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# Effects of Experience on the Parental Responses of Male Mongolian Gerbils

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***ABSTRACT:*** *We examined responses of adult male Mongolian gerbils to nest site and young during the hours preceding and days following birth of a litter. We found that (a) male attendance at the nest site was markedly reduced for several hours following the birth of pups; (b) this lack of contact by males with nest and pups did not result from active exclusion of males from the nest by their mates; (c) males lacking previous experience of pups, but not those familiar with pups, avoided contact with pups on the day of their birth; and (4) 3-day-old gerbil pups were attractive even to males encountering young for the first time.* *© 2000 John Wiley & Sons, Inc.* Dev Psychobiol 36: 177–185, 2000

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## INTRODUCTION

Most female rodents rear their young without assistance, but in some rodent species males exhibit all of the caregiving activities performed by conspecific females, except for lactation (for reviews, see Brown, 1986, 1993; Carter & Roberts, 1997; Elwood, 1983; Gubernick, 1994; Hartung & Dewsbury, 1979; Wang & Insel, 1996). Even in those rodent species in which males exhibit extensive parental care, males may spend little time in contact with newborn young and usually take hours or days to achieve levels of nest attendance comparable to those of their mates (Clark & Galef, 1999; Elwood, 1975; McCarty & Southwick, 1977; Priestnall & Young, 1978).

Two explanations have been proposed for the relatively infrequent attendance of males at nests containing newborn young. First, females of some species eject males from the nest site before or during parturition, and may prevent males from contacting neonates (Eisenberg, 1962; Elwood, 1975; McGuire, 1997; Mennella & Moltz, 1988; Oliveras & Novak, 1986; Solomon, 1992; Storey, Bradbury, & Joyce, 1994). In other species in which fathers do not interact with neonatal young, they, like virgin female rats (Fleming & Luebke, 1981; Fleming & Rosenblatt, 1974; Mayer & Rosenblatt, 1979), seem to find conspecific neonates aversive and avoid contact with them (Clark & Galef, 1999).

We have recently reported that male Mongolian gerbils, *Meriones unguiculatus*, are seldom present in their nest on the day young are born, but on subsequent days spend almost as much time in the nest with young as do their mates (Clark & Galef, 1999). Our informal observations suggested that female gerbils neither expelled males from nest sites before parturition nor interfered with their mates' entering nests containing newborn young. Rather, males approached the nest

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containing neonates, sniffed at them, and then withdrew rapidly, responding to neonates as though they were novel objects (which gerbils invariably approach and explore) that emitted an aversive odor.

In the present series of studies, we first describe systematic observations that confirm our informal finding that infrequent attendance by adult male gerbils at nests containing neonates reflects male avoidance of newborn young on the day of their birth, not female exclusion of males from the nest (Experiment 1). We then provide experimental evidence that (Experiment 2) male avoidance of contact with neonates is mitigated by previous experience with young, and (Experiment 3) that stimuli emitted by neonates, but not by older pups, are aversive to males lacking previous experience of conspecific young.

## EXPERIMENT 1: OBSERVATION OF PATERNAL BEHAVIOR DURING THE HOURS SURROUNDING BIRTH OF A LITTER

In Experiment 1, we used time-lapse videography during the hours immediately preceding and following birth of a litter to examine attendance of mated pairs of Mongolian gerbils at nest sites containing young. We also observed mated pairs directly to determine their behavior toward pups during the week following birth of young. The purposes of this first experiment were both to confirm our previous observation of infrequent attendance by male gerbils at nests containing neonates, and to determine whether this infrequent contact of fathers with neonates resulted from recently parturient females actively excluding males from nest sites.

### Method

***Subjects.*** Thirteen male and 13 female adult Mongolian gerbils randomly selected from 24 litters born and reared in the vivarium of the McMaster University Department of Psychology to descendents of breeding stock acquired from Tumblebrook Farm (Brookfield, MA) served as subjects.

We weaned subjects at 32 days of age and placed them in same-sex groups of 3 or 4 in opaque polypropylene cages (35 × 30 × 15 cm) housed in a temperature- and humidity-controlled colony room brightly lit for 12 hr/day (light onset at 0500 hr) and, to permit videography, illuminated with three 40-W, red light bulbs during the "dark" portion of the cycle.

Throughout life, subjects had ad libitum access to pellets of Purina Rodent Laboratory Chow 5001 (Ralston-Purina, Woodstock, Ontario) and tap water.

***Apparatus.*** During the experiment, subjects lived in opaque, polypropelene, shoe-box cages measuring 35 × 30 × 15 cm. The top of each cage was closed with ½-in. (1.3-cm) hardware cloth, and its floor was covered with a layer of wood-chip bedding. At the appropriate time (see Procedure), we placed a nest box measuring 28 × 12.7 × 12.7 cm at one end of each shoe-box cage (Figure 1). Each nest box, constructed of transparent Plexiglas and divided into two identical compartments by a 12.7 cm square transparent Plexiglas partition, had two entrance holes, 5 cm in diameter, that permitted subjects direct access into nest-box compartments from the 23.3 × 30 cm open area in each cage. A third 5 cm diameter opening cut at the top of the partition dividing the nest box into separate compartments permitted adults to pass directly from one compartment to the other. Hinged lids of transparent Plexiglas allowed the experimenter access to each compartment of the nest box, and holes drilled through these lids provided ventilation within the nest box. When we placed a nest box in a shoe-box cage, we also provided 5 g of cotton batting for use as nesting material.

***Procedure.*** When each female subject was 60 days old, we placed her together with a virgin adult male in a shoe-box cage and noted the date on which the pair first copulated with the expectation that a female would deliver a litter 25 days after we saw her mate.

Ten days before the expected day of delivery of each dam's litter, we placed a nest box and nesting material in her cage and, to facilitate individual identification during subsequent observations, shaved a small patch of fur from the back of her mate.

For 24 hr before and 24 hr after an expected delivery, a time-lapse videocassette recorder with a time–date generator (Panasonic AG 6720) continuously recorded the behavior of each pair at one-fourth real time. We considered the time at which an observer reviewing the videotape first saw a newly delivered pup to be the moment of parturition. All videorecordings for the 6 hr preceding and 7 hr following this event were scored for (a) seconds that the male and female spent either together or alone in the chamber of the nest-box containing, at first the nest and, after parturition, the nest and young; (b) the number of times a male entered the nest-box chamber containing the nest or nest and young; (c) the number of times the male partially entered that nest chamber (inserted only his head and forelimbs through the entrance and immediately withdrew), and any instances of aggres-

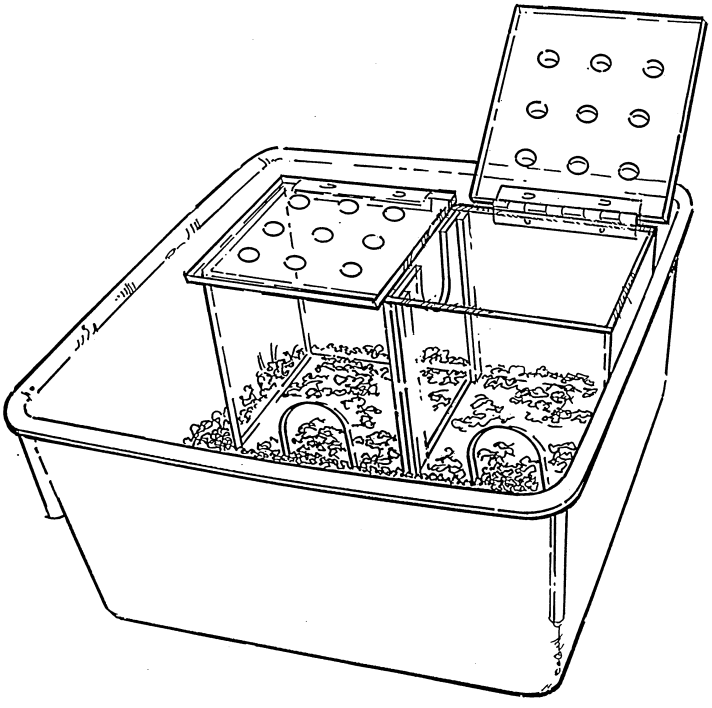

**FIGURE 1** Multichambered home cages used in the experiments.

sion (fighting, chasing, wrestling) directed by the female toward the male.

Four hours after light onset, on each day from the day of birth of a litter (Day 1) to Day 7 postpartum, an experimenter directly observed each pair and recorded once each 20 s, for 15 consecutive min, whether each adult was present in the compartment of the nest box containing the litter. Though brief, such 15-min samples of behavior are sufficiently sensitive to detect differences in the parental behavior of males in different hormonal states (Clark & Galef, 1999).

## Results and Discussion

The main results of Experiment 1 are shown in the left panel of Figure 2 which presents data describing the time male and female gerbils spent in the nest-box compartment containing the nest during the 6 hr preceding and 7 hr following the moment of parturition. During the hours preceding birth of young, males and females were frequently seen together in the nest, and males were as likely to be seen there alone as were females.

At the time of parturition, male presence in the nest dropped precipitously and remained low for the following 7 hr. Female attendance at the nest increased for 3 hr following parturition (the time we estimate was required for delivery of a litter of seven young), and then gradually returned to baseline levels.

The right panel of Figure 2 shows the mean percent of 45 observations (15 min $\times$ 3 observations/min) that male and female gerbils were in the nest-box compartment containing nest and litter on each of the 7 days following parturition. As is evident from examination of the panel, and as reported in Clark and Galef (1999), males made contact with pups infrequently on the day of their birth and on subsequent days males were in contact with pups with roughly the same frequency as were dams.

As can be seen in Figure 3, which shows the number of times that males both entered and withdrew after partially entering the nest-box chamber containing the nest, parturition resulted in males making numerous partial entrances, a behavior not seen before parturition and one that returned to baseline during the 7 hr following parturition. In reviewing videotapes of perinatal behavior, we did not see females chase or attack their mates, and we did not see any indication of behavior on the part of females that interfered with males approaching the nest and young. Rather, males seemed to be repelled by something they encountered in the nest during the hours immediately following parturition.

Informal observations were consistent with the hypothesis that females were not motivated to prevent their mates from contacting neonatal young and that males found either neonatal young or recently parturient females aversive. Shortly after delivery, 3 fe-

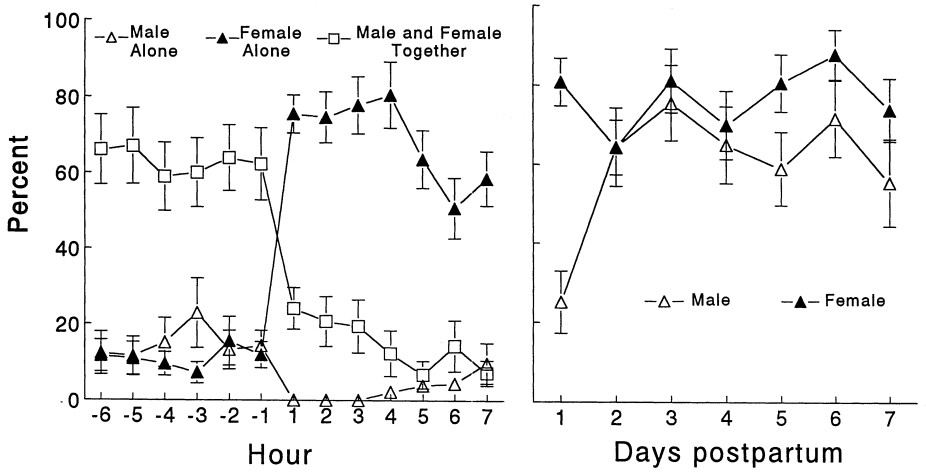


**FIGURE 2** Left panel: Mean percent of each hour surrounding the moment of parturition that male and female gerbils were either alone or together in the nest-box compartment containing the nest and litter. Right panel: Mean percent of 45 intervals during which male and female were in the nest-box compartment containing pups and litter on the day of parturition (Day 1) and subsequent days. Flags = ±1 *SEM*.

males transported their litters from the nest-box compartment where they had delivered to the nest site compartment that their consort was occupying. Two of the 3 males immediately left the compartment into which the female had moved her litter and took up residence in the compartment that had previously contained the nest.

Although our observations suggest that males were actively avoiding neonates during the hours following their birth, observation alone is not sufficient to rule out the possibility that some unobserved stimuli emitted by females caused males to avoid contact with the nest site and young. The question of whether neonatal pups are aversive to male gerbils is addressed directly in Experiment 2.

## EXPERIMENT 2: EFFECTS OF PREVIOUS EXPOSURE TO PUPS ON RESPONSE TO NEONATES

If males' initial failure to contact neonates and subsequent increased frequency of contact with maturing young result from avoidance of unfamiliar, unattractive stimuli emitted by neonates followed by a gradual habituation to those stimuli (Fleming & Rosenblatt,

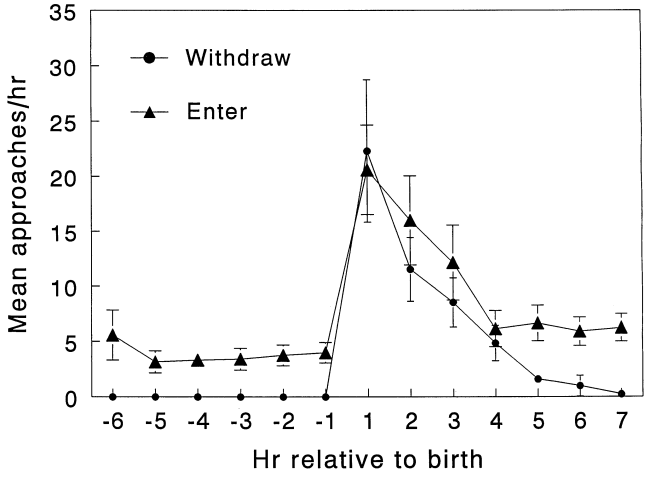


**FIGURE 3** Mean number of times during each hour surrounding delivery of a litter that males approached and either entered the nest-box compartment containing the nest and litter or withdrew after partially entering. Flags = ±1 *SEM*.

1974; Mayer & Rosenblatt, 1979), then males with previous exposure to pups should be less likely to avoid neonates than males lacking previous experience with pups. To the contrary, if recently parturient females exclude males from the nest site and thus prevent them from contacting neonates, or if recently parturient females are themselves unattractive to males, then previous exposure of males to pups should have no effect on males' frequency of contact with neonates.

## Method

***Subjects.*** Twenty-six male Mongolian gerbils from 26 litters born and reared in the vivarium of the McMaster University Psychology Department served as subjects. Each male was reared in a standard shoe-box cage by a mated pair of gerbils as part of a foster litter of 8 pups given to the pair on the day of birth of their own litter.

***Exposure.*** When the foster litter each pair was rearing was 32 days old, we removed the adult male and 7 of the pups for use in other experiments, and left 1 randomly selected male with his foster mother.

Twenty-four hours before the female in each pair was due to deliver the litter she had conceived in postpartum estrus (Female gerbils impregnated in postpartum estrus exhibit substantially delayed implantation.), we placed a ½-in. (1.3-cm) hardware-cloth partition between the subject male and his foster mother. As soon as the female delivered her litter, we removed the partition and the female's litter from the cages holding half the male subjects and the partition from the cages holding the remaining male subjects.

After removal, we left cage residents undisturbed for 1 week, and then placed each male subject in a cage with 2 or 3 other males.

***Observations.*** When each male subject was 70 days old, we placed him in the cage of an unfamiliar virgin female but separated from her by a hardware-cloth partition. Twenty-four hours later, we removed the partition and, when the female was conspicuously pregnant, a dual-chambered nest box (see Figure 1) and nesting material in the cage with the pair.

On each of the 7 days following parturition, an experimenter who was unaware of the group assignment of males observed males and their mates. The observer recorded on each day, once each 20 s for 15 min, whether each adult was in the nest box in physical contact with one or more members of its foster litter (Clark, Vonk, & Galef, 1998).

***Choice between nest and pups.*** On the day pups in a litter were born, 2 hr after the 15-min period of observation had ended, we tested either 6 or 7 of the male subjects assigned to each of the two conditions for their preferences between pups and nest site.

To perform a preference test, we first moved both adults to a holding cage, then removed the litter a pair was rearing and replaced it with 8 neonates born to a female in our breeding colony. We then placed the male in the open area of its home cage, facing away from the nest box, and waited 5 min. During the following 30 min, an observer who was unaware of the group assignment of male subjects recorded the time the male spent in the nest-box compartment containing the pups and nest and in the empty nest-box compartment.

We awarded each male a preference score calculated by dividing the time that he spent in the nest-box compartment with the pups by the total time that he spent in both nest-box compartments.

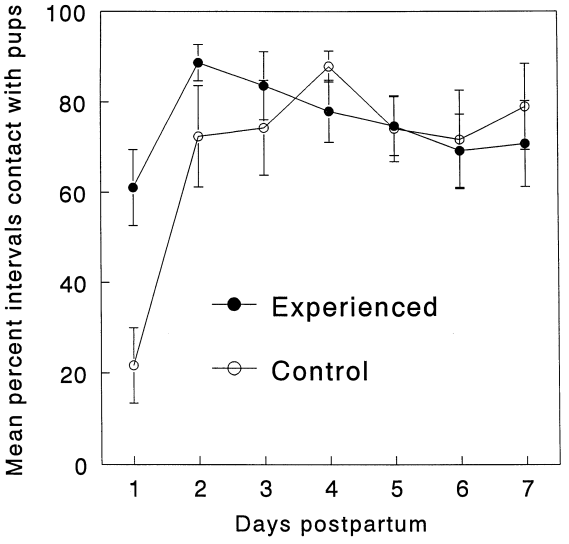


**FIGURE 4** Mean percent of intervals that males with previous experience of pups and control males spent in the nest-box compartment containing nest and litter. Flags = ±1 *SEM*.

## Results

Data from one pair was lost when the litter they were rearing died.

The main results of Experiment 2 are presented in Figure 4, which shows the mean percent of 20-s intervals that males previously exposed to pups and males lacking exposure to pups were observed in the nest box containing the pups and in contact with the young. As can be seen in Figure 4, on the day of parturition (Day 1), males that had been exposed to pups spent significantly more time than did males lacking

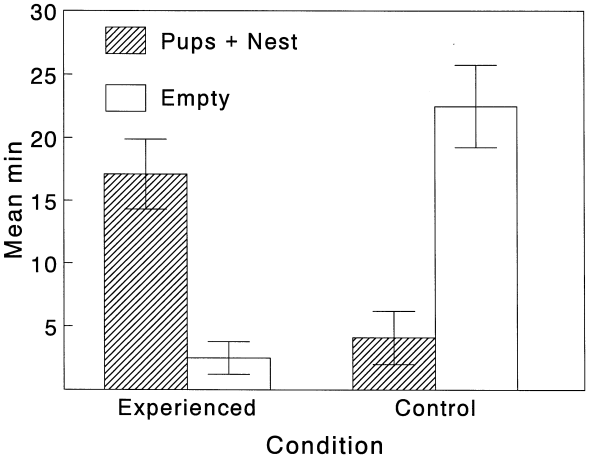


**FIGURE 5** Mean number of min out of 30 that males with previous exposure to pups and control males spent in contact with strange neonates. Flags = ±1 *SEM*.

previous exposure to pups in contact with newborn young, Student's *t* test, $t(23) = 3.44$, $p < .003$.

A between groups, within subjects ANOVA revealed that, when data from Day 1 were excluded from the analysis, males with and without previous experience with pups spent equivalent amounts of time in contact with them, $F(1, 23) = .02$, n.s. During days 2 to 7 of observation there was no main effect of days, $F(5, 115) = .825$, n.s., nor any interaction between group assignment and days, $F(5, 115) = .96$, n.s.

The results of our determination of males' preferences between nest compartments on Day 1 are presented in Figure 5, which shows the mean number of min out of 30 that males spent in the two nest compartments, one containing nest and pups, the other empty. As can be seen in Figure 5, during the 30-min test, males that had previous experience with pups spent more time in the nest-box compartment containing the nest and neonates than in the empty nest-box compartment whereas males lacking previous experience of pups spent more time in the empty nest-box compartment than in that containing the nest and litter; a between conditions, within subjects ANOVA revealed a significant Conditions × Nest Chamber interaction, $F(1, 11) = 34.11$, $p < .0003$.

Because females were not present in the test situation during determination of males' preferences, this measure provides strong evidence that males' failure to contact neonatal pups is not dependent on either activities of females or stimuli emitted by them.

When we repeated the choice test using another sample of 10 adult males that lacked previous experience of pups and offered them the opportunity to choose for 30 min between an empty nest-box chamber and one containing just the nest (without pups or dam), the subjects spent an average of 13.9 ± 2.8 min in the nest-box chamber containing the nest and 7.9 ± 2.9 min in the empty nest-box chamber, matched-pairs *t* test, $t(9) = 1.16$, n.s. Clearly, males find neonatal pups unattractive, not the nest holding them.

### Discussion

The results of Experiment 2 showed that exposure of adult male gerbils to conspecific pups affected the willingness of males' to contact pups on the day of their birth, but had no effect on males' subsequent parental behavior. The data are consistent with the hypothesis that male avoidance of pups on Day 1 and subsequent attendance to pups reflects males' response to unfamiliar, aversive stimuli emitted by pups and rapid habituation of males to those stimuli.

The results of the present experiment are also consistent with results of previous work showing (a) that female rats exposed, as adolescents, to neonatal pups show shorter latencies to induction of maternal behavior than do those lacking such adolescent experience (Moretto, Paclik, & Fleming, 1986; Stern & Rogers, 1988), and (b) that prairie voles with alloparenting experience display higher levels of parental care in their first reproductive effort than do control animals lacking such experience (Wang & Insel, 1996).

Alloparental care by older siblings of a litter conceived in postpartum estrus is common in rodents (Gilbert, Burgoon, Sullivan, & Adler, 1983; Ostermeyer & Elwood, 1984; Powell & Fried, 1992; Solomon, 1991) and, as Salo and French (1989) have proposed, may facilitate expression of parental behavior and thus affect reproductive success.

## EXPERIMENT 3: RESPONSES OF MALES WITH DIFFERENT EXPERIENCE OF PUPS TO PUPS OF DIFFERENT AGES

The results of Experiment 2 showed that exposure of males to pups decreased males' avoidance of newborn young. This finding suggests that the observed increase in males' attendance to pups in the days after their birth may result from exposure of males to pups during the day of their birth and consequent habituation to whatever aversive stimuli pups emit (Storey & Joyce, 1995; Storey & Walsh, 1994). However, it is also possible that as pups mature they cease to emit stimuli that are aversive to males. In the present experiment, we examined effects of both males' previous

experience of young and pup age on males' attendance at the nest.

## Method

***Subjects.*** Forty male and 40 female Mongolian gerbils born and reared in the vivarium of the McMaster University Psychology Department to breeding pairs acquired directly from Tumblebrook Farms served as subjects.

***Apparatus.*** The apparatus was that used in Experiments 1 and 2.

***Procedure.*** Subjects were reared, mated, and housed as described in Experiment 1. When 60 days of age, each male was mated with a female and randomly assigned to one of four groups in a 2 × 2 design ($n$ = 10/group). We tested independent groups of males either on the day of birth of the litter they fathered or on the 3rd day after birth of that litter for their preference between an empty nest-box chamber and one containing a nest and either an unfamiliar newborn litter or an unfamiliar litter of 3-day-old pups.

To begin a test session, we removed both parents from their home cage, placed them in a holding cage, removed the pair's litter to a separate holding cage, and placed in the nest another litter of either neonates or 3-day-old pups taken from a breeding pair in our colony. We then returned the adult male to his home cage and waited 5 min. During the subsequent 30 min, an observer who was unaware of the design of the experiment recorded the amount of time that the male spent in each nest-box compartment, one containing the nest and unfamiliar pups, the other empty.

## Results and Discussion

The main results of Experiment 3 are presented in Figure 6, which shows the minutes that fathers of newborn and 3-day-old litters spent in the two chambers of the nest box, one containing a nest and unfamiliar young, the other empty. As can be seen in Figure 6, both a male's experience with pups (Compare upper and lower panels of Figure 6.) and the age of the pups with which a male was tested (Compare striped and open bars in the upper panel of Figure 6.) had pronounced effects on males' attendance to young. There were significant main effects of both pup age and fathers' experience with pups on the percentage of time fathers spent in the nest-box compartment containing the young, $F$s(1, 36) > 8.04, $p$s < .007.

As can be seen in the lower panel of Figure 6, all males found unfamiliar, 3-day-old conspecific young

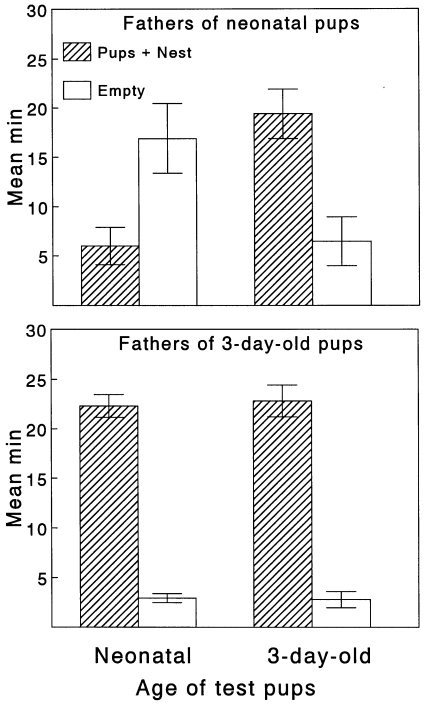


**FIGURE 6** Mean number of min out of 30 that fathers of 3-day-old litters and fathers of newborn litters spent in the nest-box compartment containing a nest and neonatal or 3-day-old pups. Flags = ±1 *SEM*.

attractive whereas, as can be seen in the upper panel of Figure 6, only males that had interacted with their own young for 3 days found unfamiliar, newborn young attractive.

It remains possible that mating with a female in postpartum estrus changes the behavior of males toward young (Huck, Soltis, & Coopersmith, 1982; Menella & Moltz, 1988). That possibility was not excluded in fathers of 3-day-old pups in the present experiment, and remains to be explored. On the other hand, when we tested fathers of neonatal pups, their mates had not yet come into postpartum estrus and males had not mated with them, thus preferences of fathers of newborn young for 3-day-old young could not have been a consequence of mating with females in postpartum estrus.

# GENERAL DISCUSSION

Most information concerning parent–young interaction in rodents is based on studies of the behavior of mothers toward their offspring. Only relatively recently has male care of young received the same attention as have mother–infant relations.

In both the California mouse (*Peromyscus californicus*; Gubernick & Alberts, 1987) and dwarf hamster (*Phodopus campbelli*; Jones & Wynne-Edwards, in press; Wynne-Edwards, 1995), males may exhibit all parental activities, except for lactation, to the same extent as do females. In other rodent species, such as southern grass-hopper mice, *Onychomys torridus* (McCarty & Southwick, 1977) and the Mongolian gerbils whose parental behavior is described in this study, in Elwood (1975), and in Clark and Galef (1999) (a) males are almost as attentive to young as are females throughout some of lactation, but (b) do not participate in the birth process as do male *P. californicus* and *P. campbelli*, and (c) take hours or days before they start to interact with juveniles with approximately the same frequency as do females.

The results of Experiment 1 indicate that, contrary to Elwood's (1975) suggestion based on informal observations, delay in onset of paternal behavior in male Mongolian gerbils does not result from exclusion of males from the nest site by recently parturient females. Rather, males avoid unfamiliar stimuli emitted by newborn pups.

The results of Experiments 2 and 3 indicate that the increase seen in male attendance to young in the nest in the days following parturition is a result both of habituation of males to the stimuli emitted by pups and to age-related changes in pups that make them acceptable to adult males. Thus, in adult male Mongolian gerbils, as in virgin female Norway rats (Fleming & Rosenblatt, 1974), emergence of parental behaviors appears to depend both on habituation to aversive stimuli emitted by conspecific young and changes in the stimuli that are emitted by the young themselves.

## NOTES

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