

MALE PARENTAL CARE  
AND CUES TO PATERNITY IN HOUSE MICE

by

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## ABSTRACT

Twenty-five male mice (Mus musculus) were observed on three consecutive days following parturition to determine the effect of four factors on the occurrence and duration of male parental care. These factors were 1) mating experience, 2) genetic relatedness of pups, 3) continuous cohabitation with a pregnant female and 4) absence of the odour of strange males on the female. The first three factors have been shown to have a significant effect on infanticide in male mice and are believed to act as cues to paternity. The males were divided into three groups which differed in the number of cues to paternity present in the males' environment. All four cues were present in the 4cue condition, only two (mating experience and genetic relatedness of pups) were present in the second condition (2cue) and all cues were absent in the last condition (Nocue). The results indicated that 4cue males displayed more parental and fewer non-parental behaviours than Nocue males. The 2cue males were intermediate on several measures and did not differ significantly from the 4cue or Nocue males. The duration of several behaviours changed significantly over days. In general parental behaviours increased over days while non-parental behaviours decreased. This suggests that exposure to pups or to a lactating female increased male parental behaviour.

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Traditionally, research in animal behaviour has neglected the role of the male in parental care. In most mammals the mother-offspring relationship is assumed to be a unique and important one and the father-offspring relationship one of minimal value. Recent interest in male parental care in rodents, however, has shown that not only is male parental care in these species prevalent and predictable, but that it may also confer a selective advantage on those males who engage in it.

Male parental care has been observed in many mouse species including the house mouse, Mus musculus (Leblond & Nelson, 1936; Beniast-Noirot, 1958; Eisenberg, 1962; Gandelman, Paschke, Zarrow & Denenberg, 1970; Priestnall & Young, 1978), the pocket mouse, Blomys taylori (Blair, 1941), the California mouse, Peromyscus californicus (Eisenberg, 1962; Dudley, 1974), the deer mouse, P. maniculatus (Horner, 1947; Hartung & Dewsbury, 1979), the white-footed mouse, P. leucopus (McCarty & Southwick, 1977; Hartung & Dewsbury, 1979), the northern grasshopper mouse, Onychomys leucogaster (Ruffer, 1965), the southern grasshopper mouse, O. torridus (Horner & Taylor, 1968; McCarty & Southwick, 1977), the meadow vole, Microtus pennsylvanicus, the California vole, M. californicus (Hatfield, 1935), the prairie vole, M. ochrogaster, and the montane vole, M. montanus (Hartung &

Dewsbury, 1979). The parental behaviours typically observed in these species consist of activities such as pup retrieval, nest-building, pup licking and the assumption of a nursing posture. These behaviours are identical to those exhibited by lactating females and virgin females exposed to pups (Beniest-Noirot, 1958). In some species, e.g., MUS MUSCULUS, males have been reported to display the same level of parental care as lactating females (Priestnall & Young, 1978). The information available on this species is therefore a potential source for determining the conditions under which paternal care is facilitated.

In general, paternal care of the young is thought to occur in those species which are monogamous, or where strong pair-bonds are formed and where mating partners continue to associate after parturition (Kleimann, 1977). There is also evidence that species living in tightly structured social units also tend to exhibit male parental care (Beach, 1967).

Why these particular social conditions seem to facilitate male parental care has been explained by the sociobiological theory of kin selection and the concepts of inclusive fitness and parental investment (Hamilton, 1964; Trivers, 1972; Wilson, 1975). According to this perspective, a behaviour is adaptive if it increases an individual's inclusive fitness or the total number of copies of an individual's genes contributed to the future gene pool. Since kin carry copies of an individual's genes, fitness can be maximized by behaving 'altruistically'

towards one's kin to ensure their survival and reproduction. One example of this 'kin selective' behaviour is the helping behaviour exhibited by parents towards their offspring, termed parental investment (Trivers, 1972).

In mammals the mechanisms of internal fertilization and gestation assure the female that her putative offspring are actually related to her. But the probability of parenthood is lower for the male as his putative offspring could be the result of kleptogamy (May & Robertson, 1980) and are not necessarily his biological offspring. Therefore, to avoid investing in offspring that are not related, males may have evolved various alternative strategies to increase their inclusive fitness (Trivers, 1972).

For example, it may be adaptive for a male to invest little time and energy in each putative offspring but attempt to conceive as many offspring as possible by mating with many females. The problem with this strategy is that it leads to a situation of diminishing returns. The less time and energy a male spends with each female and her offspring, the lower the probability of paternity and the less likely are his offspring to survive. Another alternative is to remain with his mate but to develop mechanisms to ensure and assess his paternity. For example, in species where pair-bonds are formed or where there is a highly structured social organization it may be possible for a male to determine his parenthood to a reasonable degree of accuracy. Such social conditions allow a male to monitor his

mate's activities as well as assess the relatedness of offspring by phenotypic cues. Perhaps this is why monogamy and pair-bond formation are usually associated with high levels of male parental care.

There is evidence that wild Mus musculus live in highly structured social units (Bronson, 1979). Under these conditions the males of this species have the opportunity to assess paternity. The specific factors which could serve as cues for a male mouse in assessing the degree of relatedness between himself and offspring have not yet been elucidated. By examining recent studies of infanticide in male mice, however, it may be possible to deduce such factors and predict more precisely the conditions under which parental care will occur.

Infanticide is a non-parental or anti-parental behaviour and is one of the alternative strategies that a male can adopt to improve his inclusive fitness. Killing of another male's offspring may increase the fitness of an infanticidal male, by reducing the number of competing genes in the gene pool (Hrdy, 1977). It may also increase fitness if the male, by killing a female's offspring, induces her into estrus and is then able to mate with her (Hrdy, 1977; vom Saal & Howard, 1982). Thus when the probability that an offspring is not related to a male is high, or when the cues to paternity are lacking in his environment, it may be profitable for the male to be infanticidal. Thus the presence or absence of cues which signal paternity may be important in determining whether a male will be

infanticidal as well as parental.

The studies of infanticide in male mice (Labov, 1980; vom Saal & Howard, 1982) isolated several factors which affect levels of infanticide and which may serve as cues for determining whether or not an offspring is related.

1. Mating experience. Whether a male mates before he is exposed to offspring seems to be one of the most important factors in predicting whether a male will commit infanticide. In both the Labov (1980) and vom Saal & Howard (1982) studies males that mated, regardless of the other conditions, exhibited lower levels of infanticide than those that did not.
2. Genetic relatedness. Whether the young are actually related to a male should have an effect on the level of infanticide. Genetic relatedness may be communicated by phenotypic properties of the young such as colouration and odours (Ostermeyer & Elwood, 1983). Genetic relatedness may also be inferred by prior mating or cohabitation experience with the mother. A preliminary study by Labov (1980) indicated that males were more likely to kill unrelated versus related offspring.
3. Cohabitation. Continuous cohabitation or association with a pregnant female before parturition has been shown to reduce infanticide in both experienced and virgin males (Labov, 1980). The longer a male cohabited with a female before she gave birth the less likely he was to kill her offspring,

irrespective of whether he sired them. A recent interpretation (Lown, 1980) of two studies concerned with parental care in mice (Gandelman et al., 1970; Priestnall & Young, 1978) has also pointed out that association with a female seems to facilitate paternal care.

My informal observations on laboratory mice, Mus musculus, have indicated that a high degree of male parental care occurs in this species. The purpose of this research, therefore, was to determine what factors influence paternal care in mice. Therefore, factors previously used to predict infanticide in male mice, mating experience, genetic relatedness of young and continuous cohabitation, were varied in order to observe their influence on paternal care. Because odours play such an important role in the communication system of mice (Bronson, 1974) an additional factor, the absence of the odour of strange males, was also employed. In a pilot study males reacted very negatively to their mates after they had been painted with the urine of an unfamiliar or strange male.

Adding or subtracting these four factors from the social conditions of the male results in 16 possible combinations or groups. Of these, three groups were chosen for the present research. The testing of those groups excluded was left for future research. The groups chosen were those that best represent the lowest, highest and intermediate number of cues to paternity. These groups should provide an adequate preliminary test of the hypothesis that the occurrence and intensity of male

parental care is determined by the number of cues to paternity present in a male's environment.

The experimental design thus involved the observation of three groups of male mice. This design is outlined in Table 1. In the 4cue group, the male was mated and then cohabited continuously with his mate throughout gestation. The males in this group were therefore the biological fathers of the pups they were observed with. In the second group, 2cue, the males were also mated but the females were removed shortly after mating, during the time that exposure to a strange or unfamiliar male can lead to the female resorbing the litter and mating again with the new male (Bruce, 1960). Thus the males in this group did not cohabit continuously with their mates. Instead females were reintroduced into the male's home cage several days before parturition. Furthermore females were painted with the urine of several strange males just before being reintroduced. As in the 4cue group, the males were the sires of the offspring they were observed with. Only two cues to paternity were thus present in this condition --mating experience and genetic relatedness of pups. In the 0cue group the male did not mate or cohabit continuously with a female nor was he the sire of the pups with whom he was observed. In this group pregnant females, previously mated with other males and painted with the urine of strange males, were introduced into the male's home cage just before parturition. Therefore none of the four cues to paternity were present in this condition.

Table 1. Experimental design.

Cues to paternity	Groups		
	4cue	2cue	Nocue
Mating experience	The male is mated.	The male is mated.	The male is not mated.
Relatedness of offspring	The male is the sire of the pups he is observed with.	The male is the sire of the pups he is observed with.	The male is not the sire of the pups he is observed with.
Continuous cohabitation	The male cohabits with a female throughout gestation.	The female is removed for 10 days.	A pregnant female is introduced just before parturition.
Odour of strange males	No urine of strange males is painted on the female.	Urine of strange males is painted on the female.	Urine of strange males is painted on the female.



Predictions about the level of parental care exhibited by the males in each group followed the general hypothesis that more parental care and fewer non-parental behaviours were expected where there were more cues to paternity. The specific predictions were thus:

1. 4cue males, with the maximum number of cues to paternity, will exhibit the highest levels of parental care and the lowest levels of non-parental behaviour.
2. 2cue males, with an intermediate number of cues to paternity will exhibit intermediate levels of paternal care and non-parental behaviour.
3. Nocue males, with no cues to paternity will display the lowest levels of paternal care and the highest levels of non-parental behaviour.

Pairwise comparisons of the behaviours displayed in these three groups allowed the assessment of the relative strengths of the different cues in pairs. For instance, if, as in the studies of infanticide, the first two cues of mating experience and genetic relatedness of pups have a greater effect than continuous cohabitation and strange male urine then we might expect the 2cue group to be intermediate but more closely resemble the 4cue group than the Nocue group. If these two pairs of cues are similar in strength then we would expect the 2cue group to lie directly between the 4cue and Nocue groups on these behaviours.

## Methods

### Animals

Twelve single males and 36 male/female pairs of virgin CD-1 albino house mice, Mus musculus, were obtained from a closed colony at the University of British Columbia. All mice were maintained under standard laboratory conditions for mice, with the temperature set at 20 degrees C. and humidity at 50%. A light cycle of 12D/12L was set with lights on at 0700 hrs. All mice were housed in polypropylene shoebox cages with opaque sides and fitted wire lids. Purina Lab Chow and water were provided ad libitum.

### Procedure

Mouse pairs were divided randomly into the three groups, 4cue, 2cue and Nocue, and mated. (The mated Nocue males were later discarded and replaced by the 12 single virgin males on whom the observations were recorded.) The 12 single males were housed in groups and then in individual cages to correspond to the time the 4cue and 2cue males were housed with their mates or alone. On the fifth day of mating females from the 2cue and Nocue groups were removed and isolated from their mates. The

4cue females remained with their mates for the duration of the experiment. After ten days of separation 2cue females were returned to their mate's cages. Before being returned, these females were painted, with urine obtained from unfamiliar mature males, on both the posterior anogenital and anterior regions of the body. At this same time, Nocue females were painted and introduced to the Nocue virgin males housed singly. At this point, females that were not visibly pregnant and their mates were removed from the experiment. At the end of this procedure 25 pairs remained--seven in the 4cue group and nine in each of the other experimental groups. All pairs were then left undisturbed until parturition.

#### Observations

Observations of each male's behaviour with the young were made between 1200 and 1800 hours on three consecutive days starting the day following parturition. Observations were recorded with the male in the home cage for a period of 20 minutes. Food and water bottle were left intact to ensure a situation comparable to normal housing conditions. The female was removed from the cage during this time and placed some distance from the home cage. To facilitate testing for pup retrieval behaviour two pups were removed from the nest and placed in the corner of the cage diagonally opposite the nest at the beginning of each day. During each day the parental

behaviours of licking, retrieving, covering, nesting and nursing (listed in Table 2, adapted from Priestnall & Young, 1978 and Hartung & Dewsbury, 1979) were recorded. Three measures of non-parental behaviour, active, biting and infanticide (see Table 2), were also recorded. The last two behaviours are routinely recorded in infanticide studies. The first behaviour is a measure of hyperactivity rather than normal activity. A pilot study revealed that males often became hyperactive and moved rapidly about in the cage. During this time they would often totally ignore the young, leaving them uncovered and sometimes stomping on them in the nest. Therefore this behaviour was categorized as non-parental. Behaviours that were neither parental nor non-parental were recorded under a separate "neutral" category and are not reported here. These included behaviours such as eating, drinking and self-grooming. Each behaviour was recorded on a More event-recorder in terms of frequency, duration and time of occurrence. Observations were recorded double-blind. A study of interobserver reliability revealed significant correlations ( $0.78 \leq r \leq 0.99$ ,  $p \leq 0.02$ ) between the scores of both observers for the total duration of behaviours. Details of this test for each variable are given in Appendix A.

Table 2. Behaviour categories used in the observation procedure.

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Parental behaviours

Licking	The male is licking any part of a pup's body, usually concentrating on the ano-genital region.
Retrieving	The male is carrying or attempting to carry a pup in the direction of the nest by holding it in its mouth.
Covering	The male is carrying nesting material to the nest in its mouth and either covers the young with this material or drops it in the near vicinity (within 1 inch) of the nest.
Nesting	The male is sitting or lying in the nest with the young. All four feet are within the nest area and there is ventral contact with the pups or nest substrate.
Nursing	The male's body is arched, in a nursing posture over one or more pups in the nest and no other movement is apparent.

Non-parental behaviours

Active	The male is hyperactive in the cage, i.e., moving rapidly back and forth in the cage or swinging from the bars but not carrying a pup or nesting material.
Biting	The male is biting a pup. The pup is not severely wounded.
Infanticide	The male, after initially biting a pup, attempts to eat it or a portion of it. The pup is severely wounded or dies subsequently.

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## Results

The total amount of time per observation period that males engaged in each category of behaviour, except "retrieving" was computed. The non-parental categories of "biting" and "infanticide" were dropped from the analysis since neither of these behaviours were observed in the formal observation periods, although both were observed and recorded as casual observations. Because level of parental care may be influenced by litter size an ANOVA (repeated measures) was used to test for differences in litter size between groups over the three day observation period. Litter size did not differ significantly between groups or over days ( $p \geq 0.05$ ).

Only data from the first day's observations were included in the analysis of group differences because several behavioural categories showed significant changes in duration over the three day observation period. Table 3 contains the average duration of each behaviour summed over groups for each day. An ANOVA (repeated measures) was used to test for differences between days. Sample sizes differ slightly because a few extreme values were not included in the computations. These values were shown to be significantly discordant ( $p \leq 0.01$ ) from the rest of the sample values (Barnett & Lewis, 1978). The duration of parental behaviours, with the exception of "covering", increased over days while the duration of non-parental behaviours decreased.

Table 3. Effect of day on duration (seconds) of parental and non-parental behaviours in all groups combined. (Mean  $\pm$  SE)

Behaviour	N <sup>a</sup>	Days			Day factor <sup>b</sup>
		1	2	3	
Licking	25	33.0 $\pm$ 10.1	45.5 $\pm$ 16.4	46.5 $\pm$ 11.3	n.s.
Covering	24	15.0 $\pm$ 4.5	11.4 $\pm$ 3.1	15.4 $\pm$ 3.1	n.s.
Nesting	25	221.2 $\pm$ 57.9	367.4 $\pm$ 79.8	566.4 $\pm$ 72.9	**
Nursing	25	11.7 $\pm$ 5.3	84.4 $\pm$ 34.4	128.7 $\pm$ 48.1	*
Active	22	197.4 $\pm$ 45.4	116.0 $\pm$ 31.7	59.1 $\pm$ 20.5	*

\*  $p \leq 0.05$

\*\*  $p \leq 0.01$

<sup>a</sup> N's differ for behaviours because significantly discordant ( $p \leq 0.01$ ) values (Barnett & Lewis, 1978) were not included in the computations.

<sup>b</sup> Determined by ANOVA repeated measures.

These differences were significant for "nursing" ( $p \leq 0.05$ ), "nesting" ( $p \leq 0.01$ ) and active ( $p \leq 0.05$ ). The greatest group differences were observed in the first days and these differences gradually diminished. Fig. 1 contains a plot of the changes in behaviour "nesting" over days and across groups and is an excellent example of this day effect. A significant Group x Trial interaction was not present for any of the observed behaviours.

Planned pairwise comparisons (one-tailed), (Keppel, 1982) were used to test the predicted differences between the three groups. Table 4 contains the average duration of each behaviour across groups in the first days. Removal of extreme values (by the same criteria used in the day effect data) resulted in slightly different sample sizes across behaviours. The 4cue mice exhibited more parental (licking, covering, nursing, nesting) and fewer non-parental behaviours (active) than Nocue mice. The differences were significant ( $p \leq 0.05$ ) between 4cue and Nocue groups on all measures except "licking" and "nursing", where trends in the predicted direction were present ( $p \leq 0.1$ ). A large amount of variance in the data contributed to the lack of significance on these two variables. The 4cue and 2cue groups did not differ significantly on any measures, although the nonsignificant differences were in the predicted direction. The 2cue and Nocue groups also did not differ significantly on any measures except for "nursing" where a trend ( $p \leq 0.1$ ) in the predicted direction was found.



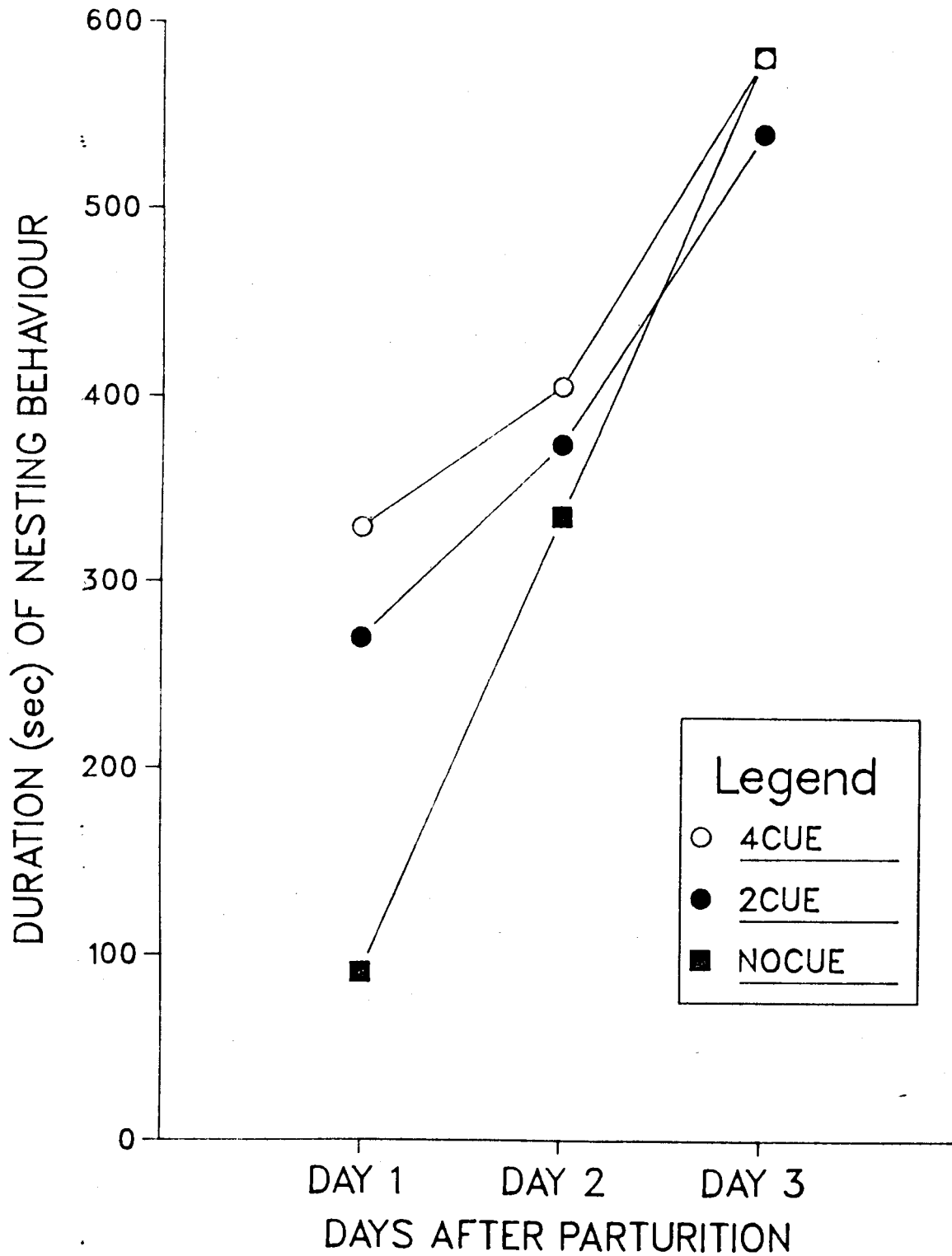


Fig. 1. Effect of day on the duration (seconds) of nesting behaviour between groups.

Table 4. Duration (seconds) of parental and non-parental behaviours between groups on Day 1. (Mean  $\pm$  SE)

Behaviour	N <sup>a</sup>	4cue	2cue	Nocue	Comparisons of group means
Licking	25	56.9 $\pm$ 28.5	26.9 $\pm$ 13.9	20.7 $\pm$ 10.1	4cue > Nocue * 4cue > 2cue n.s. 2cue > Nocue n.s.
Covering	24	24.9 $\pm$ 10.5	14.4 $\pm$ 7.1	5.6 $\pm$ 5.2	4cue > Nocue ** 4cue > 2cue n.s. 2cue > Nocue n.s.
Nesting	25	328.7 $\pm$ 143.4	269.2 $\pm$ 99.3	89.6 $\pm$ 49.7	4cue > Nocue ** 4cue > 2cue n.s. 2cue > Nocue n.s.
Nursing	23	7.8 $\pm$ 4.7	7.7 $\pm$ 4.9	0.0 $\pm$ 0.0	4cue > Nocue * 4cue > 2cue n.s. 2cue > Nocue *
Active	25	106.0 $\pm$ 48.8	221.0 $\pm$ 78.7	279.8 $\pm$ 73.9	4cue < Nocue ** 4cue < 2cue n.s. 2cue < Nocue n.s.

\*  $p \leq 0.1$

\*\*  $p \leq 0.05$

<sup>a</sup> N's differ for behaviours because extreme values that were significantly discordant ( $p \leq 0.01$ ) (Barnett and Lewis, 1978) were not included in the computations.

"Retrieving" was analysed separately from the other variables because it was not meaningful to examine the total duration of this behaviour. Instead the number of pups retrieved and the latency to retrieve the first pup was examined. Table 5 contains the mean number of pups retrieved for each group on each day. Groups differed only slightly ( $p \geq 0.05$ ) on the mean number of pups retrieved and the number of pups retrieved did not differ over days ( $p \geq 0.1$ ).

In general most males retrieved both pups soon after the beginning of the observation period. In 81.3% of the 75 observation periods both pups were retrieved, in 16.0% none were retrieved and in 2.6% only one pup was retrieved. Of the males that did retrieve at least one pup the average time to retrieve the first pup did not differ significantly between groups ( $p \geq 0.1$ ). Group scores were then combined in an ANOVA (repeated measures) to test for differences across groups. Fig. 2 is a plot of the latency to retrieve the first pup over days summed across groups. There was a significant day effect ( $p \leq 0.05$ ) with the latency to first retrieval dropping substantially across days.

Table 5. Number of pups retrieved in each group over all days. (Mean  $\pm$  SE)

Group <sup>a</sup>	Day <sup>b</sup>		
	1	2	3
4cue	1.4 $\pm$ 0.4	1.4 $\pm$ 0.4	1.6 $\pm$ 0.3
2cue	1.6 $\pm$ 0.3	2.0 $\pm$ 0.0	2.0 $\pm$ 0.0
Nocue	1.4 $\pm$ 0.3	1.8 $\pm$ 0.2	1.6 $\pm$ 0.3

<sup>a</sup> Group factor n.s. ANOVA repeated measures (N=25)

<sup>b</sup> Day factor n.s. ANOVA repeated measures

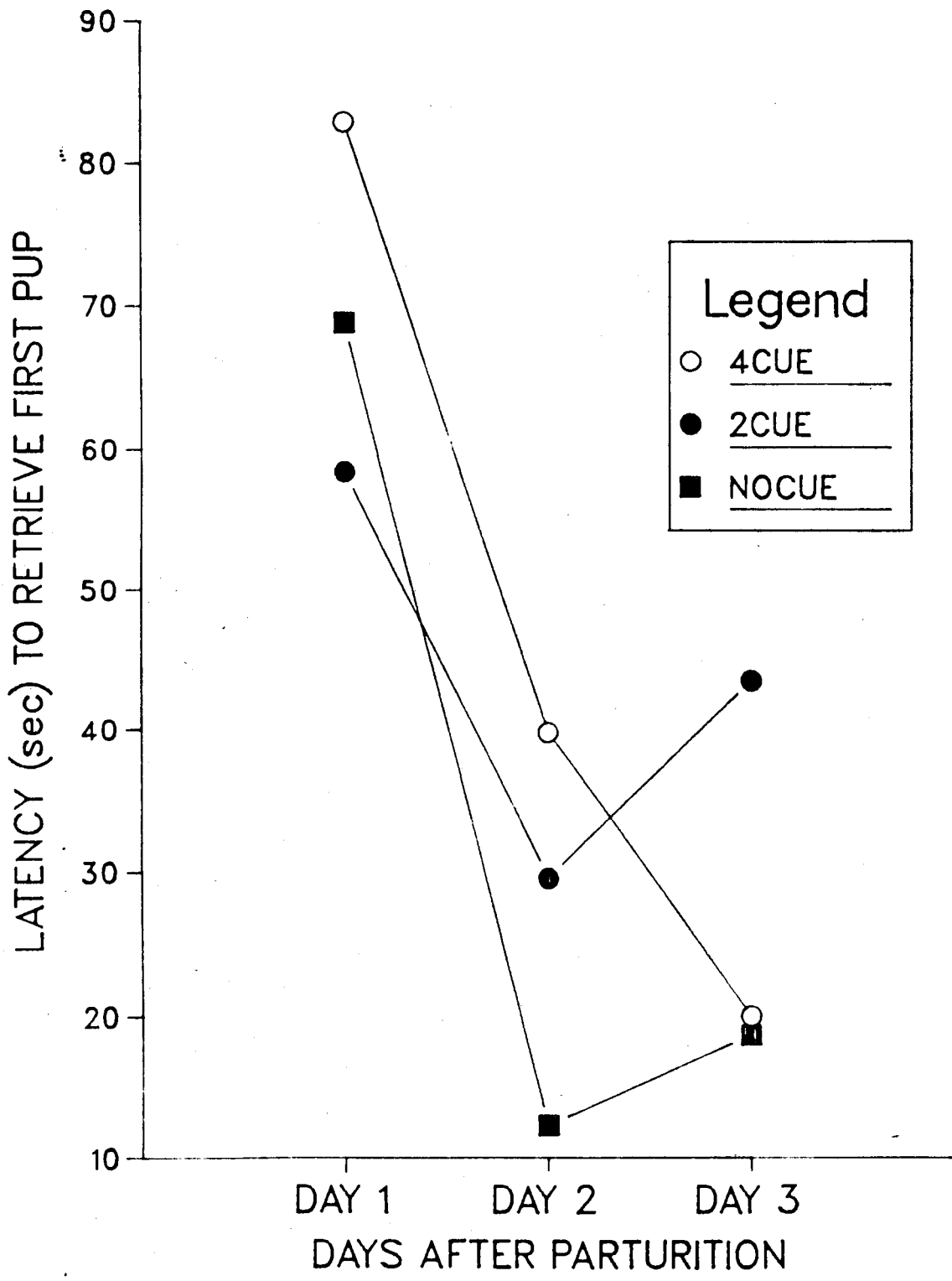


Fig. 2. Effect of day on the latency (seconds) to retrieve first pup between groups.

## Discussion

In general an appreciable amount of parental care was exhibited by the males in all groups. Males were often observed crouching over a portion of the litter in their own nest. "Pup stealing", where a male would take a pup from under the female and place it in his own nest, was not uncommon. One 4cue male and female were seen having a "tug of war" with several pups. Another 4cue male was observed helping at the birth of the litter by licking off the embryonic sacs. Virgin females have also been observed assisting at the birth of a litter (Gandelman et. al., 1970) but to my knowledge this is the first report of a male doing so.

Although most males displayed parental behaviours there were significant differences and trends in the predicted direction between the 4cue and Nocue groups. The behaviour "retrieving" was the only exception to this. Males retrieved pups almost automatically even though this may have been the first opportunity they had to retrieve. Retrievals were often clumsy at first but became more precise and efficient by the third day.

Because 2cue males did not differ significantly from either the 4cue or Nocue males it was not possible to determine which pair of cues had the greater influence on male parental care. Rather the results tend to indicate that the two pairs of cues

were of equivalent importance, assuming no interactions were present. Only further research will allow the separation of the relative effects of each factor examined in the present research.

The presence of a day effect in the data was not hypothesized but is not surprising. It seemed that both 4cue and 2cue males were 'primed' to exhibit parental behaviour while it took 0cue males longer to display these behaviours. It has been postulated that exposure to pups (Rosenblatt, 1967; Brown, 1981) or to a lactating female's urinary metabolites may induce a male to behave parentally (Elwood, 1977). Exposure to pups has been used as a method to rehabilitate infanticidal male rats (Brown, 1981). Males often lick the female's ano-genital region and ingestion of progesterone metabolites may influence their behaviour. In the present study males were also frequently observed eating feces and thus may have ingested female metabolites this way. It would certainly be to the female's advantage if she could induce parental care in unrelated males while inhibiting infanticide.

Another possible explanation for the day effect is that mating during post-partum estrus may have triggered parental care in the days after birth. Although, it seems unlikely that a male would undergo such a rapid behavioural change. One study of infanticide in male mice (vom Saal et. al., 1982) reported that to inhibit infanticide a male must have mated three weeks prior to being exposed to pups. This suggests that either the onset of

paternal behaviours is timed to begin at parturition or that it took three weeks after mating for the male to develop parental care.

No infanticide or biting a pup were observed in the formal observation periods. In general few non-parental, particularly aggressive, behaviours were observed. It is possible that these behaviours could have occurred at other times but the fact that there was not a significant decrease in litter size from birth to four days post partum argues against this possibility. It is also possible that the females protected the young from aggression by the males. Female rats demonstrate post-partum aggression (Gandelman & Simon, 1980) and are believed to "condition" males to avoid the young (Brown, 1981). Unlike the studies of infanticide in mice, where the males were tested with isolated pups (e.g., Labov, 1980), the females in this study were always present in the cage except during observation periods and therefore could have protected the pups.

The one case of infanticide by a male that I informally observed, coupled with the knowledge that I have compiled from working with these animals, does not support the likelihood of maternal protection of pups. In this case a Nogue male ate and killed approximately one half of the litter as it was being born. The female did not respond to the male's activities and made no attempt to protect or retrieve the pups to the nest as they were pulled away by the male.



Two other cases of infanticide or suspected infanticide were observed outside of the formal observation periods. One female (Nocue) ate a portion of her litter. In another case (Nocue) several bitten carcasses were found shortly after birth but there was no indication as to whether the female or male was involved. It should be noted that in all cases of infanticide observed in this lab the pups were treated as food rather than openly attacked. In general the adult picked up the pup, turned it over in its paws and began eating it, much as it would a food pellet. It seems that only juveniles and adults are attacked in an adult fashion.

In summary, the results indicated that the 4cue males displayed more parental and fewer nonparental behaviours than the Nocue males. The 2cue males were intermediate on several measures but did not differ significantly from the 4cue or Nocue males. Thus this research demonstrated that at least one of the cues of mating experience, genetic relatedness of pups, continuous cohabitation with a female or absence of the odour of strange males influences the intensity of male parental care. It was not possible, however, to determine the relative effects of the individual cues. The differences between groups were greatest the first day following parturition and then diminished on subsequent days.

The prevalence of male parental care may indicate its importance in the evolution of this species. Although no research has confirmed the function of male parental care in

house mice it is possible that a male who displays parental behaviours may increase the survival of his offspring by maintaining their body temperature, retrieving them should they stray from the nest, stimulating and cleaning them and by staying in the nest to perhaps protect them from conspecific as well as extra specific intruders. Future longitudinal research might begin to address the question of the specific adaptive benefit of paternal care in this species.

APPENDIX A

Table 1. Significance tests for interobserver reliability.

Behaviour <sup>a</sup>	Reliability <sup>b</sup>	Significance level
Licking	0.78	$p \leq 0.02$
Retrieving	0.99	$p \leq 0.01$
Covering	0.99	$p \leq 0.01$
Nesting	0.99	$p \leq 0.01$
Nursing	0.99	$p \leq 0.01$
Active	0.96	$p \leq 0.01$

<sup>a</sup> The total duration of each behaviour, except "retrieving", was used in the computations. Latency to retrieval of first pups was examined in this test instead of total duration. (N=25)

<sup>b</sup> Pearson coefficient of correlation.

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