the survival of her offspring has already been established for female collared lemmings by Mallory and Brooks (1978), who observed that lactating female collared lemmings were successful at preventing an intruder male from exhibiting infanticide on the third day postpartum but not on the 1st day postpartum (during that time of postpartum estrus). We have now replicated this finding with wild-type female house mice. Virtually all males succeeded in killing the entire litters of lactating wild-type female mice on Day 2 postpartum, and there was no evidence of aggression toward the male intruder by any of the lactating females. But, only 33% of wild-type males succeeded in killing the entire litters of lactating wild-type females on Day 7 postpartum, and some males were killed or wounded by the females.

In Experiments I and II we did not find that there was a significant increase in the frequency of infanticide in comparisons of juvenile, young-adult, and adult CF-1 male mice. But, there was a small increase in the percentage of adult CF-1 males that exhibit infanticide (about 45–50%) relative to juvenile and young-adult CF-1 males (about 30–35%). In a previous study using larger sample sizes, this difference in behavior toward young between young-adult and adult CF-1 males was found to be statistically significant (vom Saal, 1985).

We also found that juvenile CF-1 and wild-type males were equally likely to exhibit infanticide, but that the frequency of infanticide was much higher for wild-type males

than CF-1 males in adulthood. While there are many possible explanations for this finding, one hypothesis that we have recently tested is that CF-1 males are exposed to higher concentrations of testosterone during fetal development than are wild-type males. This hypothesis was based on the results of previous studies that have revealed that, in contrast to other behaviors that are activated by testosterone after puberty and organized by testosterone exposure during early life (e.g., intermale aggression, sexual behavior; vom Saal, 1983b), infanticide is inhibited by exposure to testosterone during the perinatal period in mice. Thus, during early life testosterone has the effect of "organizing" the neural substrate(s) mediating infanticide and parental behavior such that high levels of testosterone lead to an enhanced likelihood of parental behavior being exhibited and a decreased likelihood of infanticide being exhibited in adulthood (Gandelman & vom Saal, 1977; vom Saal, 1983a).

Male mouse fetuses have high blood titers of testosterone during the last 4 days of pregnancy relative to the levels found after birth but before puberty (Barkley & Goldman, 1977; vom Saal & Bronson, 1980; vom Saal, Even, Khan, & Ganjam, 1985). It is possible that a significant proportion of circulating testosterone in fetuses is secreted by the placenta rather than the testes (Soares & Talamentes, 1982). We measured serum levels of testosterone by radioimmunoassay (using procedures similar to those previously described; vom Saal, Grant, McMullen, & Laves, 1983) in CF-1 and wild-type male mouse fetuses on Day 17 of pregnancy (mating = Day 0), and CF-1 male fetuses had over twice the serum concentrations of testosterone (mean ± SEM: 5.4 ± 0.2 ng/ml) than did wild-type male fetuses [2.2 ± 0.3 ng/ml; $F(1,12) = 38.7$, $p < .001$]. While this represents only one time point in development, this finding suggests that a difference in testosterone exposure during fetal life may play a role in mediating the difference in infanticide between CF-1 and wild-type male mice.

In summary, the results of these studies lead to several conclusions. Whether virgin wild-type males exhibit infanticide after being isolated for a prolonged period of time depends on the testing procedure that is utilized. Virtually all virgin wild-type males exhibit infanticide whether they are tested in their home cages or placed with lactating females and their 2-day-old young. But, if the lactating females are more than 3 days postpartum, and therefore likely to attack an intruder into the nest area, then some females succeeded in preventing a male intruder from exhibiting infanticide. There are differences in infanticidal behavior between CF-1 and wild-type male mice. Juvenile CF-1 and wild-type males are equally infanticidal, but adult wild-type males are significantly more likely to exhibit infanticide than are adult CF-1 males. The differences between CF-1 and wild-type males in the frequency of infanticide in adulthood may be the result of differences in the concentrations of steroids that the males are exposed to during fetal life and/or due to selective breeding in the laboratory.

Notes

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