Inhibition of Infanticide after Mating by Wild Male House Mice

MARGARET M. McCARTHY
Division of Biological Sciences

AND

FREDERICK S. VOM SAAL
Division of Biological Sciences, Department of Psychology and
John M. Dalton Research Center, University of Missouri—Columbia, Columbia, MO 65211

Received 7 March 1985

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 a variety of domestic stocks of mice, and the work presented in this paper looks at the effects of mating on the behavior of wild male mice toward young. The wild mice were large, older than 6 months, and had pups of varying ages. Virtually all wild males exhibit infanticide prior to mating, but virtually all wild males were inhibited from exhibiting infanticide 4 weeks after mating. In contrast, wild males that had not exhibited infanticide prior to mating were inhibited from exhibiting infanticide 2 weeks after mating. The results of this study are consistent with the idea that mating has a specific effect on the behavior of male house mice toward young. Mating did not affect the behavior of wild male mice 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 certain 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 Parental care

I N 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 preweaning young) after mating [2, 9, 27, 28].

In CF-1 mice, the 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 preweaning young. There is also a facilitation of infanticide within the first 2 days after mating in CF-1 male mice that behaved paren tally toward young prior to mating. Facilitation during coitus (rather than the act of mounting, intromitting, or just copulating with a female but not mating) serves to induce changes in the behavior of CF-1 male mice toward young following 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 Ostermeier [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 C57 male mice. But, Elwood [4] was unable to confirm his previous finding, and, instead, reported that mating alone served to significantly inhibit infanticide by 3 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

1Requests for reprints should be addressed to Frederick S. vom Saal, 200 Leverett Hall, Division of Biological Sciences, University of Missouri—Columbia, Columbia, MO 65211.
defined by Darwin [24]; sexually-selected traits in males increase their ability to either attract or gain access to females. The sexual-mating behavior of infantilized males leads to three testable predictions, which were first outlined by Hrdy [8]. First, infantilization by males must result in a shortened birth interval in females whose litters are killed by the males. Second, infantilized males must avoid killing their own offspring if they are kept in an experimental chamber. Third, if mating-induced inhibition of infantilization 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 inhibition, infantilized males was also examined, since in some domestic stocks of mice [9] but not others [38], familiarity with the nursing female appears to play a role in determining whether males exhibit infantilization after mating.

METHOD

Animals and Housing

Wild house mice (Mus domesticus) 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 Boones County, Missouri. Approximately 100 males were trapped and 100 females (at least 60 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 F1 offspring of the wild mice were utilized in the present experiments. These animals were reared and tested utilizing the same procedures described for the wild mice. All animals were housed in rooms maintained at 22±2°C on a 12:12 hr light-dark cycle with lights on at 0600 hr. Animals were housed in polypropylene cages (18×29×13 cm) with aspen bedding. Parent 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 infantilism [8]. Two alternative testing procedures have predominated. Either the male mouse has been isolated and allowed to adapt to his cage, after which one or two pups were placed into each male's cage and its behavior toward them was reported [16, 22, 27, 38], or, alternatively, a male has been taken from his home cage and placed into the cage of a lactating female and her litter, and its subsequent behavior toward the litter has been reported [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 the lactating female, and the animals were left undisturbed for 30 min. If the male was found in the nest bowing over the pup and the pup was warm, the behavior was recorded as "parental," 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 stocks 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 the 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 infantilism 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 parturition (when most males were tested using this procedure), a female mouse no longer in postpartum estrus, which occurs during the first 2-3 days after parturition, is returned to the cage of the male that was given 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 female mice exhibit aggression toward males that are placed into the female cages [16].

Infanticidal behavior in CF-1 males was found to kill 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 infantilization 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

I. Influence of Sexual Experience on Infantilism in Wild-Type Males: Tested with Novel Male Females

The purpose of this experiment was to determine if the phenomenon of mating-induced inhibition of infantilism that has been observed in CF-1 male mice could also be observed in wild-type mice. It has been proposed that infantilized 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
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 unacquainted 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 mice (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.
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 exhibiting infanticide on the behavior of sexually-experienced wild-type males toward young, the identical experiment was repeated utilizing CF-1 males. Virgin, CF-1 females 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 matched and then tested for their behavior toward young 2 days after their female mates delivered young using the same procedure described in the previous experiment.

Twelve infanticide-experienced CF-1 males were placed into cages with novel females 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 when separated from the female partner within 2 sec of copulating (27). In this experiment 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 three weeks after a single pup was 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 IV. 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 (3,180). 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 behavior toward young using the same procedure (87% exhibited infanticide; see [16]; 7% <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 clear 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 stressed by the test male) was placed into each male's home cage. Of the 12 males tested, 12% exhibited infanticide and 88% exhibited parental behavior toward
INHIBITION OF INFANTICIDE IN MALE MICE

The pup. This proportion of males exhibiting infanticide is not significantly different from the behavior of sexually-naïve, wild-type males toward young when tested in their home cages (87% exhibited infanticide; see [16], χ² = 0.1). When tested in the same 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, CF-1 males were placed with lactating females on the day that the females delivered. All of the males were thus able to immediately recognize 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 sized by the CF-1 males that did not exhibit infanticide was about 7 days longer than the interval for the delivery of litters sized 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 whereas wild-type males 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 the 15 males were placed with the females until the litters sized by the test males were born was 24.9±0.4 days (range 12-29 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 cages when they were 23 days old). The mean (+SEM) interval from the time that the 16 noninfanticidal males were placed with the female until the 10 males' own offspring were born was 38.8±6.4 days (two-thirds of the litters were born on Days 38 and 39; range=36-44 days; Fig. 2). Therefore, infanticidal wild-type males produced their own offspring after a significantly shorter interval than did noninfanticidal males, F(1,29)=46.7, 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 (noninfanticidal males) mated with the females when the nursing young were 20 or 21 days old (at which time weaning 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 mating with an ovarectomized 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; χ² > 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±3.5 days. This interval is significantly longer than the interval for the previously infanticidial males, 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 instigate 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 interesting in that they both confirm and contradict results obtained with domestic-rocks 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 estrus 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 [27, 28]. Infanticidal behavior in male mice has thus been proposed not to be directly determined by the degree of genotypic relatedness of the male 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. Newcomb 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 Schwartzkopf [2], utilizing both DBA and C3H/10 strains, reported that recognition of a particular lactating female is a necessary condition for 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 ejaculation during copulation 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, support 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 conclusion 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 females' 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 with them (see 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 VI). 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.

Defactory stimuli are the major cues by which mice communicate information concerning, among other reproductive states [25]. It thus seems logical to assume that defactory 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 pheromonal 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 cues mediate the inhibition of infanticide after mating in wild-type male mice that have not previously
exhibited infanticide. The results of Experiment II demon-
strated that cooperation with an ovariectomized female 
without mating did not result in an inhibition of infanticide in 
wild-type males, while the results of Experiment I demon-
strated that recognition of the prior female presents 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 cohabitation contact 
with a female might lead to differences in the behavior 
of wild-type males toward young preyed on by being placed 
into the home cage of a lactating female. But, it is possible 
that the act of ejaculating during coitus mediates the inhibi-
tion of infanticide after mating in wild-type male mice that 
have not previously exhibited infanticide, since ejaculation, 
whether or not mounting, intromittent, 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-selection 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 experi-
ments thus further support the hypothesis that infan-
ticide in male mice evolved due to sexual selection.

ACKNOWLEDGEMENTS

This research was conducted in partial fulfillment of the M.A. 
degree by MMH and was supported by grants to FvS from NIH
(NS 20775), NSF (BNS 8023770), and the University of Missouri Re-
search Council (University of Missouri Biomedical Research Sup-
port Grant BRR 07951 from NIGMS).

REFERENCES

infanticide and discrimination of estrous and estrus nonestrus 
hibiting hormone by steroids in the mouse. Endocrinology 106: 
4. Elwood, R. The inhibition of infanticide and the onset of paternal 
care in male mice. M. Musculus. J. Comp. Psychol. in press.
Mongolian gerbils: Ontogeny, causation and function. In: In-
fanticide in Co-operation and Evolution in Animals. edited by C.
ulating preferences among conspecifics in mice. Anim. Behav. 31: 
81-85, 1983.
8. Hols, S. Infanticide among marmosets: A review, classification 
and examination of the implications for the reproductive strat-
9. Hula, W., R. Solmo and C. Cooperseith. Infanticide in male 
larvatory mice: Effect of social status, prior sexual experi-
ence and sex for discrimination between related and unrelated 
non-lactating Mus musculus: Influence of genotype, family 
11. Laton, J. Factors influencing infanticidal behavior in wild 
mouse male mice (Mus musculus). Behav. Ecol. Sociobiol. 46: 297-303, 
1980.
strategies in the colored marmoset, Callithrix jacchus. Nature 272: 
13. Mammelka, S. and M. Kinchel. Frequency and extent of 
delayed implantation in lactating mice and mice. J. Reprod. Fertil. 
14. McCarthy, M., J. Base and F. vom Saal. Infanticide and parent-
tal behavior in wild female house mice (Mus musculus): effects of 
ovariectomy, adenohypophyseal administration of oxytocin and 
16. McCarthy, M. and F. vom Saal. Infanticide by virgin CF-1 and 
wild male house mice (Mus musculus): Effects of age, prolonged 
17. Osterringer, M. and R. Elwood. Pup recognition in Mus 
musculus: Parental discrimination between their own and alien 
1956.
21. Swase, B. Maternal aggression in mammals: In: Parental Care 
in Mammals, edited by D. Gubler and P. Klopfer. New York: 
22. Swase, B. and M. Moynihan. Infanticide: Genetic, developmental 
and hormonal influences in mice. Physiol. Behav. 27: 421-427, 
1981.
23. Swase, B. and M. Moynihan. Infanticide: Genetic, developmental 
and hormonal influences in mice. Physiol. Behav. 27: 421-427, 
1981.
Selection and the Descent of Man, edited by J. Campbell. 
25. Vandenbergh, J. Hormonal, phenotypic and behavior. In: 
Hormonal Correlates of Behavior. Vol. 2, edited by S. Ehr-
271-288.
26. vom Saal, F. Postpartum and ultimate causes of infanticide in 
house mouse males: In: Infanticide: Comparative and Evolutionary 
Aspects, edited by C. Haufler and S. Bluffer-Holy. New York: 
27. vom Saal, F. Time-constant change in infanticide and parental 
behavior induced by ejaculation in male mice. Physiol. Behav. 34: 
28. vom Saal, F. and L. Howard. The regulation of infanticide and 
parental behavior: implications for reproductive success in male 