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Inhibition of Infanticide after Mating by Wild Male House Mice

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McCARTHY, M. M., AND F. S. VOM SAAL. *Inhibition of infanticide after mating by wild male house mice.* PHYSIOL BEHAV 36(2) 203–209, 1986.—The effect of mating on the behavior of male house mice (*Mus musculus*) toward young has been examined in numerous domestic stocks of mice, and the somewhat contradictory results led us to examine the effects of mating on the behavior of wild male mice toward young. The wild mice were the F_1–F_4 offspring of mice trapped in Missouri. Virtually all wild males exhibit infanticide prior to mating, but virrually all wild males were inhibited from exhibiting infanticide 3 weeks after mating whether they were placed into the cage of their former mate and her litter or into the cage of an unfamiliar female and her litter, similar to the effect of mating on the behavior of CF-1 male mice toward young. In contrast, wild males that had exhibited infanticide prior to mating were inhibited from exhibiting infanticide 3 weeks after mating when placed with their former mates and their 2-day-old young but not when placed with unfamiliar females and their 2-day-old young. When wild males were tested for their behavior toward young using the procedure of placing a single pup into each male's home cage, mating did not result in an inhibition of infanticide (about 90% of the males exhibited infanticide). Cohabitation with a female without mating also did not influence the behavior of wild males toward young. Wild males that exhibited infanticide when placed with a lactating female produced their own young more rapidly than did noninfanticidal males, thus providing further support for the hypothesis that under some conditions, infanticide can be an adaptive trait. But, virgin, infanticidal males took significantly longer to inseminate the females whose litters had been killed than did infanticidal males with prior sexual experience.

Infanticide Parental behavior Sexual behavior Paternal care

IN studies conducted with domestic stocks of house mice (*Mus musculus*), it has been reported that previously infanticidal male mice are inhibited from exhibiting infanticide (the killing of preweanling young) after mating [2, 9, 27, 28]. In CF-1 mice this period of inhibition of infanticide occurs between 12 and 50 days following mating, after which most males exhibit infanticide. It appears, therefore, that mating serves to inhibit male mice from exhibiting infanticide at almost the exact times (± a few days) that males would be likely to encounter their own preweanling young. There is also a facilitation of infanticide within the first 4 days after mating in CF-1 male mice that behaved parentally toward young prior to mating. Ejaculating during coitus (rather than the act of mounting, intromitting, or just cohabiting with a female but not mating) serves to induce these changes in the behavior of CF-1 male mice toward young after mating [27].

There has been some controversy as to exactly what mechanism inhibits infanticide in male mice around the time their young are likely to be present. In one recent report by Elwood and Ostermeyer [5], the finding by vom Saal [27] that the act of ejaculating inhibits infanticide was not replicated; instead, mating and continued cohabitation with the female partner was reported as being necessary for an inhibition of infanticide to occur in CS-1 male mice. But, Elwood [4] was unable to confirm his previous finding, and, instead, reported that mating alone served to significantly inhibit infanticide by 13 days after mating. In addition, Elwood [4] reported that for a significant increase in parental behavior to be observed, mating as well as cohabitation with the female for 1 day after mating was required. Thus, Elwood concluded that some aspect of the interaction between the male and the female during the first day after mating served to facilitate parental behavior after mating (see also, [6].

The sexual-competition hypothesis proposes that male mice exhibit infanticide when competition between males for access to receptive females makes it advantageous for one male to kill the offspring of another male. This type of infanticide is believed to have evolved due to sexual selection as

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defined by Darwin [24]; sexually-selected traits in males increase their ability to either attract or gain access to females. The sexual-competition hypothesis of infanticide leads to three testable predictions, which were first outlined by Hrdy [8]. First, infanticide by males must result in a shortened birth interval in females whose litters are killed by the males. Second, infanticidal males must avoid killing their own offspring, and third, infanticide must be, at least in part, mediated genetically and thus heritable [28]. In the present studies we tested the first two predictions of this model utilizing both CF-1 and wild-type male mice.

It is always risky to speculate concerning the adaptive significance to animals living in the wild of a behavior that is only observed in a domesticated species, and previously we had only examined infanticide in domestic stocks of mice. This led to the question as to whether the phenomenon of mating-induced inhibition of infanticide would also be observed in wild male mice when tested utilizing two different procedures. Whether familiarity with the prior female partner would be found to mediate this phenomenon in wild male mice was also examined, since in some domestic stocks of mice [9] but not others [28], familiarity with the nursing female appears to play a role in determining whether males exhibit infanticide after mating.

METHOD

Animals and Housing

Wild house mice (*Mus musculus*) were trapped using Sherman live traps in an abandoned building in a field on the Charles W. Green Experimental and Research Wildlife Management Area located on Boone County, Missouri. Approximately 100 mice were originally trapped (roughly 40 males and 60 females) and were then bred (one male and one 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 the beginning of an experiment. All wild-type males were between 90–120 days old at the time of testing.

CF-1 albino house mice were used in some of the experiments. A breeding stock of CF-1 mice was purchased from Charles River Farms (Wilmington, MA) in 1979 and randomly bred in a closed colony. 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 polypropylene cages (18×29×13 cm) with aspen bedding. Purina breeder chow and water were available ad lib.

Testing Procedure

There has been some concern about the manner in which rodents should be tested for infanticide [6]. Two alternative testing procedures have predominated. Either a male mouse has been isolated and allowed to adapt to his cage, after which one or two pups were placed into each males' cage and his behavior toward them has been reported (cf. [16, 22, 27, 28]), or, alternatively, a male has been taken from his home cage and placed into the cage of a lactating female and her litter, and his subsequent behavior toward the litter has been reported (cf. [9, 11, 12, 16, 28]).

Both of the above testing procedures were utilized in the present studies. In the first testing procedure, one 2-day-old pup was quietly placed into the corner of the cage 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." It has been observed that isolated male mice from domestic stocks do not behave differently toward pups of different strains [23], and wild male mice trapped in Israel do not behave differently toward wild or domestic-stock mouse pups [10]. In addition, previous studies with wild-type male and female mice in our colony revealed that they also do not behave differently toward laboratory stock and wild-type pups [14, 15, 16]. Therefore, all testing of isolated animals was done with CF-1 mouse pups.

The second testing procedure involved the test male being placed into the cage of a lactating female and her litter. Wild-type males were always placed with wild-type females and their pups while CF-1 males were always placed with CF-1 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." 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 their cages [15], but no litter that contained fewer than 4 pups or more than 7 pups was utilized. On the second day after delivering (when most males were tested using this procedure), a female mouse no longer is in postpartum estrus, which occurs during the first night after parturition. Maternal aggression (intense aggression toward male or female mice that come near the nest area) is first observed on Day 3 in female mice [21]. On the second day after parturition, we have observed that a lactating wild-type female mouse does not actively defend her litter and does not engage in mating behavior. But, by seven days after parturition females exhibit aggression toward males that are placed into the females' cages [16].

In these experiments infanticidal males always killed the entire litter of a female rather than just a few pups. Therefore, when the litter of a lactating female was killed by a test male, a single infanticidal event was considered to have occurred. The inappropriate use of the death of each pup in a litter as an independent act of infanticide by other investigators [9, 11, 12] has greatly complicated interpreting the results of these studies.

RESULTS

1. Influence of Sexual Experience on Infanticide in Wild-Type Males Tested with Novel or Familiar Females

The purpose of this experiment was to determine if the phenomenon of mating-induced inhibition of infanticide that has been observed in CF-1 male mice would also be observed in wild-type males. It has been proposed that infanticidal males may avoid killing their own offspring by recognition of their former mate rather than by direct recognition of the young [9]. If some sort of recognition system were to

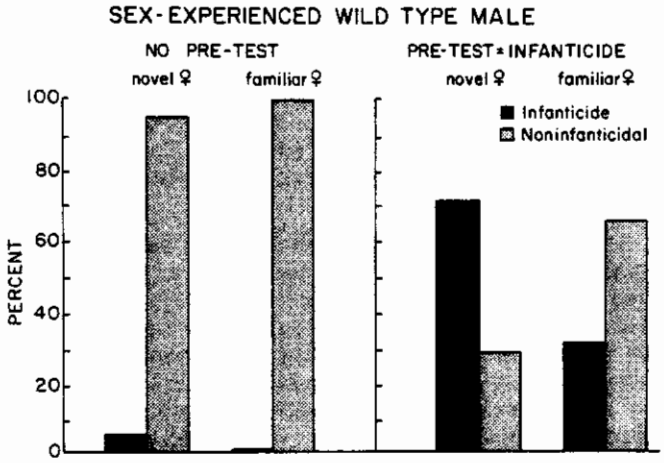

FIG. 1. Wild-type males were pretested for their behavior toward a single 2-day-old pup that was placed into each males' home cage for 30 min, and only males that exhibited infanticide on this pretest were used (PRE-TEST INFANTICIDE GROUP; 87% exhibited infanticide on the pretest). Other wild-type males were not pretested for infanticide (NO PRE-TEST GROUP). All pretested and nonpretested males were then mated with a female, and when a male's prior female partner delivered young, the male was placed back into the cage of the prior partner (familiar female) and her 2-day-old litter or into the cage of a novel female and her 2-day-old litter. The behavior toward young was recorded as "infanticide" if the litter was killed and "noninfanticidal" if the litter was unharmed. The percent of each group of males that were infanticidal and noninfanticidal is presented. Group sizes are: NO PRE-TEST GROUPS: NOVEL FEMALE=20, FAMILIAR FEMALE=10. PRE-TEST INFANTICIDE GROUP: NOVEL FEMALE=21, FAMILIAR FEMALE=15.

operate to inhibit infanticide toward specific pups, it is reasonable to propose that recognition of a prior mate might be involved.

To examine this hypothesis, virgin, wild-type males were paired with females and allowed to cohabit for 2 weeks, after which the males were isolated. The females were then observed for the day of parturition. On the second day after parturition, the wild-type males whose mates delivered young were placed into a cage containing either the female with which they had mated, referred to as a "familiar" female, or a cage containing a female that the male was unrelated to and had not been paired with, referred to as a "novel" female. The cage of each female was changed between the time of removal of the male partner and delivery in order to eliminate any olfactory cues other than those emitted by the female and her litter.

Ten wild-type males were placed into the cage of their former mates and their litters, and none of these males exhibited infanticide. Twenty wild-type males were placed into cages with novel females and their litters, and one of these males (5%) exhibited infanticide (Fig. 1). The results of Experiments II and VI (see below) revealed that most virgin, wild-type males (88%–94%) placed into the cage of lactating females and their 2-day-old young exhibited infanticide. Therefore, wild-type males were inhibited from exhibiting infanticide 3 weeks after mating, and the inhibition of infanticide was not dependent on recognition of the female with which the male had mated.

II. The Influence of Cohabitation with a Female without Mating on Infanticide by Virgin, Wild-Type Males

Other studies of the regulation of infanticide in laboratory stocks of mice have led to the hypothesis that cohabitation with a female rather than mating plays a role in the inhibition of infanticide that we have observed after mating in both wild-type and CF-1 male mice [4,5]. The purpose of this experiment was to determine if a period of cohabitation with a female without mating with her would result in an inhibition of infanticide in naive, virgin, wild-type male mice.

Adult, virgin males were paired with females that had been ovariectomized, and the males and females remained together for 3 weeks. None of the ovariectomized females were observed to be attacked or wounded during this period. After 3 weeks the males were housed individually. Three to 5 days later, the males were placed into the cages of lactating, wild-type females and their 2-day-old litters. The animals were examined after 14 hr and of the 17 males tested, 88% exhibited infanticide (the entire litters were killed) while 12% were noninfanticidal. Cohabiting with an ovariectomized female for 3 weeks thus did not have an inhibitory effect on infanticide in wild-type male mice.

III. Influence of Prior Experience Exhibiting Infanticide on the Behavior of Wild-type Males toward Young after Mating

Prior experience exhibiting infanticide has been shown to be without effect on the inhibition of infanticide and facilitation of parental behavior between 2 and 7 weeks after mating in sexually-experienced, isolated, CF-1 males. In addition, mating *per se* inhibited infanticide and facilitated parental behavior in CF-1 males [27,28]. Elwood and Ostermeyer [5] and Elwood [4] only tested CS-1 male mice with prior experience exhibiting infanticide and reported that mating alone did not facilitate parental behavior although infanticide was inhibited. This difference between CF-1 and CS-1 males in the effect of mating on infanticide and parental behavior could thus be the result of an interaction between prior experience exhibiting infanticide and mating in terms of the behavior of males toward young. The purpose of this experiment was to examine whether prior experience exhibiting infanticide would influence the inhibition of infanticide 3 weeks after mating in wild-type male mice.

Virgin, wild-type males were tested for infanticide while singly housed by placing a pup into each male's cage (87% of the 60 males screened exhibited infanticide). Thirty-six of the males that had previously exhibited infanticide were subsequently paired with a female and allowed to cohabit for 2 weeks, after which the males were housed individually. Two days after a male's former mate delivered, each male was placed into the cage of his former mate or a novel female as described in Experiment I. Fifteen males were placed with their former mates (familiar females), and 33% exhibited infanticide toward their own offspring. Twenty-one males were each placed with a novel female, and 71% exhibited infanticide (Fig. 1). In all cases in which infanticide occurred the entire litter was killed; all other males were noninfanticidal toward the entire litter, and none of the pups in the litter were harmed.

Infanticide-experienced males placed with novel females tended to be more likely to exhibit infanticide than infanticide-experienced males placed with their former mates, although the difference was not statistically significant, $\chi^2(1)=3.72$, $p=0.055$; this comparison is not statistically significant at $p<0.05$ if the correction for continuity is

included in the calculation; ([20], p. 110). But, the infanticide-experienced males placed with novel females were equally likely to exhibit infanticide (71%) as were the males that were allowed to cohabit with an ovariectomized female and were then tested with novel lactating females in Experiment II (88% exhibited infanticide; $\chi^2, p>0.1$). In contrast, significantly fewer of the previously-infanticidal males placed with familiar females (33%) exhibited infanticide after mating than did the males that were allowed to cohabit with an ovariectomized female and were then tested with novel lactating females in Experiment II (88% exhibited infanticide; $\chi^2(1)=8.0, p<0.01$).

In terms of the effects of prior experience exhibiting infanticide on the behavior of wild-type male mice 3 weeks after mating, the males with prior experience exhibiting infanticide that were placed with novel females (71%) were significantly more likely to exhibit infanticide than were the males with no prior experience exhibiting infanticide that were also placed with novel females after mating in Experiment I, 5% were infanticidal; $\chi^2(1)=16.3, p<0.001$. In contrast, there was no significant effect of prior infanticide experience on the behavior of wild-type males toward young when males were placed with their prior mates (in Experiment I, 0 of 10 males exhibited infanticide, and in the present experiment 5 of 15 male exhibited infanticide; Fisher Exact Probability Test, $p>0.1$).

With regard to the above Chi Square analyses, it is not really appropriate to compare data from males that were screened on a pretest with data from males that were not pretested for their behavior toward young, since the prescreened males do not represent a random sample of males. But, only 8 of 60 males that were initially screened for their behavior toward young did not exhibit infanticide on the pretest. Thus, the large difference in the frequency of infanticide between the previously infanticidal males (71%; Experiment III) vs. the non-infanticide-experienced males (5%; Experiment I) that were placed with novel females is not likely to be accounted for based on a sampling bias. But, for the males that were placed with familiar females (see Fig. 1), a sampling bias could account for the smaller (although not statistically significant) difference in the frequency of infanticide between the males with no pretest for infanticide (0%; Experiment I) vs. the males that exhibited infanticide on the pretest (33%; Experiment III).

IV. Influence of Prior Experience Exhibiting Infanticide on the Behavior of CF-1 Males toward Young after Mating

Because the results of Experiment III suggested that there might be an effect of prior experience exhbiting infanticide on the behavior of sexually-experienced wild-type males toward young, the identical procedure was repeated utilizing CF-1 males. Virgin, CF-1 males were tested for infanticide while individually housed by placing a pup into each male's cage. The males that exhibited infanticide (about 45%, which is typical for this stock; [16, 27, 28, 29]) were mated and then tested for their behavior toward young 2 days after their former mates delivered young using the same procedure described in the previous experiment.

Ten infanticide-experienced, CF-1 males were placed into cages with their former mates and their litters, and none of the males exhibited infanticide. Twelve infanticide-experienced CF-1 males were placed into cages with novel females and their litters, and none of the males exhibited infanticide. Therefore, in CF-1 males that have previously exhibited infanticide, there is an inhibition of infanticide and facilitation of parental behavior 3 weeks after mating whether or not the males are placed with novel females or their former mates.

V. The Effect of the Length of Postmating Contact with a Female on Infanticide by Wild-Type males Tested in Their Home Cages

Sexually-experienced, CF-1 males have been tested for infanticide by placing a pup into the cage of an isolated male three weeks after mating or by placing a male into the cage of a lactating female on the day of parturition, and infanticide was found to be inhibited in these males regardless of the testing procedure [27,28]. In addition, CF-1 males were inhibited from exhibiting infanticide after mating even when separated from the female partner within 2 sec of ejaculating [27]. In the previous experiments wild-type males were tested by being placed into the cages of nursing females. In this experiment wild-type males were tested in their home cages for their behavior toward a single pup 3 weeks after mating to determine whether the testing procedure would influence the behavior of wild-type males toward young after mating. About 90% of virgin, wild-type male mice exhibit infanticide utilizing either of the above two testing procedures ([16]; see also Experiments II and VI). We also examined whether a short or a long period of postmating cohabitation with the female partner would influence the behavior of wild-type males toward young after mating.

(A). Wild-type males with a short postmating period of cohabitation. Adult, virgin, wild-type males were paired with wild-type females, and the females were examined each morning for a vaginal plug. When a plug was found, the male was removed and housed individually. Mice typically mate during the middle of the night around the time that females ovulate (about 6 hr after the preovulatory surge in luteinizing hormone release at the onset of the dark phase of the light: dark cycle; [3,18]). It is likely, therefore, that these males were with the females less than 10 hr after mating. Twenty days after mating each male whose mate delivered young was tested for infanticide by placing a single 2-day-old pup into the male's cage. Of 28 males tested, 86% exhibited infanticide and 14% behaved parentally. This frequency of infanticide is not significantly different from that of virgin, wild-type males that were previously tested for their behavior toward young using the same procedure (87% exhibited infanticide; see [16]; χ^2; $p>0.1$). This finding reveals that sexual experience does not inhibit infanticide in wild male house mice when the males are tested by placing a pup into their home cages and the males are removed from the females' cages shortly after mating.

(B). Wild-type males with a long postmating period of cohabitation. The results of the previous experiment suggest that either the procedure of testing in the home cage or the absence of a prolonged period of postmating contact with the female partner resulted in an absence of the inhibition of infanticide 3 weeks after mating in wild-type male mice. In this experiment the males were paired with wild-type females, and the animals were not disturbed for 17 days, after which the males were housed in clean cages. Two days after the prior female partner delivered her litter (parturition occurs on Day 18 of pregnancy in wild mice), a single 2-day-old pup (not sired by the test male) was placed into each male's home cage. Of the 12 males tested, 92% exhibited infanticide and 8% exhibited parental behavior toward

the pup. This proportion of males exhibiting infanticide is not significantly different from the behavior of sexually-naive, wild-type males toward young when tested in their home cages (87% exhibited infanticide; see [16]; χ^2; $p>0.1$). Wild-type males that are tested in their home cages 20 days after mating are thus not inhibited from exhibiting infanticide regardless of whether they cohabit with the female partner for a few hours or for about two weeks after mating.

VI. The Interval to Produce Young in Infanticidal and Noninfanticidal Wild-Type Males

It has been observed that CF-1 male mice that exhibited infanticide when placed with nursing females produced their own young more rapidly than did noninfanticidal males [28]. In this prior study [28] CF-1 males were placed with lactating females on the day that the females delivered. All of males were thus able to immediately inseminate the females regardless of whether or not they exhibited infanticide, since the males were placed with the females prior to postpartum estrus, which occurs during the night following parturition. The interval required for the female to deliver the litter sired by the CF-1 males that did not exhibit infanticide was about 7 days longer than the interval for the delivery of litters sired by the infanticidal males [28]. This difference was consistent with the duration of embryonic diapause in CF-1 females (implantation of embryos is delayed in nursing females that become pregnant during postpartum estrus, and the duration of time of diapause is a function of the number of pups that the female is nursing; [13]).

In the present experiment the possibility that infanticidal wild-type males would produce a litter in a significantly shorter period of time than noninfanticidal males was examined. This experiment utilized the same wild-type males that were tested in Experiment III; some of the males exhibited infanticide when placed with a lactating female while other males did not kill any of the pups (based on whether the males were placed with novel or familiar females). These males were placed with the lactating females on the second day after parturition (after postpartum estrus). Thus, any male that did not exhibit infanticide would not have the opportunity to mate with the female until about the time of weaning of her litter, since constant suckling stimulation, which is provided by a litter of pups, completely inhibits ovulation in house mice as well as most other mammals [19]. This testing procedure thus differed from that previously used with CF-1 male mice, since the CF-1 males were placed with lactating females prior to postpartum estrus [28].

Fifteen of the sexually-experienced, wild-type males that exhibited infanticide when placed with lactating females in Experiment III were chosen at random and allowed to cohabit with the test female until a second litter was delivered. The mean (±SEM) interval from the time that these 15 males were placed with the females until the litters sired by the test males were born was 24.9±0.4 days (range=22–29 days), and none of these previously infanticidal males killed the litter that they had sired. The 16 noninfanticidal males from Experiment III were allowed to cohabit with females throughout the time that they were nursing their first litters (the pups were removed from the cage when they were 23 days old). The mean (±SEM) interval from the time that these 16 noninfanticidal males were placed with the female until the males' own offspring were born was 38.8±0.4 days (two-thirds of the litters were born on Days 38 and 39; range=36–44 days; Fig. 2). Therefore, infanticidal wild-type

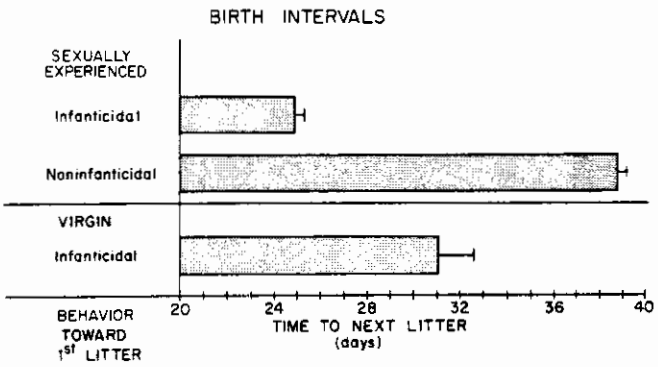

FIG. 2. Wild-type males were placed into the cage of a lactating wild-type female and here 2-day-old young. Some of the males had mated with other females (sexually-experienced groups; see Experiment III), while other males had no prior sexual experience. The sexually-experienced males were catagorized as to whether they were infanticidal (N=15) or noninfanticidal (N=16) when placed with the lactating female. Fifteen out of 16 virgin males that were placed with the lactating females exhibited infanticide, and only the 15 males that exhibited infanticide were included in this experiment. The mean (+SEM) number of days until the females delivered litters sired by the test males is shown.

males produced their own offspring after a significantly shorter interval than did noninfanticidal males, $F(1,29)=467$, $p<0.001$. Since the males were placed with the females on the second day after they delivered, and pregnancy in wild mice lasts 18 days, most of the noninfanticidal males inseminated the females when the nursing young were 20 or 21 days old (at which time preweanling young are eating solid food). In contrast, the females that had had their litters killed by the infanticidal males appeared to have ovulated and mated 6–7 days after the death of their litters.

A third group of males was also examined in this experiment. Sixteen wild-type males that had not previously mated with a female or been tested for infanticide were placed with lactating females and their 2-day-old young as described above, and 15 (94%) of the males exhibited infanticide. The proportion of these virgin males that exhibited infanticide is not statistically different from the proportion of virgin males in Experiment II that exhibited infanticide after cohabiting with an ovariectomized female and then tested for infanticide by being placed into a cage with a lactating female and her 2-day-old young (88% exhibited infanticide; χ^2; $p>0.1$).

The 15 virgin males that exhibited infanticide were allowed to remain with the test females until the litters that they had sired were delivered, and the interval to delivery of the litters was calculated. The mean (±SEM) interval to the production of their own litters from the time that the males were placed with the lactating females (on Day 2 postpartum) was 31.1±1.5 days. This interval is significantly longer than the interval for the previously described infanticidal males with prior sexual experience, N=15, mean interval=24.9±0.4 days; $F(1,28)=13.7$, $p<0.01$. Both the virgin and sexually-experienced males were between 90 and 120 days old at the time that they were paired with the lactating females at the beginning of the experiment, so there was no significant difference in the mean age of these 2 groups of males at the time of testing. Therefore, infanticidal, virgin,

wild-type male mice required a longer period of time to inseminate a female whose litter had been killed than did infanticidal, sexually-experienced, wild-type males (Fig. 2).

DISCUSSION

The current findings from studies with wild mice are intersting in that they both confirm and contradict results obtained with domestic-stocks of mice. Infanticidal CF-1 male mice have previously been reported to produce a litter after a significantly shorter period of time than noninfanticidal males when placed with lactating females [28], and this has now been repeated for wild-type male house mice in Experiment VI. The current results thus provide further support for the first prediction of the sexual-competition hypothesis of infanticide, namely, that under the appropriate conditions (for instance, when males encounter lactating females), males that exhibit infanticide produce offspring more rapidly than do males that do not exhibit infanticide. One interesting observation, however, is that virgin, infanticidal, wild-type males required significantly longer to inseminate females after killing their litters than did sexually-experienced, infanticidal, wild-type males. Examination of the data revealed that the additional time that the infanticidal virgin males required to inseminate the females (5–6 days) was equal to about one estrous cycle in female mice. It thus appears that the virgin males did not successfully inseminate their female partners during the first estrus exhibited after the litters were killed, and the males then had to wait until the females became receptive again, at which time virtually all males successfully inseminated their partners.

We also tested the second prediction of the sexual-competition hypothesis, namely, that infanticidal males must have some mechanism for avoiding exhibiting infanticide toward their own young. There is already considerable evidence that the characteristics of nursing young (the sex, age or stock) do not influence the proportion of male mice that exhibit infanticide [2, 10, 11, 22, 27, 28]. Infanticidal behavior in male mice has thus been proposed to not be directly determined by the degree of genetic relatedness of the males to the young.

The results of Experiment I reveal that wild-type males were inhibited from exhibiting infanticide 3 weeks after mating when placed into cages with either novel females and their litters or with their former mates and the males' own offspring. Huck *et al.* [9] reported that in Swiss-Webster mice, cues emitted by the prior female partner served to regulate whether males that had not previously been tested for their behavior toward young exhibited infanticide after mating. But, vom Saal and Howard [28], utilizing CF-1 mice, as well as Brooks and Schwarzkopf [2], utilizing both DBA and C57B1/6J strains, reported that recognition of a particular lactating female did not mediate the inhibition of infanticide and facilitation of parental behavior which they observed 3 weeks after males had mated. Subsequently, vom Saal [27] reported that the act of ejaculating during coitus mediated the inhibition of infanticide 3 weeks after mating rather than cohabitation with a female before or after mating in CF-1 mice. The prior findings, in conjunction with our current findings from Experiment I utilizing wild-type male mice that had not previously exhibited infanticide, suggest that the conclusion of Huck *et al.* [9], that recognition of the prior female partner is the only factor that mediates the inhibition of infanticide after mating in male mice, is not true in wild-type male mice that have not previously encountered young and exhibited infanticide.

In contrast to the above finding with wild-type males that had not previously exhibited infanticide prior to mating, the results of Experiment III provide support for the contention of Huck *et al.* [9] that recognition of the prior female partner mediates the inhibition of infanticide after mating in male mice, since the behavior toward young of wild-type males that had previously exhibited infanticide was regulated by cues associated with the lactating females: most previously infanticidal males placed with novel females 3 weeks after mating were similar to sexually-naive, wild-type males (tested using the same procedure) in that they exhibited infanticide. But, previously infanticidal, wild-type males placed with their former mates were significantly less likely to exhibit infanticide than were sexually-naive males that were placed into the cages of lactating female mice and their 2-day-old young. All males that exhibited infanticide when placed into the cage of a lactating female did not exhibit infanticide toward the litter that they subsequently sired (see Experiment VI). How or why experience exhibiting infanticide results in a switch in the regulation of the inhibition of infanticide after mating in wild-type male mice from infanticide being inhibited solely as a function of mating with a female (without any recognition of the specific female) to the inhibition of infanticide being based on recognition of the prior female partner is unknown. What is becoming obvious, however, is that the phenomenon of mating-induced inhibition of infanticide in male mice is extremely complex.

Quite different results were obtained with CF-1 male mice. The results of Experiment IV demonstrated that the behavior of previously infanticidal CF-1 males toward young was not influenced by whether the males were placed with novel females or their prior mates, confirming the results of previous studies utilizing CF-1 male mice [26, 27, 28]. In addition, CF-1 male mice were inhibited from exhibiting infanticide after mating when tested in their home cages [27,28] or when placed into the cages of lactating females (novel or familiar) and their litters (Experiment IV). But, the phenomenon of mating-induced inhibition of infanticide was only observed in wild-type males (without previous infanticide experience) when they were tested by being placed into the cages of lactating females (Experiment I), not when they were tested by having a single pup placed into their home cages (Experiment V). The testing procedure utilized to examine this phenomenon with different genetic stocks of house mice is thus obviously quite important. It was because we had observed that testing wild-type male mice with a single pup did not result in an inhibition of infanticide after mating that the other experiments described above were conducted by placing males into the cages of lactating females and their litters.

Olfactory stimuli are the major cues by which mice communicate information concerning sex, age and reproductive state [25]. It thus seems logical to assume that olfactory cues emitted by a female could have served as the stimuli which regulated whether or not the previously infanticidal, wild-type males in Experiment III exhibited infanticide when placed with a lactating female. It is also possible that some of the variability in a mouse's phermonal profile has been lost in inbred mice, and that male mice from the CF-1 stock (which is random bred in our laboratory but derived from an inbred strain) are less able to distinguish between individual CF-1 females than are wild-type mice (cf. [1, 7, 17]).

The present experiments did not directly address the question of which cue(s) mediate the inhibition of infanticide after mating in wild-type male mice that have not previously

exhibited infanticide. The results of Experiment II demonstrated that cohabitation with an ovariectomized female without mating did not result in an inhibition of infanticide in wild-type males, while the results of Experiment I demonstrated that recognition of the prior female partner also did not mediate the inhibition of infanticide in wild-type males without prior experience exhibiting infanticide. We did not examine whether different periods of postmating contact with a female might lead to differences in the behavior of wild-type males toward young when tested by being placed into the home cage of a lactating female. But, it is possible that the act of ejaculating during coitus mediates the inhibition of infanticide after mating in wild-type male mice that have not previously exhibited infanticide, since ejaculation, rather than mounting, intromitting, or cohabitation with a female prior to or after mating mediates this phenomenon in CF-1 male mice [27].

The inhibition of infanticide after mating reduces the probability of male mice killing their own offspring and thus satisfies the requirement of the sexual-competition hypothesis that there must be a mechanism for parental recognition to inhibit males from killing their own offspring. Since male mice that exhibit infanticide also produce young more rapidly than noninfanticidal males, exhibiting infanticide could increase the reproductive success of male mice under some ecological circumstances. The results of these experiments thus add further support to the hypothesis that infanticide in male house mice evolved due to sexual selection.

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