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BRIEF COMMUNICATION

A Male Gerbil's Intrauterine Position Affects Female Response to His Scent Marks

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CLARK, M. M. AND B. G. GALEF, JR. *A male gerbil's intrauterine position affects female response to his scent marks.* *PHYSIOL BEHAV* 55(6) 1137–1139, 1994.—Female Mongolian gerbils scent marked more frequently in response to scent marks deposited by adult male conspecifics that, as fetuses, had resided in intrauterine positions between two male fetuses (2M males) than in response to scent marks deposited by adult male conspecifics that had resided in intrauterine positions between two female fetuses (2F males). Because 2M male gerbils are significantly more likely than are 2F male gerbils to impregnate females, and because female gerbils are able to discriminate among males after exposure to their scent marks, the ability of female gerbils to discriminate scent marks of 2M males from those of 2F males may serve as a basis for female identification of males likely to make suitable mates.

Intrauterine position Scent marking Female choice

THE reproductive potential of an adult male Mongolian gerbil (*Meriones unguiculatus*) is correlated with the intrauterine position that he occupied as a fetus. When adult, those male gerbils that matured in utero between two male fetuses (2M males) impregnate a significantly greater proportion of the females with whom they are mated than do those male gerbils that developed in utero between two female fetuses (2F males). Further, those 2F male gerbils that do succeed in impregnating females tend to sire smaller litters than do their 2M fellows (3).

Adult 2F and 2M male gerbils differ along dimensions other than that of reproductive potential. For example, and most relevant to the present experiment, 2M male gerbils have larger scent glands and scent mark more frequently than do their 2F brothers (2).

The experiment described here was undertaken to determine whether female gerbils could discriminate the scent marks of 2M males from those of 2F males.

METHOD

Subjects

Our subjects were 12 vaginally delivered, virgin female and 24 caesarian-delivered, virgin male Mongolian gerbils

taken from 36 litters conceived, gestated, and delivered in the vivarium of the McMaster University Psychology Department by breeding stock acquired from Tumblebrook Farm (Brookfield, MA).

Apparatus

The experiment was carried out in a 92 × 92 cm arena with an opaque, white Plexiglas floor and shellacked wooden walls 62 cm high. The arena floor was divided into 16 squares (23 × 23 cm) by black lines painted on the floor surface, and a black, 1/2-cm high Plexiglas peg (1 × 2 cm) was attached to the floor at each of the nine points of intersection of the painted lines.

Procedure

Male subjects. Each male gerbil was caesarian delivered on the last day of its gestation while its dam was deeply anesthetized with halothane. Each caesarian-delivered male subject and its litter mates were foster reared by a dam that had delivered a litter vaginally on the day of caesarian delivery of the litter she was to foster rear [detailed descriptions of techniques of caesarian delivery, fostering, and rearing can be found in (1,2)].

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As fetuses, 12 of the 24 male subjects had matured in utero between two males; the remaining 12 males had matured in utero between two females.

Subject selection. The 12 2F males that served as subjects were selected from a pool of 16 2F males on the basis of their scent marking frequency when placed in the apparatus during a screening session conducted 14 days before the experiment proper was carried out. When each male subject was 75 to 90 days old, it was placed in the apparatus for 10 min, and only those males that scent marked six or more times during the 10-min screening period were subsequently used in the experiment proper. Four of the 16 2F males did not scent mark six times while in the apparatus and were discarded. All 12 2M male subjects marked when placed in the apparatus, and there was no need to select among 2M male subjects.

We did not determine the stage in the estrous cycle of females at the time of their participation in the experiment.

Behavioral testing. When subjects were 90–100 days of age, we initiated behavioral testing in a room separate from the colony room where subjects had been maintained.

Before beginning the experiment proper, we randomly assigned: 1) each male and each female subject to one of 12 experimental trios each composed of one female, one 2F male, and one 2M male, 2) three of the nine pegs in the test arena to be marked by the 2M male member of a trio, three to be marked by the 2F male member of a trio, and three to be left unmarked. We controlled marking of pegs by males by placing small glass jars over any pegs that we did not wish a male to mark while it was in the apparatus. The same method was employed to limit each male to depositing three scent marks on one randomly selected peg of the three that he was allowed to mark, two scent marks on a second randomly selected peg and one scent mark on the third.

Before beginning testing, we also randomly assigned one of the three unmarked pegs to serve as a control for the two pegs scent marked once, one as a control for the two pegs scent marked twice, and the third as a control for the two pegs marked three times by male subjects.

To start the experiment proper, we introduced, in counterbalanced order, either the 2M or 2F male from a trio into the apparatus and constrained his behavior so that he deposited six scent marks on the three pegs he was allowed to mark. Once the first male had completed his assigned task, we removed him from the apparatus, covered the three pegs that he had marked with glass jars, and removed the glass jars covering the three pegs that his male trio mate was to mark. We then placed the male trio mate of the removed male in the enclosure and allowed him to place six scent marks on the three pegs he was to mark (three marks on one randomly selected peg, two marks on a second, and one on a third).

Once the second male in a trio had completed marking his assigned pegs, he was removed from the apparatus; the floor of the enclosure was cleaned with 95% ethanol and rinsed with distilled water. Then, all glass jars were removed from the enclosure. These procedures took 4–5 min to complete.

Finally, the female member of the trio was placed in a randomly selected corner of the apparatus, facing its center, and released. During the next 10 min, an observer, who was unaware of the previous treatment of pegs, recorded the number of scent marks that a female deposited on each peg.

Once testing of the female member of a trio had been completed, the floor of the apparatus and each of the nine pegs were cleaned with 95% ethanol and then rinsed with distilled water.

The entire procedure was carried out with each of the 12 trios of subjects participating in the experiment.

Data Analysis

To equate the contribution of each subject to the data pool, we analyzed the proportion of scent marks each female trio member directed toward each of the nine pegs to which she was exposed. Proportions were arcsine transformed prior to ANOVA to normalize the distribution of percentage scores.

RESULTS AND DISCUSSION

Figure 1 shows the mean proportion of scent marks that female subjects directed toward each of the nine pegs to which they were exposed. There was a significant effect of the intrauterine position of male subjects on the distribution of scent marks by females [repeated measures ANOVA, $F(2, 22) = 9.27, p < 0.002$], but no effect of the number of scent marks that males had deposited on pegs on subsequent female scent marking of those pegs, $F(2, 22) = 2.70, NS$, and no significant interaction between number of scent marks and male intrauterine position, $F(4, 44) = 1.26, NS$.

Post hoc LSD tests revealed that the proportion of scent marks deposited by females on the three pegs marked by 2M males (52.3%) was significantly greater than was the proportion of marks deposited on either the three unmarked pegs (24.7%) or the three pegs marked by 2F males (21.0%; LSD tests, both $p < 0.01$). Further, there was no reliable difference in the proportion of marks deposited by females on pegs that had been marked by 2F males and on unmarked pegs (LSD test, NS).

Statistical analysis (repeated measures ANOVA) of the number of scent marks deposited by female subjects on the six pegs actually marked by 2M and 2F males revealed a significant effect of both intrauterine position of males [$F(1, 11) = 22.4, p < 0.001$] and number of marks/peg [$F(2, 22) = 3.42, p < 0.05$] on scent marking by female subjects.

The failure to find any difference in the mean proportion of scent marks deposited by female subjects on pegs marked by 2F males and on unmarked pegs is consistent with the hypothesis that females may not have been able to detect the presence of scent marks deposited by 2F males. It is also possible that females can detect the presence of scent marks deposited by 2F males but

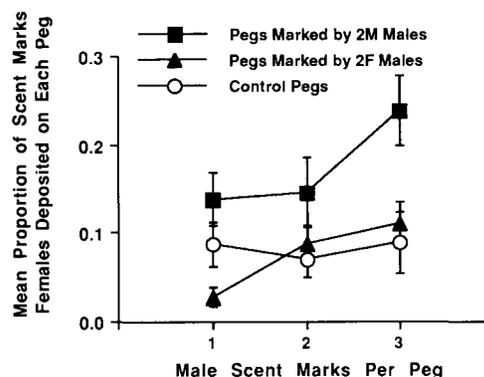


FIG. 1. Mean proportion of scent marks deposited by female subjects during a 10-min test on: 1) pegs previously marked 1, 2, or 3 times by either 2M or 2F male gerbils or 2) unmarked pegs. Unmarked pegs had been randomly assigned before the start of testing as controls for pegs marked 1, 2, or 3 times by males.

fail to respond to those marks by scent marking over them. There is, however, no question that female gerbils can both discriminate between and respond differently to scent marks deposited by 2M males and 2F males of their species. The ability to discriminate the odors of males from different intrauterine positions may not be universal in rodents (6).

Female gerbils often react aggressively in response to sexual advances by males and are able to determine whether a male succeeds in mating with them (4). The ability of female Mongolian gerbils both to discriminate familiar from unfamiliar males (4,5) and 2M from 2F males on the basis of their scent marks, taken together with the finding that 2M males are more likely than 2F males to successfully impregnate their consorts (3), suggests that scent marks deposited by male

Mongolian gerbils may provide female gerbils with a way to select relatively potent 2M males as consorts. Whether female gerbils living in natural circumstances actually identify individual males from their scent marks (7) and use the ability to discriminate scent marks of 2M males from those of 2F males to increase their probabilities of mating with potent males will be difficult to determine.

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