



# Mongolian gerbil fathers avoid newborn male pups, but not newborn female pups: olfactory control of early paternal behaviour

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We examined effects on the parental behaviour of male Mongolian gerbils, *Meriones unguiculatus*, of the sex and number of pups in a litter. Recent fathers interacting with foster litters consisting entirely of newborn males decreased the time that they spent in contact with a litter the greater the number of pups it contained. However, fathers that interacted with litters composed entirely of newborn females showed no change in the time they spent in contact with a litter as a function of its size. Fathers responded similarly to litters of 1- and 3-day-old female pups, but their responses to male pups changed from avoidance to approach as the age of males increased from 1 day to 3 days, and fathers made anosmic by intranasal administration of zinc-sulfate solution did not avoid neonatal litters. Results of a correlational study revealed that the more time males spent with newborn young during a 30-min test, the greater their latency to mate with their partners in postpartum oestrus and the shorter the duration of their mating effort during the 24 h immediately after parturition. We discuss these findings as consistent with the view that androgen-mediated olfactory stimuli produced by newborn male Mongolian gerbils make them unattractive to fathers, possibly functioning to increase the time that recent fathers mate-guard while their partners are in postpartum oestrus.

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On the day that a litter of Mongolian gerbils, *Meriones unguiculatus*, is born, the father spends far less time in the nest with the young than does the mother (Elwood 1975; Clark & Galef 1999). This delay in onset of paternal behaviour is not a result of recently parturient females excluding their mates from the nest site (Clark & Galef 2000). Rather, male Mongolian gerbils, like virgin female rats (Fleming & Rosenblatt 1974), appear to find conspecific neonates aversive and are reluctant to approach a nest containing a newborn litter (Clark & Galef 2000).

To a human observer, the appearance and behaviour of newborn and 3-day-old gerbil pups are quite similar. However, fathers' avoidance of their young ends before the young are 3 days of age, and from day 3 postpartum to weaning, gerbil fathers spend almost as much time with their young as do mothers (Clark & Galef 2000; Clark et al. 2001).

Around the time of birth, newborn male gerbils (Probst 1987), like the young of many other mammalian species (e.g. rats: Corbier et al. 1978; vom Saal et al. 1992; mice:

Jean-Faucher et al. 1978; ferrets: Erskine et al. 1988), experience an endogenous surge in testosterone (T) that results in their having T titres as high as those seen in adult males of their species. Circulating levels of T in neonatal males peak within 2–4 h following birth (Rhoda et al. 1984; Erskine et al. 1988) and return to more moderate levels within 2–3 days (vom Saal et al. 1992).

Perinatal elevation of T titres affects sexual differentiation in mammals (e.g. Corbier et al. 1983; Roffi et al. 1987), and can therefore alter stimulus characteristics of young that might mediate any differences in parental responses to sons and daughters (reviewed in Moore 1995). For example, mother rats (Moore & Morelli 1979) and mother gerbils (Clark et al. 1990) lick the anogenital areas of sons more frequently than they lick those of daughters, and injecting daughters with T induces mother rats to treat daughters as they treat sons (Moore 1982).

In biparental species, such as the Mongolian gerbil, fathers, like mothers, might be expected to be sensitive to the endocrine status of the young that they assist in rearing (Clark et al. 1990). If so, fathers should respond differently towards sons than towards daughters, and possibly respond differently towards neonatal sons

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undergoing the postnatal elevation in circulating levels of T than towards older sons whose T titres have declined to lower levels (Clark & Galef 2000).

In the present series of experiments, we first examined responses of adult male Mongolian gerbils whose mates had recently delivered litters to both male and female neonates (experiment 1). We then established the role of pup age (experiment 2) and of olfactory stimuli produced by pups (experiment 3) in mediating responses of recent fathers to young. Last (experiment 4), we took a first step in evaluating possible reproductive consequences of variation in the time that fathers spend with newborn litters.

### EXPERIMENT 1: EFFECTS OF NUMBER OF NEWBORN YOUNG ON PARENTAL BEHAVIOUR OF FATHERS

If avoidance of newborn young by Mongolian gerbil fathers (Clark & Galef 2000; Clark et al. 2001) is a response to T-mediated stimuli produced by male neonates, then fathers might be expected to avoid litters composed of males, but not litters composed of females. Furthermore, fathers might be expected to show greater avoidance of all-male litters as a function of an increase in the number of pups they contain, but not to show comparable increased avoidance of all-female litters as they increase in size.

#### Methods

##### Subjects

Subjects were 125 male and 125 female Mongolian gerbils taken from 110 litters born and reared in the vivarium of the McMaster University Department of Psychology to third-generation descendants of breeding pairs acquired from Charles River Breeding Farms (Wilmington, Massachusetts, U.S.A.). All subjects resided in a single temperature- and humidity-controlled colony room illuminated on a 12:12 h light:dark cycle with light onset at 0500 hours.

We weaned subjects at 32 days of age, and placed them in same-sex groups of three or four in opaque polypropylene shoebox cages (35 × 30 × 15 cm). The top of each cage was closed with a 0.5-in (1.26-cm) hardware-cloth lid, and its floor was covered with a layer of wood-chip bedding. Throughout life, all subjects had ad libitum access to tap water and pellets of Purina Rodent Laboratory Chow 5001 (Ralston-Purina, Woodstock, Ontario, Canada).

##### Apparatus

During the experiment, adult subjects lived as mated pairs in cages identical to those in which they had resided earlier in life. At the appropriate time (see Procedure), we placed at one end of each cage a nestbox (28 × 12.7 × 12.7 cm), constructed of transparent Plexiglas (Fig. 1). Nestboxes, divided into two identical compartments by a 12.7-cm square transparent Plexiglas partition, had two entrance holes, each 5 cm in diameter, that allowed subjects access to compartments from the

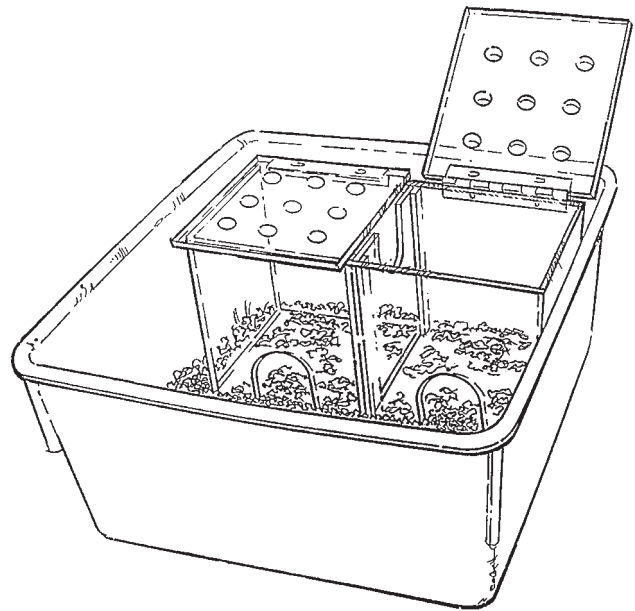


Figure 1. Multichambered cages used in experiments.

23.3 × 30-cm open area in each cage. A third 5-cm diameter opening was cut into the top of the partition dividing the nestbox into separate compartments, that permitted adults, but not pups, to pass directly from one compartment to the other. Hinged lids of transparent Plexiglas gave experimenters access to each compartment, and holes drilled through these lids provided ventilation within the nestbox. When we placed a nestbox into a cage, we also provided 5 g of paper toweling for subjects to use as nesting material.

##### Procedure

**Breeding.** When a female reached 60 days of age, we placed her in a shoebox cage together with an unrelated, virgin male. We noted the date on which the pair first copulated, expecting females to deliver a litter 25–26 days after we saw them mate.

Ten days before the expected date of delivery of a female, we placed a nestbox and nesting material in her cage. We subsequently examined each cage twice daily at 0800 and 1600 hours to identify the date of birth of her litter (day 1), which we defined as the day when we first saw a litter in a cage.

**Preference testing.** Between 0800 and 1100 hours on day 1, we tested each father's preference between the empty nestbox compartment and the nestbox compartment containing the nest built by a pair. To perform a preference test, we first removed both adults from their home cage to a holding cage, then removed their litter to a separate holding cage. Next, we placed into the nest either nothing ( $N=20$  males), one neonate ( $N=30$  males), three neonates ( $N=30$  males) or six neonates ( $N=45$  males).

Forty-five males presented with pups in the test situation received all-male litters, 45 received all-female litters and 15 received litters composed of three male and

three female pups. The 20 males that had no pups added to their nest chose between a nestbox compartment containing an empty nest and a nestbox compartment with neither nest nor pups. To facilitate subsequent statistical analyses, we randomly assigned 10 males that had no pups added to their nests to a 'no-male neonates' condition and the remaining 10 to a 'no-female neonates' condition.

After we had made the appropriate adjustment to nest contents, we placed the male member of each pair in the open area of his home cage, facing away from the nestbox. During the next 30 min, an observer who was unaware of the sex of any pups in a nest recorded the time that the male spent in each nestbox compartment.

### Statistical analysis

To assess effects of the contents of a nestbox compartment on a male's preference, we divided the time that each male spent in the nestbox compartment containing the nest and young (if any) by the total time he spent in both nestbox compartments and multiplied the result by 100. To assure homogeneity of variance, before undertaking statistical analyses, we arcsine transformed these percentage scores

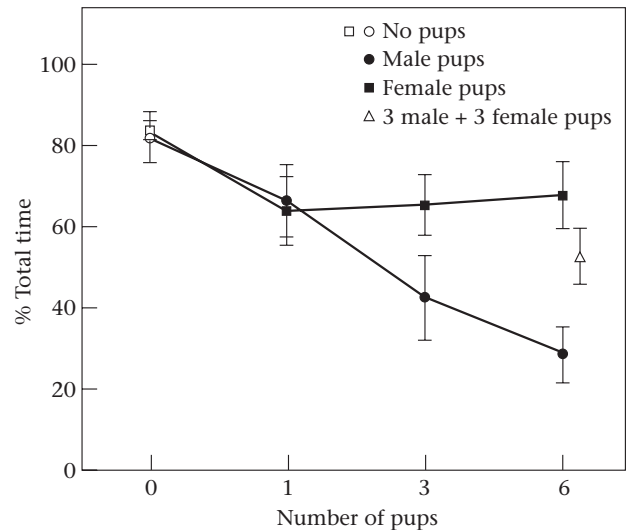
## Results and Discussion

### Effects of number and sex of pups in a litter

The mean  $\pm$  SE total time that males assigned to the various groups spent in both nestbox compartments ranged from  $17.5 \pm 2.0$  min to  $21.3 \pm 1.3$  min, and did not differ as a function of either the number (ANOVA:  $F_{3,102}=1.93$ , NS) or sex of pups in the litters ( $F_{1,102}=0.47$ , NS) that we had introduced into nests. However, males' preferences for the nestbox compartment containing a nest and/or pups was significantly affected by both the number ( $F_{3,102}=5.86$ ,  $P<0.002$ ) and sex ( $F_{1,102}=6.06$ ,  $P<0.02$ ) of pups in the nest, and there was a significant interaction between these main effects ( $F_{3,102}=2.95$ ,  $P<0.04$ ) resulting from fathers' preferences for male (linear trend analysis:  $F_{1,42}=19.10$ ,  $P<0.0001$ ), but not for female pups ( $F_{1,42}=0.55$ , NS), decreasing as the number of pups in a nest increased (Fig. 2).

### Response to litters containing pups of both sexes

We found no effect of sex ratio of litters on the mean total time that males spent in both nestbox compartments in the three groups in which one nestbox compartment held the nest and six pups ( $F_{2,42}=0.30$ , NS). However, we did find a significant effect of litter sex ratio on the percentage of time that males spent in the nestbox compartment containing the nest and pups ( $F_{2,42}=7.70$ ,  $P<0.002$ ; Fig. 2). Males choosing between an empty nestbox compartment and a nestbox compartment containing six male pups spent a smaller percentage of the test time in the nestbox compartment containing the pups than did males choosing between an empty nestbox compartment and one containing three male and three female pups (Dunnett's Multiple-Comparison test:  $q=2.49$ ,  $P<0.05$ ; Fig. 2). On the other hand, males



**Figure 2.** Mean  $\pm$  SE time that adult male subjects in experiment 1 spent in the nestbox compartment containing a nest or nest and pups as a percentage of the total time that they spent in both nestbox compartments.

choosing between an empty compartment and a compartment containing a nest, three male and three female pups spent as much time in the latter compartment as did males choosing between an empty compartment and a nest containing three male pups ( $q=1.38$ , NS; Fig. 2). Apparently, number of male pups in a litter, rather than total number of pups in a litter, determined a male's preference for that litter.

## EXPERIMENT 2: EFFECTS OF AGE OF PUPS ON FATHERS' RESPONSES TO THEM

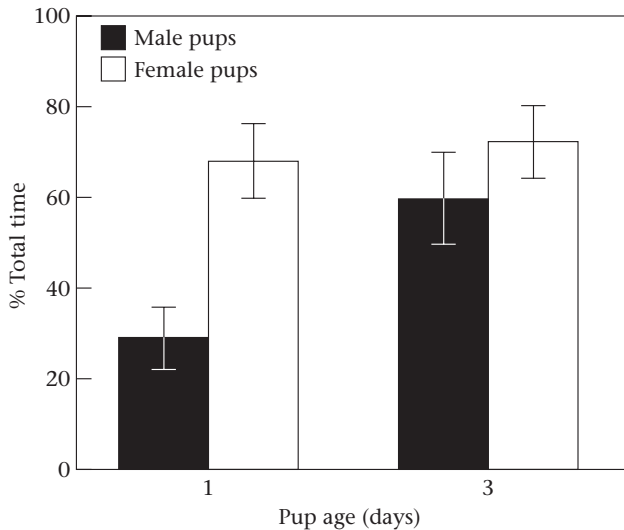
Our previous experiments with Mongolian gerbils have shown that recent fathers, although avoiding a nest containing a litter of neonates, are attracted to a nest containing 3-day-old pups (Clark & Galef 2000). If this change in fathers' response to young reflects a change in their response to male pups as they increase in age, then the response of recent fathers to male, but not to female, pups should change as pups increase in age.

We randomly assigned adult males to experiments 1 and 2 at the same time to permit statistical comparisons between subjects in the two experiments. Experiments 1 and 2 are presented as separate experiments only to facilitate exposition. In experiment 2, we tested recent fathers' preferences between an empty nestbox compartment and a nestbox compartment containing either six male or six female pups when those pups were 3 days of age.

## Methods

### Subjects

Subjects were 30 adult male gerbils whose mates had given birth within 24 h and 90 3-day-old pups of each sex served as stimuli.



**Figure 3.** Mean  $\pm$  SE time that adult male subjects in experiment 2 spent in the nestbox compartment containing a nest and pups as a percentage of the total time that they spent in both nestbox compartments when pups were 3 days of age. Data from fathers in experiment 1 that chose between an empty nestbox compartment and one containing either six newborn males or six newborn females are included for comparison.

#### Apparatus and procedure

The apparatus and procedure were the same as those used in experiment 1 except that we tested responses of 30 fathers to nests containing either six 3-day-old males or six 3-day-old females rather than to six neonatal pups. We compared the behaviour of these 30 fathers with that of the 30 fathers in experiment 1 that chose between an empty nestbox compartment and one containing either six newborn male or six newborn female pups.

#### Results and Discussion

The time that fathers assigned to the four groups spent in both nestbox compartments ranged from  $18.3 \pm 1.98$  to  $21.3 \pm 1.59$  min and did not differ as a function of group assignment (one-way ANOVA:  $F_{3,56} = 1.00$ , NS).

As would be expected from the hypothesis that the change in response of fathers to litters of young as the young mature reflects a change in fathers' response to male, but not to female pups, a one-way ANOVA performed on arcsine-transformed preference scores revealed a marked effect of group assignment on preference for the nestbox containing a nest and pups ( $F_{3,56} = 5.24$ ,  $P < 0.003$ ; Fig. 3). Post hoc LSD tests revealed that fathers found newborn male pups less attractive than either 3-day-old male pups ( $P < 0.05$ ) or newborn female pups ( $P < 0.01$ ) and found 3-day-old male pups as attractive as both 3-day-old and 1-day-old female pups (both LSD tests NS).

#### EXPERIMENT 3: THE ROLE OF OLFACTORY CUES

The results of experiments 1 and 2 indicate that fathers found newborn males but not newborn females aversive. Evidence from experiments with Norway rats indicates

both that mothers distinguish male from female young on the basis of their smell (Moore 1981) and that rendering virgin females anosmic facilitates their expression of maternal behaviour (Fleming & Rosenblatt 1974). On the day of the birth of a litter, male gerbils repeatedly initiate entrance into the nestbox compartment containing a nest and conspecific young, but withdraw before contacting the pups, suggesting that newborn gerbils may produce olfactory stimuli that recent fathers find aversive (Clark & Galef 2000).

In the present experiment, we used peripheral induction of a transitory anosmia (Alberts & Galef 1971) to determine whether Mongolian gerbil fathers are responding to aversive olfactory cues when they avoid contact with newborn young.

#### Methods

##### Subjects

Subjects were 20 adult male Mongolian gerbils, maintained and bred as described in the Methods of experiment 1, and 120 pups of each sex, born on the day that mates of the adult male subjects delivered their litters, served as stimuli.

##### Procedure

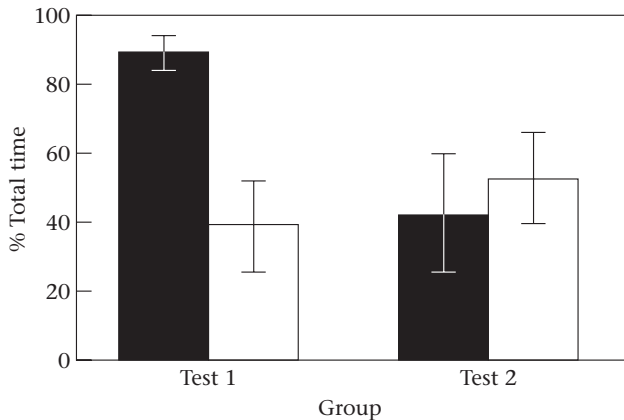
When the mate of each male subject was in the last week of her second pregnancy, we anaesthetized him by intraperitoneal injection with 50 mg/kg sodium pentobarbital, and treated his nasal passages with either isotonic zinc-sulfate solution (zs group,  $N = 10$ ) or tap water (water group,  $N = 10$ ). Irrigation of the olfactory mucosa with zinc-sulfate solution causes an anosmia that lasts a few days (Alberts 1974); irrigation of the nasal passages with water has no known effect on olfactory sensitivity (Wamboldt & Insel 1987).

On the day following treatment, we tested each male for his response to a cotton-tipped applicator soaked with vinegar (Maille Wine and Tarragon Vinegar, Maille, Dijon, France) and held near his nose. We considered any subject that did not attempt to avoid the applicator to be anosmic. We also tested each male assigned to both the zs and water conditions for response to vinegar shortly after the birth of his mate's third litter. During the latter test, all males vigorously avoided the cotton applicator, indicating that they were not anosmic.

On the day of birth of the second litter delivered by the mate of each male subject, we tested him, as in experiment 1, with three male and three female pups in the nest. After the test, each male remained with his mate for 30 or more days, until the day following delivery of her third litter, when we again tested him for his preference between a nestbox compartment containing three male and three female pups and an empty nestbox compartment.

#### Results and Discussion

We lost data from seven males. One father assigned to the zs condition failed the first anosmia test, and mates of



**Figure 4.** Mean  $\pm$  SE time that adult male subjects assigned to the zs (■) and water (□) conditions spent in the nestbox compartment containing a nest and pups as a percentage of total time that they spent in both nestbox compartments.

three males assigned to the zs condition failed to produce a third litter, as did mates of two males assigned to the water condition.

During the first preference test, zinc-sulfate-treated (anosmic) males spent an average of  $26.8 \pm 1.24$  min in both nestbox compartments, and the remaining subjects spent from  $21.5 \pm 3.62$  to  $16.3 \pm 3.50$  min (one-way ANOVA:  $F_{3,24}=2.48$ , NS).

There was no main effect of condition or test on the percentage of time that subjects spent in the nestbox compartment containing pups (both  $F_{s_{1,12}} < 1.91$ , both NS; Fig. 4), but there was a significant interaction between main effects ( $F_{1,12}=6.02$ ,  $P < 0.03$ ; Fig. 4), resulting largely from the greater percentage of time that subjects assigned to the zs condition spent in the nestbox compartment containing pups during the first test, when they were anosmic. Anosmic males showed no avoidance of neonatal pups.

#### EXPERIMENT 4: FATHERING DELAYS MATING

In a species such as the Mongolian gerbil, in which females are fertile soon after giving birth and both parents are parental, the hours following parturition should be a time of conflicting demands on both parents, and fathers in particular. To enhance his future reproductive success, a father, although motivated to care for his newborn young, must mate with his partner while she is fertile. In Mongolian gerbils, the pressure on fathers to inseminate partners soon after parturition is particularly pronounced because female gerbils do not have lactational oestrus. Within a week of parturition, an epithelial membrane covers a female's vagina, preventing insemination until lactation ends (Meckley & Ginther 1972; Clark & Galef 1992). Consequently, a male gerbil who fails to mate with his partner during her postpartum oestrus has to wait at least 30 days before he has another opportunity to father her young.

That male gerbils living in natural circumstances compete for sexual access to their recently parturient mates is suggested by the observation that, in captivity, soon after the birth of a litter, the father engages in a series of bouts of mounting, intromission and ejaculation that lasts 4–9 h. Such prolonged mating activity is not needed to inseminate a female; as a single ejaculation will inseminate 70% of females in postpartum oestrus, and two ejaculations (which males can easily achieve in less than 1 h) are sufficient to inseminate essentially all females (Agren 1990).

It has been suggested that these hours of sexual activity following the birth of a litter serve as a form of mate guarding (Dewsbury 1984; Parker 1984), increasing a male's probability of fathering any litter his mate conceives in postpartum oestrus. Mate guarding would appear important in that female gerbils in oestrus actively solicit copulations (Burley 1980), and free-living gerbil females will seek matings with males other than their respective partners (Agren et al. 1989). Obviously, recent fathers can ill afford to be distracted by paternal urges during the hours following their mate's delivery, and behavioural mechanisms might be expected to have evolved to ensure gerbil fathers' attention to mates, rather than to newborn young, for as long as their mate is in oestrus. In experiment 4, we looked for possible reproductive correlates of fathers spending time in the nest with young rather than interacting with a mate in postpartum oestrus.

## Methods

### Subjects

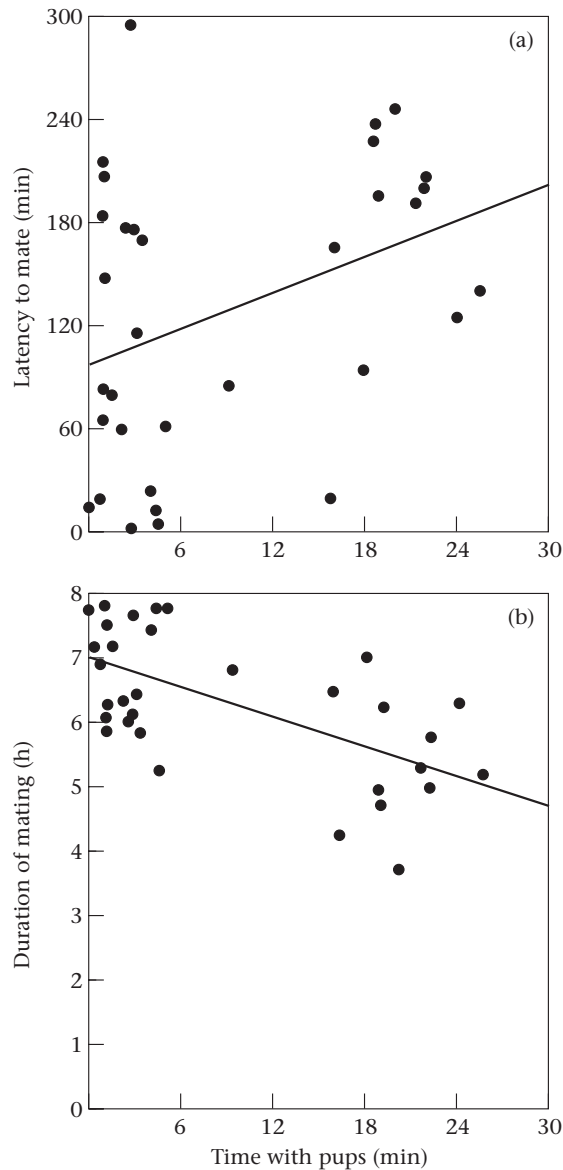
Subjects were 35 reproductively experienced male gerbils, 4–6 months of age at the time of testing, and 105 gerbil neonates that were born on the days that mates of male subjects delivered litters served as stimuli.

### Apparatus

We used the same apparatus used in experiments 1, 2 and 3.

### Procedure

On the day of birth of a litter, we tested the male partner of the recently delivered dam for 30 min for his preference between an empty nestbox compartment and one containing the nest, three male and three female foster pups born that day. After testing a male, we returned both the male and his mate to their home cage together with the foster litter with which the male had been tested. We used a time-lapse video-cassette recorder (Panasonic AG 6740) to tape the behaviour of males during the next 24 h, and scored the tapes to determine the latency to first intromission and the time to cessation of mating of each male. We considered mating to have ended at the start of the first 3-h period in which no mating took place. Once 3 h had passed without a male mating with a female in postpartum oestrus, he never initiated a new mating sequence.



**Figure 5.** Relation between the time that males spent with a litter of newborn young and (a) their subsequent latency to mount their partner during her postpartum oestrus and (b) the duration of their sexual activity.

## Results and Discussion

We found a significant positive correlation between the time that males spent in the nestbox compartment containing the nest and litter and their latency to initiate sexual behaviour (Pearson's correlation:  $r_{33}=0.39$ ,  $P<0.02$ ; Fig. 5a) as well as a significant negative correlation between the time that males spent in the nestbox compartment containing the nest and litter and the duration of their mating ( $r_{33} = -0.57$ ,  $P<0.01$ ; Fig. 5b). In summary, males with a tendency to spend time with pups also had a tendency to delay mating and to spend relatively less time mating with a partners during her postpartum oestrus.

## GENERAL DISCUSSION

Results of the present series of experiments indicate that the previously observed reluctance of male Mongolian gerbils to make contact with litters on the day of their birth, but not 2 days later, results from recent fathers' response to odours produced by male but not by female neonates. The results also provide a preliminary indication that a father's avoidance of newborn young may influence his future reproductive success, in that increased attention to a litter may result in less time spent guarding a mate during her fertile period in the hours immediately following parturition.

Although the proximal cause of avoidance of newborn litters by gerbil fathers appears straightforward, it is difficult to discern why, as the present results suggest, a behavioural process focusing a male's attention on his fertile mate, rather than on his offspring, should depend on stimuli produced only by newborn sons. In future studies of parent–young interactions in Mongolian gerbils, it will be interesting to see how the sex ratios of natural litters influence both parental care and sexual behaviour during the hours immediately following the birth of a litter. Perhaps such studies will cast some light on why responses to neonatal male pups so dominate the behaviour of gerbil fathers in the hours immediately following the birth of offspring.

## Acknowledgments

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