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Fetal Uterine Position Affects Copulation and Scent Marking by Adult Male Gerbils

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CLARK, M. M., S. A. MALENFANT, D. A. WINTER AND B. G. GALEF, JR. *Fetal uterine position affects copulation and scent marking by adult male gerbils.* PHYSIOL BEHAV **47**(2) 301–305, 1990.—Those male Mongolian gerbils *(Meriones unguiculatus)* that as fetuses resided in uterine locations adjacent to no females, when adult, scent marked more frequently, mounted estrous females with shorter latencies, and ejaculated after fewer intromissions than did those male gerbils that as fetuses resided in uterine locations adjacent to two females. Both the scent-marking frequencies and copulatory patterns of adult males were positively correlated with three indices of their circulating levels of testosterone: ventral gland size, anogenital distance, and relative testes weights. Also, those males that scent marked relatively frequently copulated more reliably than did those males that scent marked relatively infrequently.

Sexual behavior Scent marking Copulatory patterns Uterine position Androgen Ventral gland Anogential distance Mongolian gerbil

MONGOLIAN gerbils *(Meriones unguiculatus)* are sometimes frustrating subjects for behavioral research. Because of considerable differences in the frequencies with which individual gerbils spontaneously exhibit various behaviors, it is often not possible to examine a behavior of interest in all subjects randomly selected for study from a population. For example, in many published studies of copulation and scent marking by Mongolian gerbils (behaviors explored in the experiments presented below), baseline frequencies of behavior have been used as criteria to select individuals to use as subjects. Only those gerbils that exhibited a behavior of interest "reliably" (i.e., at a relatively high frequency) during a preliminary period of observation were selected for study [see for examples (5, 7, 17)].

A growing body of literature indicates that some of the spontaneous variation in behavior, morphology, and physiology exhibited by adult litter-bearing rodents can be accounted for by reference to individuals' uterine locations relative to fetuses of the same or opposite sex (3, 4, 21, 22). Because: a) fetal uterine location is known to affect both the hormonal milieu to which fetuses are exposed and adult patterns of behavior [particularly those behaviors dependent on circulating levels of sex steroid hormones for their expression (22,23)] and b) frequencies of scent marking and copulation by adult male gerbils are known to be androgen dependent (17, 24–26), it seemed reasonable to predict that fetal uterine location might make a major contribution to previously unexplained, spontaneous variability observed in frequencies of scent marking (Experiment 1) and copulation (Experiment 2) exhibited by adult male gerbils.

GENERAL METHOD

Subjects

Adult male Mongolian gerbils *(Meriones unguiculatus)*, cesarian delivered from and foster reared by females born and raised in the McMaster vivarium, served as subjects. All subjects were second- or third-generation descendants of breeding stock acquired from Tumblebrook Farms (Brookfield, MA).

Procedure

Breeding and maintenance. At 90 to 100 days of age, virgin female gerbils were each weighed and then placed individually with a proven male. Each breeding pair was housed in a polypropylene cage (35 × 30 × 15 cm), lidded with hardware cloth (1.3 cm), and carpeted with a thin layer of wood-chip bedding (Beta chips, Northeastern Products, Warrensburg, NY). All subjects, their dams, and foster dams were maintained throughout the experiment on ad lib Purina Rodent Laboratory Chow #5001 and water in a temperature- and humidity-controlled colony room illuminated on a 12-hr light/dark schedule (light onset at 0500 hr).

The date on which each breeding pair first mated was determined using time-lapse video recording and pair members were separated 2 weeks later, when females were conspicuously pregnant. All pups were weaned on Day 25 postpartum (day of birth = Day 1) and, after weaning, male pups were maintained in groups of two or three littermates in polypropylene cages (35 × 30 × 15 cm) until initiation of experimental procedures 100 to 110 days postpartum.

Surgery and foster rearing. Twenty-four days after observed copulation (i.e., 1 day before anticipated vaginal delivery), each female that had gained weight at a rate consistent with her impregnation on the day of observed copulation was anesthetized by ether inhalation, her abdomen was opened, her uterus externalized, and her fetuses removed singly. The gender of each fetus was determined on the basis of its anogenital distance (13) and its position in its dam's uterus was recorded (22). After all fetuses had been removed from a dam, she was euthanized by anesthetic overdose.

Each infant was toe clipped at delivery for permanent identification and then, using the procedures of Clark and Galef (3), fostered to a female that had delivered a litter vaginally on the day of cesarian delivery of her foster pups.

Classification of uterine positions. To examine the effects of fetal uterine position on adult behavior and morphology, we looked at the number of female fetuses adjacent to each male fetus in utero (22). We classified those male fetuses located in utero between two female fetuses as 2F males, those male fetuses located adjacent to a single female as 1F males, and those male fetuses in contact with no females as 0F males.

We used this (22) method of classification as a matter of convenience, not because our data were sufficient to show that contiguity with females was more important in affecting male development than either ovarian-caudal location of males relative to females (10) or the overall proportion of females in a uterine horn. In fact, our data suggested that: a) the ratio of females to males in a uterine horn, b) the number of females caudal to a male and c) the number of females adjacent to a male could each be shown to affect development of male fetuses. However, to determine the relative contribution to male ontogeny of confounded variables (a), (b), and (c) would have required examination of very many more cesarian-delivered gerbil litters than we had available. Consequently, although we demonstrate below clear effects of uterine position on the behavior and morphology of adult male gerbils, we cannot yet identify the precise cause of those effects.

EXPERIMENT 1

Experiment 1 was undertaken to determine whether the frequencies with which adult male gerbils scent marked in an open field were influenced by the uterine location that each had occupied as a fetus. Because frequency of scent marking by male gerbils has been found to be correlated with circulating levels of androgens (1), we also measured three, androgen-sensitive, physical characteristics of our subjects: their ventral gland sizes (27), anogenital distances (13), and testes weights (15).

METHOD

Subjects

Sixty-three 100- to 110-day-old male Mongolian gerbils from 32 cesarian-delivered litters, reared and maintained as described in the General Method section, were tested individually to determine their respective frequencies of scent marking. Each subject was removed to an individual cage ($35 \times 30 \times 15$ cm) for the 7 days immediately preceding initiation of testing.

Procedure

Scent-marking frequency was assessed in individual subjects using a modified version of procedures developed by Thiessen, Friend and Lindzey (17). Each male was observed for 15 min/day, for 4 consecutive days, in a 92×92 cm test 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, ½-cm high Plexiglas peg (1×2 cm) was attached to the floor at each of the nine points of intersection of the painted lines.

To begin a test session, a subject's cage was removed from the colony room (where subjects had been maintained since weaning) and placed in the room containing the test arena. Two hr later, the subject was removed from its cage and placed in a corner of the arena facing the arena center. During the next 15 min, the observer recorded the number of instances of scent marking exhibited by the subject. Scent marking was defined as an active lowering of the belly and dragging of the ventral gland pad across a peg or the floor of the arena (17). Scent marking was easily discriminated from both normal locomotion and perineal dragging (18).

At the end of the 15-min test session, the subject was returned to its home cage and transported back to the colony room. The arena was then cleaned with an 80% alcohol solution and rinsed with distilled water before testing of the next subject. Order of testing of subjects was counterbalanced across the 4 days of testing and each subject was assigned a single scent-marking score equal to the mean number of scent marks it deposited per 15 min in the test arena.

After the scent-marking test was completed, each subject was sacrificed by anesthetic overdose, weighed, and both the area of its ventral gland (maximum length $\times$ maximum width) and anogenital distance were measured. The testes of each subject were then removed and weighed. Both behavioral and physical measurements were undertaken by an experimenter unaware of the uterine position occupied by individual subjects before birth.

RESULTS

The main results of Experiment 1 are presented in Table 1 which shows the mean scent-marking scores ($\pm$ 1 SE) and physical measurements ($\pm$ 1 SE) obtained from adult male gerbils that, as fetuses, had occupied 0F, 1F, and 2F uterine locations. As can be seen in Table 1 and, as statistical tests tended to confirm, the number of females adjacent to male fetuses in utero affected adult males' frequencies of scent marking, $F(2,60) = 7.65$, $p = 0.002$, ventral gland sizes, $F(2,60) = 2.83$, $p < 0.05$, anogenital distances, $F(2,60) = 3.22$, $p = 0.04$, and relative testes weights, $F(2,60) = 2.54$, $p < 0.10$. Frequency of scent marking, ventral gland sizes, anogenital distances, and relative testes weights were each significantly greater in 0F than in 2F males (Newman-Keuls tests, all $ps < 0.05$). Scent-marking frequencies across all 63 subjects were significantly, positively correlated with both their respective ventral gland sizes (Pearson's $r = .27$, $p < 0.05$) and anogenital distances (Pearson's $r = .42$, $p < 0.001$) and were marginally correlated with their relative testes weights (Spearman's $rho = 0.23$, $p = 0.07$).

DISCUSSION

The results of the present experiment indicate that a portion of the spontaneously occurring variability in the scent-marking behavior of adult male Mongolian gerbils can be accounted for by reference to the uterine positions occupied by individual males before birth. Males developing in utero adjacent to fewer female fetuses scent marked more frequently than did males developing in utero adjacent to more female fetuses.

The findings that 2F males had smaller ventral gland pads, shorter anogenital distances, and lighter testes than 0F males are consistent with the hypothesis that exposure of male fetuses to female fetuses in utero (or lack of exposure to male fetuses in utero) had demasculinizing effects on males. Indeed, 2F males in

TABLE 1

EFFECTS OF MALES' PROXIMITY TO FEMALE FETUSES IN UTERO ON ADULT SCENT-MARKING BEHAVIOR AND ADULT PHYSIOLOGY

	Uterine Position		
	0F	1F	2F
Number of males	25	28	10
Mean marks/15 min	13.1 ± 2.5	5.3 ± 1.3	1.5 ± 0.8
Anogenital distance (cm)	1.84 ± 0.02	1.79 ± 0.03	1.71 ± 0.06
Ventral gland area (cm^2)	1.78 ± 0.06	1.58 ± 0.06	1.52 ± 0.08
Relative testes weights (mg/100 g)	144.1 ± 2.7	138.3 ± 2.6	136.9 ± 1.5

the present experiment exhibited frequencies of scent-marking behavior similar to the frequencies of scent marking exhibited by either castrated males (11, 17, 25) or intact females (16, 19, 24) in other laboratories.

The reduced levels of scent marking to be observed in 2F males, relative to 0F males, like the small relative testes weights, scent-marking pads, and anogenital distances of 2F males relative to 0F males, suggest that events occurring in utero may have resulted in altered circulating levels of testicular hormones in fetal or neonatal gerbils (18–20) that, in turn, were responsible for the observed variation in adult male phenotypes.

EXPERIMENT 2

The copulatory behavior of adult male Mongolian gerbils, like their scent-marking behavior, is highly variable (7–9, 25). Male gerbils differ considerably in any index of sexual vigor one cares to measure (probability of mounting, of intromitting, or of ejaculating; latency to mount, intromit, or ejaculate; number of mounts or intromissions per ejaculation; postejaculatory interval, etc.) and, of course, the sexual behavior of male gerbils is, like their scent-marking behavior, sensitive to circulating levels of androgens (24–26).

In the present experiment, we examined both the sexual performance and scent-marking behavior of adult male gerbils as a function of their respective uterine positions relative to female sibs. The data collected in the present experiment allowed us both to extend the range of behaviors of adult male gerbils shown to be influenced by prenatal, uterine experience and to confirm the main findings of Experiment 1.

METHOD

Subjects

Twenty-nine, 6-month-old, male, Mongolian gerbils from 15 cesarian-delivered litters, reared and maintained as described in the General Method section, served as subjects. Twenty adult female gerbils that had been bilaterally ovariectomized when 90 days of age served as stimulus females. Estrus was induced in stimulus females by priming them first with 10 μg of estradiol benzoate (both 48 and 24 hr before a test session) and then with 500 μg of progesterone 4 to 6 hr before allowing them to interact with a male subject (12).

Procedure

Male sexual experience. Because sexually naive male gerbils exhibit low levels of sexual activity when paired with receptive females for the first time (8), each of the 29 males in the present experiment, housed individually from 110 days of age to completion of the experiment, was provided with sexual experience some weeks before testing. When a male reached 150 days of age, a 3- to 4-month-old female gerbil was placed in his cage and the pair was left undisturbed until they were observed to copulate. The female was then removed from each male's cage and, 1 week later, replaced with a second 3- to 4-month-old female that was again left with the male until 1 week after copulation occurred.

Sexual behavior tests. Three weeks following the second copulatory episode, each male's sexual behavior was observed after he was placed with a stimulus female in induced estrus. To begin testing, a stimulus female was injected with progesterone and she was then placed in the cage of a male subject, but on the opposite side of a hardware-cloth partition that held her separate from the male. Five hr later, the partition separating each male and female was removed and sexual behaviors were recorded until either: a) the male had achieved three ejaculations, b) 2 hr had passed without the male mounting the female, or c) ejaculation had failed to occur within 90 min of the first intromission in a postejaculatory sequence. To ensure that each male's sexual behavior was sampled adequately, each male was tested with five different stimulus females, one/week for five consecutive weeks.

During each test session, an experimenter, ignorant of the uterine position that a male had occupied, recorded: a) the male's latency to first mount, b) the number of mounts and number of intromissions preceding each ejaculation, c) the latency from the first mount in an ejaculatory series to ejaculation and d) the time from an ejaculation to the next mount.

In the course of our preliminary observations, we had observed a reliable correlate of the occurrence of ejaculation in male gerbils that we have not seen described in the literature. At ejaculation, the pelvic thrust terminated with a clearly discernable upward movement, rather than with the horizontal movement characteristic of intromissions not ending in ejaculation. We used this vertical thrust as one index of ejaculation.

Scent-marking test. One week after completing observation of each male's sexual behavior, we observed his scent-marking behavior on four consecutive days using the procedures described in the Method section of Experiment 1. Each male was then sacrificed and, as in Experiment 1, we determined its body weight, ventral gland pad size, anogenital distance, and testes weights.

Data analysis. Three subjects (two 2F males and one 1F male) failed to exhibit sexual activity during any of the five test sessions and their data were excluded from analyses of sexual behavior other than that of frequency. All 26 remaining males achieved ejaculation three times during at least three of the five observation periods. Each sexually active male was assigned a single score on each measure of sexual behavior equal to its median score on that measure across the five periods of observation.

RESULTS

Sexual Behavior

The main results of Experiment 2 are presented in Table 2 which describes the sexual performance of adult males as a function of their respective uterine locations relative to female siblings. As can be seen from examination of the data presented in Table 2, both the latencies of males to mount females, $F(2,23) = 5.45$, $p<0.02$, and the latencies of males to achieve three ejaculations, $F(2,23) = 4.2$, $p<0.02$, varied significantly with the number of female neighbors they had as fetuses. 0F males exhibited shorter latencies both to mount females and to achieve three ejaculations than did 2F males (Newman-Keuls test, both $ps<0.05$) and 0F males were more likely to achieve ejaculation than were 2F males (Fisher's Exact Probability Test, $p=0.02$).

TABLE 2

SEXUAL PERFORMANCE AND SCENT-MARKING BEHAVIOR OF MALES DEVELOPING ADJACENT TO NO, ONE, OR TWO FEMALES

Uterine position		0F	1F	2F
N		11	10	8
% Subjects showing M/I/3E*		100/100/90.9	90/90/70.0	75/75/25.0
N		11	9	6
Latency to 1st mount (sec)		351.5 (97.6)†	364.0 (82.8)	917.3 (301.6)
Latency to 3rd ejaculation (sec)		2706.8 (203.9)	3831.8 (574.6)	4452.7 (253.1)
Number of mounts per ejaculation	1‡	42.9 (3.1)	64.1 (8.7)	70.5 (4.7)
	2	18.9 (1.7)	21.3 (7.4)	27.4 (4.6)
	3	17.5 (2.9)	19.9 (2.4)	39.4 (10.5)
Number of intromissions per ejaculation	1	34.6 (2.9)	49.1 (8.8)	59.8 (5.1)
	2	17.5 (1.6)	15.7 (3.6)	24.7 (3.2)
	3	16.5 (2.9)	16.7 (2.0)	32.8 (2.6)
Latency to reach ejaculation (sec)	1	1225.8 (191.8)	2110.3 (473.7)	1924.0 (324.1)
	2	370.9 (28.3)	405.0 (75.7)	516.3 (93.7)
	3	342.6 (77.8)	371.0 (55.7)	725.8 (231.5)
Postejaculatory interval (sec)	1	313.5 (16.1)	394.4 (47.4)	410.8 (40.6)
	2	326.3 (18.5)	419.0 (35.7)	401.7 (22.3)
Mean marks/15 min		20.2 (3.5)	14.6 (3.1)	11.6 (2.8)

*Mounts/intromissions/three ejaculations during all five test sessions.
†Numbers in parentheses = ± 1 SE.
‡1, 2, 3 refer to first, second, and third ejaculatory series.

Examination of the data presented in Table 2 also reveals effects of uterine location on male behavior within ejaculatory series. Uterine location affected both the number of mounts and number of intromissions to ejaculation and the time to ejaculation exhibited by males in both the first and third ejaculatory series [both $Fs(2,23)>4.1$, all $ps<0.05$]. Differences among 0F, 1F and 2F males in the second ejaculatory series were in the same direction as were those in the first and third ejaculatory series but were not significant. Newman-Keuls tests revealed that for each measure in the first, second, and third ejaculatory series 0F males were more rapid or efficient ejaculators than were 2F males (all $ps<0.05$).

Postejaculatory intervals were significantly affected by uterine position following the second ejaculatory series (Kruskal-Wallis, $H=7.02$, $p<0.02$), but not following the first ($H=3.2$, $p>0.10$), though once again the behavior of 0F males differed significantly from that of 2F males (Mann-Whitney $U=9$, $p<0.02$), with 2F males exhibiting significantly longer postejaculatory intervals following first ejaculation than 0F males.

Scent Marking

Examination of frequencies of scent marking behavior exhibited by 0F, 1F, and 2F males (shown in the bottom row of Table 2) reveals that, as in Experiment 1, uterine location significantly affected frequency of scent marking by adult male gerbils, $F(2,26)=3.20$, $p<0.05$. Once again a Newman-Keuls test revealed that 0F males scent marked significantly more frequently than did 2F males ($p<0.05$).

Scent Marking and Sexual Behavior

For the entire sample of 29 males, frequency of scent marking and time required to achieve three ejaculations were significantly, negatively correlated (Spearman's $rho=-.44$, $p<0.02$). Yahr and co-workers (25) have also reported negative correlations between scent-marking frequency and sexual vigor in gerbils.

Physical Measurements

As we observed in Experiment 1, uterine location significantly affected the size of males' ventral gland pads, anogenital distances [both $Fs(2,26)>3.85$, both $ps<0.05$], and relative testes weights (Kruskal-Wallis $H=5.31$, $0.10>p>0.05$). Student's t-tests showed that 0F males had larger ventral glands, greater anogenital distances, and greater relative testes weights than did 2F males (all $ts>4.94$, all $ps<0.001$).

DISCUSSION

Comparison of the data describing scent-marking behavior in Tables 1 and 2 reveals that males from 0F, 1F, and 2F uterine locations in the present experiment (Table 2) scent marked more frequently than did corresponding subjects in Experiment 1 (Table

1). Both the greater ages (11) of subjects in Experiment 2 than in Experiment 1 and the relatively extended period during which subjects in Experiment 2 were kept in social isolation (14) may have contributed to the different frequencies of scent-marking behavior observed in the two experiments.

The results of the present experiment are similar to those previously reported in studies of effects of uterine position on the copulatory behavior of both house mice and Norway rats (23). Mongolian gerbils can thus be added to the growing list of litter-bearing, laboratory rodent species in which it has been found that the uterine positions of male fetuses relative to members of the opposite sex is correlated with their patterns of copulatory behavior in adulthood.

GENERAL DISCUSSION

Taken together, the results of the present experiments clearly indicate that some of the spontaneous variability observed in the copulatory and scent-marking behavior exhibited by adult male Mongolian gerbils is attributable to the uterine environments that they occupied as fetuses. Those males that developed adjacent to two female fetuses exhibited both lower frequencies of scent-marking behavior and were less efficient copulators than were those males developing adjacent to no female fetuses.

Although, the causes of the changes in scent-marking and copulatory activities we observed in males developing adjacent to two females are not known, early exposure to gonadal hormones can affect the levels of scent-marking and copulatory behaviors exhibited by adult male gerbils (11, 18–20, 24). It seems likely that the uterine positions of male gerbils, like those of male mice and rats (22,23), influence both the levels and types of hormones to which individuals are exposed during sensitive periods in ontogeny. Of course, in the present experiments, evidence of differences in the internal hormonal milieu of both fetal and adult male gerbils as a function of their respective uterine positions was indirect. Further investigations will be required to provide direct measurement of hormonal correlates of the variations in morphology, scent marking, and copulatory patterns described here. However, regardless of the physical substrate mediating effects of uterine position on phenotypes of adult male gerbils, attention to uterine position-correlated, prenatal experiences and their sequelae (2, 6, 20) will be required to explain the variability in spontaneous behavior that has rendered behavioral study of adult male gerbils more difficult than it might otherwise be.

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