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Factors Influencing Infanticidal Behavior in Wild Male House Mice (*Mus musculus*)

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Summary. 1. Infanticidal behavior was examined in wild-strain male house mice *(Mus musculus)*. Preliminary studies established that male house mice killed significantly more unrelated than related pups. Several factors influencing a male's tendency to kill unrelated young were then systematically investigated. Independent variables included the length of time a male cohabited with a pregnant female (10, 6, 3, or 1 days), the phenotype of the unrelated offspring (wild or albino), and whether the male copulated with an estrous female before cohabiting with a pregnant female. In the latter case, the estrous female was 'painted' with urine from the pregnant female with which the male was later paired. The dependent variable in all cases was pup survival to five days postpartum.

2. Males which copulated before cohabitation killed significantly fewer young than males which did not mate. Increased length of cohabitation significantly reduced infanticide by males which mated, but did not affect the number of pups killed by males which did not copulate. Offspring phenotype was not an important factor in preventing infanticide.

Introduction

Male house mice *(Mus musculus)* produce pheromones which induce pregnancy termination and a return to estrus in female conspecifics recently inseminated by a different male (Bruce, 1959, 1960, 1961; Chipman and Fox, 1966; Chipman et al., 1966; Hoppe, 1975). The ability to block pregnancies has been interpreted as an adaptive 'strategy' to (a) increase the representation of an individual male's genes in future generations at the expense of other males, and (b) prevent a male's providing parental investment to genetically unrelated offspring (Trivers, 1972; Wilson, 1975; Dewsbury, 1978).

Female house mice are not susceptible to pregnancy blocking after the embryos implant in the uterus. Therefore, unless new males encounter females during their earliest stages of gestation, the advantages outlined above could not be realized. Under such conditions, Wilson (1975) predicted that selective pressure would favor males capable of employing other methods to reduce the number of progeny carrying genes of male competitors. Wilson suggested infanticide of unrelated offspring as one such alternative. Although infanticidal behavior has been reported in lions (Bertram, 1975), langurs and other primates (reviewed in Hrdy, 1977), and collared lemmings (Mallory and Brooks, 1978), there has been no systematic investigation to ascertain stimuli which induce males to kill neonates.

Preliminary experiments established that wild-strain male house mice introduced to unfamiliar pregnant females three days before parturition significantly reduced offspring survival compared with stud males which remained with their mates during gestation and parturition or isolated female controls (71%, 99%, and 96% survival, respectively, $P < 0.001$). A multifactorial experiment was then established to examine the role of, and interactions between, several other parameters which might influence male infanticidal behavior. These included:

1. The Role of a Male's Previous Experience with a Pregnant Female. Infanticide would not increase male reproductive success if practiced indiscriminately. Males may recognize their own offspring by past association with the mother. If previous experience with a female is important, then males which are reunited with pregnant females they previously inseminated should kill fewer offspring than males which are paired with unfamiliar pregnant females.

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2. Cohabitation Period of a Male and Pregnant Female Before the Birth of Pups. If males recognize genetically related offspring only by past association with their mother, then increasing the time a male and female cohabit may inhibit male infanticidal behavior. However, increasing the cohabitation period with a female carrying unrelated embryos should not reduce a male's infanticidal behavior to any extent.

3. Characteristics of the Offspring. Pups may provide information to an adult male about kinship. If cues from offspring are salient, then infants whose phenotypes differ from the adult male should be killed more frequently than offspring with a similar phenotype.

4. Whether the Male Tested for Infanticidal Behavior Copulated with the Pregnant Female. When a strange male usurped the status of the dominant male in troops of langurs, pregnant females exhibited behavioral (but not physiological) estrus and copulated with the stranger (Hrdy, 1977). Hrdy proposed that copulating with a pregnant female somehow inhibited the male from destroying her infant. The effects of mating on infanticidal behavior of male house mice were tested in these experiments.

Materials and Methods

Subjects

Male house mice tested for infanticidal behavior (referred to below as test males) were wild-strain animals maintained in a colony at the University of Rhode Island. Some males used in these experiments were trapped locally and maintained for several months before testing; others were born into the colony. Assignment of a male to any experimental cell was random. Each test male had previously demonstrated the ability to impregnate a female. Males were isolated for a minimum of three weeks before pregnant females were introduced to them in plastic cages (13 x 28 x 15.5 cm). Both wild and Swiss albino males inseminated the females which were later introduced to test males. These stud males were isolated in plastic cages since weaning at 21–25 days. None had a previous sexual experience.

All females utilized in these experiments were from a Swiss albino strain colony at the University of Rhode Island. Five to eight nulliparous animals were housed together in stainless-steel stock cages (24 x 30 x 15.5 cm) from weaning until they were paired individually (at 45 ± 3 days of age) with a stud male. When a copulatory plug was discovered, the female was returned to a stainless-steel stock cage (5 animals/cage maximum) until she was placed with a test male.

Other nulliparous Swiss albino females were introduced to test males for copulation experiments (see below). These females were maintained in stainless-steel stock cages since weaning and were at least 40 days old when presented to test males. Estrous cycles were checked daily by cell smears obtained via vaginal lavage (Parkes, 1926). Females were introduced to test males the evening a late proestrous smear was observed.

All animals received Purina Lab Chow and tap water ad libitum. The animal quarters had a 14:10 LD cycle (lights on at 0700 EDT). Temperature in the animal rooms ranged from 20° to 28° C. All cages held wood shavings as bedding material.

Table 1. Infanticide experiments, experimental design

Number of days postinsemination when females are introduced to test males (total number of days from pairing to birth of litters)

	8 (10)	12 (6)	15 (3)	17 (1)
Males copulate, wild-phenotype offspring				
Males copulate, albino-phenotype offspring				
Males do not copulate, wild-pheotype offspring				
Males do not copulate, albino-phenotype offspring				

Procedure

Table 1 illustrates the general design of the experiments in which test males were paired with females which carried unrelated offspring. Each cell was replicated four times. Males tested for infanticidal behavior were subjected to the following conditions:

Cohabitation Period. Pregnant females were introduced to test males' cages 8, 12, 15, or 17 days postinsemination (10, 6, 3, or 1 days before the expected birthdate of the litter). The females and any surviving offspring remained with a male for a minimum of five days after birth. Experimental males were paired with females inseminated by another male; 16 additional control males were reintroduced to females they had originally inseminated on the days listed above.

Phenotype of Offspring. Half of the 64 test males cohabited with females who were originally mated to a wild-strain stud. The other half were paired with females carrying offspring sired by an albino stud.

Copulation Prior to Cohabitation. Female house mice in the postimplantational stages of pregnancy will not copulate. Therefore, females in estrus were introduced to half of the test males at approximately 2030 the evening before pregnant females were to be placed in the males' cages. To minimize the probability that a test male would distinguish the estrous female from his future cage mate, urine from the pregnant female which was to cohabit with a test male was 'painted' over the tail base, rump, lower abdomen, and genitalia of the estrous female. The pregnant female which provided urine and the recipient estrous female were both given the same identification marks (picric acid). Pregnant females introduced to males which did not copulate were randomly marked. The breeding female was removed from the test male's cage the following morning if either a copulatory plug or sperm in a vaginal smear was observed. The estrous female was immediately replaced by the identically marked pregnant female, which remained with the test male for the remainder of the experiment. Test males which showed no evidence of having mated with the estrous female were removed from the experiment and replaced with another experienced male drawn at random from the colony, and the procedure was repeated after the new test male's required three weeks total isolation period was satisfied. In all cases, males were tested only once for infanticidal behavior.

Pregnant females were checked for births of litters at least twice a day beginning 48 h before the expected parturition date. Birthdates and number of offspring in each litter were recorded. Litters were rechecked daily for evidence of infanticide until five days postpartum. When dead offspring were found, the following data were recorded when possible:

1. The presence or absence of milk in the stomach.
2. Number of offspring partially or completely cannibalized.
3. Condition of other living infants.

A contingency $-\chi^2$ analysis was employed to test for differences in infant survival between pups subjected to unrelated males and those which lived with their biological fathers. In the experiments in which all offspring were unrelated, independent variables and higher-order interactions between and among independent variables were analyzed with the BMDP-P3F computer program (Brown et al., 1976).

Results

Factors Influencing Infanticide by Unrelated (Test) Males

Data from two litters were excluded from the analyses due to a strong probability that the test males had been used previously for infanticide experiments. Both males excluded copulated and were introduced to pregnant females on day 8 postinsemination. One male was exposed to wild offspring while the other encountered albino pups. However, data on litter size at birth were utilized from these two litters (see Discussion).

Copulation. Data are reported in Table 2. Males which mated with estrous females before cohabiting with pregnant females killed significantly fewer unrelated offspring than did males which did not copulate before cohabiting.

Length of Cohabitation. No significant trend toward increased pup killing was associated with shorter periods of cohabitation (Table 3). However, a clearer understanding emerges if the contingency table is collapsed into smaller units. There were no significant differences in the level of infanticide when females were introduced to test males on either days 8 or 12 postinsemination. Similarly, no differences were found in pup killing by males introduced on either days 15 or 17. A significant increase is indicated when pooled data from days 8 and 12 are compared with pooled results from days 15 and 17.

The data are better understood by comparing the interaction between copulatory status and length of cohabitation (Table 4). Males which did not copulate exhibited similar levels of infanticide regardless of the amount of time they spent with pregnant females (Table 4). In contrast, infanticidal behavior of males which mated was clearly influenced by the length of the cohabitation period. The percentage of surviving offspring decreased substantially from days 8 through 12 and then stabilized at a level slightly below noncopulating males. Survival of infants subjected to copulating males was significantly higher for day 8 but not for day 12. Survival was similar for both groups on days 15 and 17.

Table 2. Effects of copulation on infanticidal behavior of test males toward unrelated offspring

Condition	Number of offspring born	Number of offspring surviving to five days (% survival)
Males copulate ($n=30$)	326	251 (78)
Males do not copulate ($n=32$)	370	258 (70)

Test for difference in infanticide ($\chi^2_1=4.65$, $P<0.05$)

Table 3. Effect of cohabitation period on survival of unrelated offspring

Number of days postinsemination pairs were formed (total cohabitation time)	Number of offspring born (no. of litters)	Number of offspring surviving to five days (% survival)
8 (10 days)	166 (14)	130 (78)
12 (6 days)	165 (16)	126 (76)
15 (3 days)	188 (16)	129 (69)
17 (1 day)	177 (16)	124 (70)

Tests for differences in infanticide: all groups: $\chi^2_3=5.94$, $P=0.11$ (NS); 8 days vs 12 days postinsemination: $\chi^2_1=0.17$, NS; 15 days vs 17 days postinsemination: $\chi^2_1=0.08$, NS; 8 and 12 days (pooled data) vs 15 and 17 days (pooled data): $\chi^2_1=5.68$, $P<0.025$

Table 4. Interaction of copulation and cohabitation period on survival of unrelated offspring

Days postinsemination pairs were formed	Males copulate		Males do not copulate	
	Number born (no. litters)	Number surviving five days (% survival)	Number born (no. litters)	Number surviving five days (% survival)
8	79 (6)	78 (99)	87 (8)	52 (60)
12	70 (8)	58 (83)	93 (8)	68 (73)
15	92 (8)	59 (64)	96 (8)	70 (73)
17	85 (8)	56 (66)	92 (8)	68 (74)

Test for differences in infanticide:

$\chi^2_3=36.93$, $P<0.001$
$\chi^2_3=5.42$, NS

Table 5. Effect of offspring phenotype on survival of unrelated offspring

Offspring phenotype	Number of offspring born (no. of litters)	Number of offspring surviving to five days (% survival)
Wild	354 (30)	249 (70)
Albino	342 (32)	260 (76)

Test for difference in infanticide: $\chi_1^2 = 2.86$, $P < 0.10$ (NS)

Table 6. Interaction of copulation and offspring phenotype on survival of unrelated offspring

Offspring phenotype	Males copulate		Males do not copulate	
	Number born (no. litters)	Number surviving five days (% survival)	Number born (no. litters)	Number surviving five days (% survival)
Wild	166 (14)	123 (74)	188 (16)	126 (67)
Albino	160 (16)	128 (80)	182 (16)	132 (73)

Test for differences in infanticide:

$\chi_1^2 = 1.60$, NS
$\chi_1^2 = 1.32$, NS

Table 7. Interaction of offspring phenotype and cohabitation period on survival of unrelated offspring

Days postinsemination pairs were formed	Wild-phenotype offspring		Albino-phenotype offspring	
	Number born (no. litters)	Number surviving five days (% survival)	Number born (no. litters)	Number surviving five days (% survival)
8	87 (6)	74 (85)	79 (8)	56 (71)
12	82 (8)	46 (56)	83 (8)	80 (96)
15	97 (8)	71 (73)	91 (8)	58 (64)
17	88 (8)	58 (66)	89 (8)	66 (74)

Test for differences in infanticide:

$\chi_3^2 = 18.22$, $P < 0.001$;
$\chi_3^2 = 27.73$, $P < 0.001$

Phenotype of Offspring. Table 5 indicates the percentage of wild and albino offspring alive after five days. Although wild pups were killed more frequently, the difference was not significant. Table 6 demonstrates the lack of any interaction between copulatory status of males and offspring phenotype. Interaction between phenotype and length of cohabitation is less clear (Table 7). No pattern is apparent for either wild or albino offspring and neither set of data is homogeneous over time. The high survival rate of albino pups on day 12 is especially puzzling since survival for albinos is otherwise similar on days 8, 15, and 17.

Table 8. Offspring survival, controls

Number of days post-insemination female was reintroduced	Number born (no. litters)	Number surviving five days (% survival)
8	39 (4)	23 (59)
12	55 (4)	50 (91)
15	52 (4)	51 (98)
17	48 (4)	39 (81)

Test for differences in infanticide: $\chi_3^2 = 28.06$, $P < 0.001$

Table 9. Comparison of offspring survival in experimental and control experiments

Experimental condition	Number of offspring born (no. litters)	Number surviving five days (% survival)
Experimental, all litters	696 (62)	509 (73)
Experimental, males copulate, wild-phenotype offspring	166 (15)	123 (74)
Control	194 (16)	163 (84)

Tests for differences in infanticide: control vs experimental (all litters): $\chi_1^2 = 9.73$, $P < 0.005$; control vs experimental (males copulate, wild-phenotype offspring): $\chi_1^2 = 5.19$, $P < 0.025$

Controls

Data presented in Table 8 show no discernible pattern of infanticide in this group of males; the four cohabitation cells are not homogeneous. The high frequency of infanticide for day 8 is especially perplexing.

Statistical comparison between experimental and control males demonstrates a highly significant difference in infanticidal behavior (Table 9). Fewer offspring were killed by their fathers (control males) than by unrelated males (Table 9). A similar difference also exists when controls are compared only with test males under the closest experimental conditions, i.e., test males which copulated and were subjected to wild-phenotype offspring.

Discussion

Evidence for Infanticide by Males

Only two attacks by males on neonates were directly observed during these experiments. Possibly females could have played a role in killing pups. With males absent, infanticide by females toward large litters has been reported in hamsters (Day and Galef, 1977) and Rockland-Swiss albino house mice (Gandelman and Simon, 1978). However, it is unlikely that females participated to any significant degree in destruction of offspring in my experiments for two reasons:

1) In pilot studies, there was 96% pup survival when males were not present. Experimental females belonged to the same strain as those animals used in the pilot study. Parity and age of females were the same in both sets of experiments.

2) Many aspects of infanticide differed from those reported by Gandelman and Simon (1978), who found that females exhibited infanticidal behavior if presented with a litter of either 12 or 16 pups; the females killed offspring until approximately nine pups remained (the mean number of offspring produced by control females). In contrast, I found that of 37 litters subject to infanticide, 16 (43%) were entirely destroyed. Mean litter size at birth was similar in experimental (11.19 ± 0.82 SE), control (12.12 ± 0.66 SE), and isolated control (pilot study) (13.14 ± 0.99 SE) females ($F_{2,84} = 0.461$, NS), but litter survival after five days was very different for each group.

Pups subject to infanticide in the present experiments survived significantly less time than infants in the study by Gandelman and Simon (1978), who reported most infanticide occurred on days 3–7 postpartum (days 2–6 if parturition is called day 0 for purposes of comparison with my study). By extrapolating data from Gandelman and Simon's cumulative count of dead pups (p. 237), average pup survival from parturition (day 0) to day 5 was 2.85 ± 0.18 (SE) days. In my experiments, with strange males present, mean survival time of pups subject to infanticide was reduced to 1.65 ± 0.13 (SE) days. This estimate of survival is high because in several cases in which survival time could not be accurately determined, it was recorded as five days. Mean survival time is significantly different for the two studies ($t_{271} = 5.45$, $P < 0.001$).

Gandelman and Simon (1978) never found carcasses of the 86 pups killed. They concluded the dead young were cannibalized. In the present study with strange males present, 79% of all infant carcasses (172 of 218) were recovered. The difference between these data and those of Gandelman and Simon (1978) is highly significant ($\chi^2_1 = 156.27$, $P < 0.001$).

Gandelman and Simon (1978) stated that live young were continually nourished by their mothers, since white 'milk lines' were found in their stomachs. In addition to live young, at least 63 dead pups in my experiments also showed clear evidence of having suckled, indicating maternal care. Of the 150 unrelated offspring recovered, 99 were not dismembered. They had numerous tooth marks concentrated around the head and snout, but were otherwise intact. Similar patterns of attack have been reported in male lemmings (Mallory and Brooks, 1978). The rest of the carcasses were dismembered; some appeared cannibalized. All males did not attack unrelated offspring. Several males which did not commit infanticide exhibited parental behavior toward the litter. These behaviors included crouching over the litter in the nest and retrieving offspring outside the nest.

Adaptive Advantages for Males

Infanticide has received considerable attention by population and theoretical biologists since it has become established that the behavior is manifest in many species and elicited under various conditions. Hrdy (1979) has classified infanticide into several categories which may be adaptive to the perpetrators. They include exploitation (i.e., infants are used as a food resource), resource competition, xenophobia, accidental death due to parental manipulation, and sexual selection. This study examined the last category. The results are important for two reasons. First, *Mus musculus* can be added to the list of species in which infanticide occurs by males unrelated to the offspring involved. Second, these experiments elucidated and confirmed hypotheses proposed by others (Trivers, 1972; Hrdy, 1977, 1979) concerning the underlying causes for infanticidal behavior by males.

Hrdy (1977, 1979) predicted that males may recognize genetically related offspring by past sexual association with the mother rather than by characteristics of the offspring themselves. Although no data exist for langurs to confirm or refute the hypothesis (Hrdy, personal communication), my studies indicate a comparable situation with *Mus*. Male house mice which copulate with females are less likely to destroy those females' offspring. This relationship is indicated both by differences between experimental and control levels of infanticide, and by differences between experimental males which mated and those which did not. Similar differences were found in experimental and control male collared lemmings *(Dicrostonyx groenlandicus)* by Mallory and Brooks (1978). In contrast, the pups' phenotype did not significantly influence the likelihood of infanticide.

The interaction of mating and length of cohabitation are also significant. Males of many species prevent other male conspecifics from approaching females for varying periods both before and after mating (reviewed in Wilson, 1975; Daly and Wilson, 1978). Such behavior may establish whether the female has been previously inseminated. If offspring are born shortly after mating, a male may then somehow determine that he is genetically unrelated to them. The probability of kinship would increase with time. Thus, some minimum critical period may exist before infanticide by the male is reduced. In my experiments, cohabitation period significantly influenced infanticidal behavior of those males which mated. How a male determines elapsed time is unknown. Why the critical period would be between three and six days before parturition (Table 4) is not apparent. Perhaps infanticide could be experimentally reduced even further by increasing cohabitation. However, extending the cohabitation period much beyond ten days (i.e., earlier than eight days postinsemination) could prevent infanticide because the pair would be established while the female is still potentially susceptible to pregnancy blocking (Bruce, 1961).

In contrast, cohabitation period was not an important variable for males which did not mate. These results may also be interpreted as an adaptive 'strategy'. If copulation has not occurred, then there is no chance of a male's being genetically related to the female's offspring and infanticide should not be reduced with increasing cohabitation.

Female Strategies for Preventing Infanticide

It should be noted that these experiments may represent an artificial situation in *Mus* because pregnant females will not copulate after their embryos have implanted[1]. However, female microtine rodents *(Microtus ochrogaster* and *M. pennsylvanicus)* and the cricetine *Peromyscus maniculatus* will terminate pregnancies after implantation in response to an unfamiliar male and remate (Stehn and Richmond, 1975; Kenney et al., 1977). This prolongation of the Bruce effect may represent a female response to more severe infanticidal pressures by unfamiliar males than is found in *Mus* (Labov, 1979, and in preparation). Research should be undertaken with the aforementioned species to determine the likelihood of infanticide under similar conditions.

Further understanding of the evolutionary significance of infanticidal systems, particularly as they pertain to female reproductive success, may only be possible when more is learned about the social structures of different species. For example, house mice form small, isolated, polygynous reproductive units (demes) in which little immigration or emigration occurs; these demes may be stable over several generations (reviewed by Lacy, 1978). Thus female house mice would not be frequently confronted with unfamiliar males. Similar social structures have been reported for langurs (Hrdy, 1977) and lions (Schaller, 1972; Bertram, 1975), and the potential for infanticide should be relatively low in these species. However, in promiscuous species or those with a less rigid social structure (e.g., *Peromyscus maniculatus,* Eisenberg, 1968), the probability of a female's encountering an unfamiliar, potentially infanticidal male would be increased. Female responses should be more varied and numerous in these species. Prolongation of susceptibility to the Bruce effect may be beneficial to these females in terms of investment of both time and energy in offspring (Labov, 1979, and in preparation).

The effectiveness of other female tactics to limit offspring vulnerability should also be examined in more detail. Mallory and Brooks (1978) placed unfamiliar male collared lemmings with females and their litters either one or three days postpartum. Infanticide was reduced in the latter group because of sustained defense of litters by females. Female postpartum aggression toward both males and other females has also been demonstrated in rats and mice and appears to be hormonally mediated (reviewed by Leshner, 1978). In the present study, several females retrieved pups removed from the nest by males, but no physical attacks by females were observed.

Many female mammals are smaller than male conspecifics. Nest defense beyond some level could reduce future reproductive success due to injury. Aggressive behavior may not be as effective a strategy for females as other counterresponses such as the Bruce effect or behavioral pseudoestrus.

Many other aspects of infanticidal behavior demand future attention. Virtually nothing is known about the heritability of genes which control this behavior, or how infanticide may be modified by development, social status and experience, gender, and other influences. Although several cues for a male's recognizing genetically related pups were investigated in my experiments, the question is far from settled. For example, control males separated from their mates for up to 17 days still killed fewer offspring than test males which mated and cohabited immediately thereafter with pregnant females. Perhaps the urine from pregnant females did not entirely mask the individual odors of the recipient estrous females. This possibility should be examined by permitting males to copulate with females and then introducing the males to the same or different pregnant females after specified periods of isolation. The present experiments also did not ascertain whether males which killed

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[1] In a review of reproduction in domestic *M. musculus,* Bronson et al. (1966, p. 196) stated that "... many cases of mating at various times during pregnancy have been reported; for example Mirskaia and Crew (1930), Bilewicz and Mikiewiczowa (1954), and Bloch (1958)". However, I could find no evidence to support this statement in any of these references

unrelated pups would demonstrate similar responses toward their own offspring. Several observations suggest that infanticidal males do discern their own offspring (Labov, unpublished observations). Further systematic testing with adequate controls is warranted.

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