Androgen Mediated Effects of Male Fetuses on the Behavior of Dams Late in Pregnancy

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Two correlational studies were undertaken to explore the relationship between the sex ratio of the pups that a female Mongolian gerbil gestated and her behavior, morphology, and hormone levels late in pregnancy. In the first study, we found that the change in sex ratio between the first and second litters that a female gerbil delivered and the change in her frequency of scent marking late in her first and second pregnancies were significantly correlated. In the second study, we found significant positive correlations between both the percentage and the number of males in the litter a female delivered and (1) her plasma testosterone levels, (2) the size of her ventral gland, and (3) her frequency of scent marking, all measured late in pregnancy. Our data were entirely consistent with the hypothesis that fetal males excrete biologically significant quantities of testosterone into their dam's bloodstream and that this testosterone masculinizes both the behavior and morphology of dams late in pregnancy.

Evidence that fetal male primates release biologically significant amounts of testosterone into their dams' bloodstreams (Klinga, Bek, & Runnebaum, 1978; Meulenberg & Hofman, 1991; Resko, 1970) has instigated several investigations of

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effects of fetal gender on androgen-sensitive behaviors of gravid females (Erwin & Anderson, 1975; Nieuwenhuijsen, Slob, & de Neef, 1988; Sackett, 1981). Such efforts have not been entirely successful.

In the sole published report of effects of fetal gender on the behavior of pregnant females with a statistically reliable outcome, Sackett (1981) found that pigtail macaques (*Macaca nemistrina*) that subsequently gave birth to sons, during pregnancy, received fewer bite wounds that require veterinary attention than did pigtail macaques giving birth to daughters. He interpreted this finding as consistent with the hypothesis that fetal androgens increased the aggressiveness of those females that gestated sons.

Of course, receipt of serious wounds is, at best, an indirect index of aggressive behavior (Nieuwenhuijsen et al., 1988) and, as Sackett (1981) indicated, direct observation of effects of fetal gender on agonistic behaviors of dams was needed to demonstrate that fetal sons actually increased their mothers' levels of aggression during pregnancy. Unfortunately, results of a subsequent observational study of effects of fetal gender on aggression in pregnant stumptail macaques (*Macaca arctoides*) provided no support for Sackett's indirect observations. Females carrying sons were, if anything, more likely to be attacked by conspecifics than were females carrying daughters (Nieuwenhuijsen et al., 1988).

Regardless of outcome, experiments such as Sackett's (based on analyses of more than 2800 macaque pregnancies) or Nieuwenhuijsen and colleagues' (describing the results of nearly 3 years of observation of a large troop of captive primates) required access to research facilities not available to most investigators. Consequently, such reports do not provide the research community at large with paradigms permitting further investigation of effects of fetal gender on the behavior of female mammals during gestation. Our first experiment, therefore, was undertaken to describe effects, if any, of fetal gender on the behavior of dams late in pregnancy in a readily available species of laboratory rodent, the Mongolian gerbil (*Meriones unguiculatus*).

Experiment 1

In the present study, we looked for correlations between the gender composition of the litter that pregnant gerbils were carrying and the frequency of their scent-marking behavior late in pregnancy. Scent marking is an androgen-sensitive behavior in female gerbils (Whitsett & Thiessen, 1972; Thiessen & Lindzey, 1970; Yahr, 1976) easily quantified in the laboratory without either elaborate equipment or intrusive manipulation of subjects. Plasma testosterone levels of gerbil dams late in pregnancy are correlated with both the sex ratio of and number of males in gestated litters (Clark, Crews, & Galef, 1991).

Of course, as Sackett (1981) and others have indicated, significant correlations between the gender of fetuses carried by females and the behavior of those females during a single reproductive episode are difficult to interpret. For example, positive correlations between the number of males that female gerbils carry and their frequencies of scent marking might reflect a tendency on the part of those females with high levels of endogenous testosterone to bear sons, rather than provide evidence of androgenization of gravid females by their male fetuses. In fact, we have previously reported that female Mongolian gerbils that were themselves androgenized as fetuses (as a result of occupying a uterine location between two male fetuses), in adulthood tend both to deliver male-biased litters and to have relatively elevated levels of plasma testosterone (Clark, Crews, & Galef, 1991; Clark & Galef, 1988; Clark, Spencer, & Galef, 1986). Consequently, a positive correlation between the number of males that female gerbils carried and their behavior during pregnancy would not provide convincing evidence of an effect of fetal gender on the behavior of gravid females.

To control for correlated individual differences in baseline levels of scent-marking behavior and in probabilities of bearing male offspring, we used a within-subjects design in which female gerbils were examined during two successive pregnancies. We correlated differences in the gender composition of the two litters that each female delivered with differences in her behavior late in successive pregnancies. Such a procedure permitted observation of correlations between fetal gender and dams' behavior unaffected by individual difference either in dams' baseline levels of scent marking or in dams' tendencies to produce either male- or female-biased litters.

Methods

Subjects

Subjects were 35 nulliparous female Mongolian gerbils born in the McMaster Psychology Department vivarium to breeding stock acquired from Tumblebrook Farm (Brookfield, MA). Subjects were weaned when 30 days of age and were then maintained in groups of two or three in 15 × 30 × 15 cm shoe-box cages until they were bred.

Procedure

Mating and Maintenance

When 60 days of age, each of the 35 subjects was placed with a sexually proven adult male gerbil from the McMaster vivarium. All 35 pairs were housed individually in 15 × 30 × 15 cm polypropylene, shoe-box cages and maintained on ad lib Purina Rodent Laboratory Chow #5001 and water in a single temperature-controlled colony room that was illuminated on a 12:12 hr light/dark schedule.

The date on which each pair mated was determined by observation, with the expectation that a female would give birth 26 days after copulation was observed. Following mating, each pair was left undisturbed until the female was conspicuously pregnant (i.e., late in the 2nd week of gestation). The male was then removed from each pair's cage.

Measuring Scent Marking

On the 21st day of gestation, the scent marking frequency of each pregnant female was assessed using a modification of procedures developed by Thiessen, Friend, and Lindzey (1968). Each subject was observed for 5 min/day, for 4 consecutive days, in a 92 × 92 cm open field with an opaque, white Plexiglas floor and shellacked wooden walls 62 cm high. The floor of the field was divided into 16 squares (each 23 × 23 cm) by a grid of six black lines painted on the floor surface. 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 case was removed from the colony room and placed in the procedure room containing the open field. One hr later, the subject was removed from her cage and placed in a randomly selected corner of the open field, facing the field's center. During the next 5 min, an observer recorded the number of instances of scent marking exhibited by the subject. Scent marking was defined (Clark, Malenfant, Winter, & Galef, 1990) as an active lowering of the belly and dragging of the ventral scent pad across either a peg or the floor of the arena.

At the end of the 5-min test session, the subject was returned to its home cage and transported back to the colony room. The floor of the open field was then cleaned with a 75% alcohol solution and rinsed with distilled water before the next subject was tested.

Each subject was assigned a single scent-marking score equal to the average number of times it scent marked/5 min in the open field.

First Delivery

After testing, each female's cage was examined twice daily (10:00 A.M. and 4:00 P.M.) for delivery. As soon as a litter was found, the male and female pups were counted, and the litter was reduced to 2 male and 2 female pups. Dam and litter were then left undisturbed until the litter was weaned, 35 days after its birth.

Second Mating, Testing, and Delivery

Two days following weaning of a dam's first litter, she was once again placed in the cage of a sexually proven adult male. The cage was monitored to determine when the pair mated, and the male was removed when the female was conspicuously pregnant. Beginning on the 21st day of gestation, each dam's scent-marking behavior was observed in the open field for 5 min/day for 4 consecutive days. After testing, the cage of each pregnant female was examined twice daily for the presence of a litter and the number of both male and female pups was counted as soon as a litter was found. The experiment ended with the birth of each female's second litter.

Results

Description of First and Second Litters

Each of the 35 subjects gave birth to two litters that did not differ significantly in size, sex ratio, or in number of males that they contained (Mean ± *SE*: size of first litter = 6.8 ± 0.3 pups; size of second litter, 6.9 ± 0.3 pups; sex ratio of first litter 45.6 ± 3.3%, sex ratio of second litter 50.5 ± 3.6%; number of males in first litter 3.2 ± 0.2 males, number of males in second litter 3.5 ± 0.3 males).

Although there was a tendency for subjects to scent mark more frequently

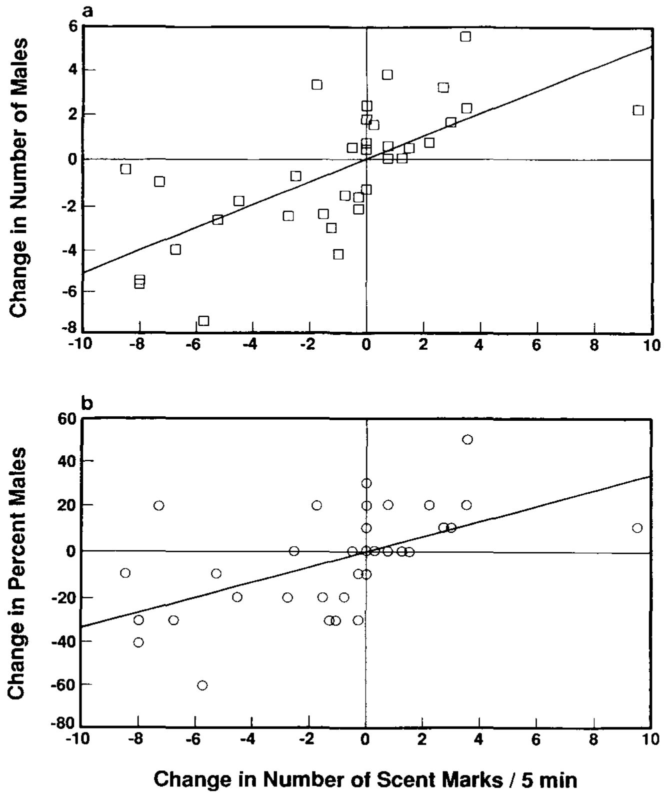

Fig. 1. (a) The relationship between the change from first to second pregnancy in each female's scent-marking scores and the change in sex ratios between her first and second litters. (b) The relationship between the change from first to second pregnancy in each female's scent-marking scores and the change in the number of males between her first and second litters.

during their second pregnancy than during their first (Mean ± *SE*: first pregnancy, 2.6 ± 0.5 scent marks/5 min; second pregnancy 3.7 ± 0.7 scent marks/5 min), this difference was not statistically reliable, related t test, $t = 1.63$, $p < 0.11$.

Interlitter Changes in Litter Composition and Behavior

The main results of Experiment 1 are presented in Figures 1a and 1b. Figure 1a shows the relationship between the change from first pregnancy to second pregnancy in each female's scent-marking score and the change from first litter to second litter in the sex ratios of each female's first two litters; Figure 1b shows the relationship between the change from first pregnancy to second pregnancy in each female's scent-marking score and the change from first litter to second litter in the number of males in each female's first two litters.

As can be seen in Figure 1a, changes in sex ratio between females' first and second litters and changes in females' scent-marking behavior during first and second pregnancies were positively correlated, Spearman's $r = 0.75$, $p < 0.01$. Sixteen of the 17 dams whose second litters contained a higher percent of males than did their first litters scent marked more frequently during their second pregnancy than during their first; only 5 of 11 females that had a lower percentage of males in their second litters than in their first showed an increase in scent marking between successive pregnancies, $\chi^2 = 14.0$, $df = 1$, $p < 0.001$.

Similarly, as can be seen in Figure 1b, changes in females' scent-marking scores between first and second pregnancies were significantly positively correlated with the change in the number of males in their first and second litters, Spearman's $r = 0.56$, $p < 0.001$. All 14 dams whose second litters contained more males than did their first litters and that exhibited a change in scent-marking frequency between first and second pregnancies scent marked more frequently during their second pregnancy than during their first pregnancy; only 2 of 10 females that had fewer males in their second litter than in their first litter and exhibited a change in scent-marking frequency marked more frequently during their second pregnancy than during their first, Fisher's exact probability test, $p < 0.001$.

As mentioned in the introduction to Experiment 1, correlations between behavior and the gender composition of gestated litters based on observation of single reproductive episodes can be difficult to interpret because of the possibility of correlated individual differences in the tendency of females to scent mark and to bear male-biased litters. Consistent with such a possibility, we found significant correlations across first and second litters both in individual female's scent-marking scores, Spearman's $r = 0.44$, $p < 0.05$, and in individual female's probabilities of delivering male-biased litters, Fisher's exact probability test, $p < 0.02$.

We also found significant positive correlations both (1) between individual female's scent-marking scores and the sex ratios of each of their first two litters, first litter, Spearman's $r = 0.35$, $p < 0.04$; second litter, Spearman's $r = 0.54$, $p < 0.01$; and (2) between individual female's scent-marking scores and the number of males in each of their first two litters, first litter, Spearman's $r = 0.33$, $p < 0.05$; second litter, Spearman's $r = 0.35$, $p < 0.04$.

Discussion

Taken together, the results of Experiment 1 show: first, that individual female gerbils tended to be consistent both in their relative frequencies of scent marking and in their tendencies to deliver male-biased or female-biased litters and, second, that the frequency of scent marking exhibited by individual females during pregnancy was modified in accord with the gender composition of the litters that they bore. Increases either in the number of fetal sons that a female carried or in the sex ratio of her litter were correlated with increases in the frequency of her scent-marking behavior.

Experiment 2

Experiment 2 was undertaken to examine potential hormonal mediators of the correlations found in Experiment 1 between the gender composition of each of the litters that dams carried and their frequencies of scent marking late in gestation.

We have previously reported, for male gerbils (Clark, vom Saal, & Galef, 1992), significant correlations among (1) testosterone levels, (2) scent-marking frequency, and (3) size of ventral glands (ventral gland size is an adrogen-sensitive morphological characteristic in both male and female gerbils: Blum & Thiessen, 1971; Thiessen et al., 1968; Yahr & Thiessen, 1972). We therefore anticipated finding positive correlations among (1) frequency of scent marking, (2) ventral gland size, and (3) testosterone levels in pregnant female gerbils. The correlations of particular interest in the present study were those between the above three correlated dependent variables and the gender composition of litters carried by pregnant females.

Methods

Subjects

Forty-eight, nulliparous female Mongolian gerbils from the McMaster Psychology Department vivarium served as subjects.

Procedure

Mating and Maintenance

Subjects were maintained and mated as described in Experiment 1.

Measuring Scent Marking

Starting on the 21st day of gestation, each female's scent-marking behavior was measured for 4 consecutive days, as described in Experiment 1.

Collection of Blood Samples

On Day 25 of gestation, 1 day before the expected date of delivery of each female and 1 day after her scent-marking test was completed, we (1) anesthetized her with ether, (2) measured the maximum length and maximum width of her ventral gland, (3) externalized her uterus and determined the sex of each of the fetuses that she was carrying (Clark & Galef, 1990), (4) collected blood samples by cardiac puncture, (5) centrifuged the blood in heparinized capillary tubes for 20 min at −4°C, and (6) stored the plasma at −110°C for later assay.

Radioimmunoassay of Plasma Samples

Plasma levels of progesterone, testosterone, estradiol, and corticosterone were analyzed using the radioimmunoassay technique described in detail in a study by Moore and colleagues (1985) with four modifications. First, plasma samples were allowed to equilibrate overnight with 1000 cpm of each radioactive steroid hormone for recovery determination. Second, corticosterone was eluted with 4.0 ml of 50% ethyl acetate in isooctane. Third, the antibodies used in assays were: for progesterone, Niswender antiprogesterone No. 337-11 BSA (Colorado State University, Ft. Collins, CO) at 1 : 2500 dilution; for testosterone, lyophilized antitesterone No. T3003 (Wien Laboratories, Succasunna, NJ) reconstituted in

30-ml Phosphate buffer saline; for estradiol, No. ED17-94 (Endocrine Sciences, Tarzana, CA) at 1 : 80 dilution; and for corticosterone, No. B21-42 Endocrine Sciences, Tarzana, CA) at 1 : 80 dilution. Finally, the tracers used for progesterone (#NET–724), testosterone (#NET-553), estradiol(#NET-517), and corticosterone (#NET-399) were supplied by New England Nuclear (Boston, MA). The intra- and interassay coefficients of variation were as follows: for progresterone, 1.1 and 13.9%, for testosterone, 1.8 and 8.4%, for estradiol, 1.4 and 10.5%, and for corticosterone, 1.3 and 15.5%, respectively. The sensitivities of the assays for progesterone, testosterone, and estradiol were 1.9 pg and for corticosterone 7.8 pg.

Results and Discussion

The main results of Experiment 2 are presented in Table 1, which shows correlations among litter characteristics, dams' characteristics, and dams' hormone levels on the last day of gestation. As can be seen in Table 1, two of the findings of Experiment 1 were replicated in Experiment 2. We found significant correlations between the scent-marking scores of dams and both (1) the sex ratios of litters and (2) the number of males in litters.

More important, the results of the present experiment demonstrate strong positive correlations between both the number of male fetuses in a litter and the sex ratios of fetal litters and (1) testosterone levels, (2) sizes of ventral glands, and (3) scent-marking frequencies exhibited by gestating dams. Those females with a relatively high proportion of male fetuses in their litters, or that delivered relatively large numbers of male pups, scent marked relatively frequently and had both relatively large ventral glands and relatively high plasma testosterone levels.

The picture that emerges from Table 1 is entirely consistent with the view that the testes of fetal male gerbils secrete testosterone, which enters the bloodstream

Table 1
Relationships Among Litter Characteristics, Dams' Behavior, Morphology, and Hormone Levels

	Scent Marks	Ventral Gland Size	Testosterone	Estradiol	Cortisol	Progesterone
# males	0.35**	0.36**	0.55***	0.36**	0.26	−0.19
sex ratio	0.47***	0.36**	0.46***	0.32*	0.20	−0.08
# females	−0.38**	−0.19	−0.31*	−0.16	−0.06	−0.10
scent marks	—	0.68****	0.27*	0.17	0.02	−0.19
ventral gland size	—	—	0.27**	0.12	0.07	−0.12
Testosterone	—	—	—	0.08	0.05	−0.15
Estradiol	—	—	—	—	0.41**	−0.04
Cortisol	—	—	—	—	—	0.05

Note. All cell entries are *r* values for Spearman rank order correlations.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table 2
Correlations Between Number of Males/Litter and Testosterone Levels, Ventral Glands Sizes and Scent Marking Frequencies of Dams Delivering Litters of 7 or 8 Pups

Litter Size	# Males & Testosterone	# Males & Gland Size	# Males & Scent Marking
7 (n = 11)	0.55*	0.20	0.71**
8 (n = 15)	0.79**	0.30	0.44*

Note. Cell entries are r values for Spearman rank order correlations.
* $p < 0.05$.
** $p < 0.01$.

of their dams and results in increases in both the size of the ventral glands of pregnant females and their frequencies of scent marking.

On this view, the significant negative correlations shown in Table 1 between the number of females in a litter and both dams' testosterone levels and scent-marking frequencies reflect the negative correlation between the number of females and number of males in litters, Spearman $r = -0.39$, $p < .007$. Also on the hypothesis that androgens from male fetuses are the hormonal mediators of observed correlations between the sex composition of litters and dams' behavior and morphology late in pregnancy, the significant positive correlations between estradiol levels and the number of males in and sex ratios of litters reflect aromatization of testosterone into estrogen.

Perhaps the most conservative way to analyze the data of the present experiment is to examine correlations between gender composition of litters of a constant size and (1) testosterone levels, (2) ventral gland sizes, and (3) frequencies of scent-marking behavior of dams late in pregnancy. Such analyses permit examination of relationships between the number of male fetuses that a female carried and other dependent variables unconfounded by any effects of the total number of pups that a female gestated on her behavior and morphology late in gestation. The present sample of 48 dams and their litters provided a sufficient number of litters containing both 7 and 8 pups to permit meaningful correlational analyses.

As can be seen in Table 2, females that delivered litters containing either 7 or 8 pups exhibited the same pattern of significant correlations between the number of males in their respective litters and their testosterone levels and frequencies of scent marking as did the total sample of 48 subjects. With increasing number or percentage of males in a litter (the two measures are perfectly correlated in litters of constant size), dams exhibited significantly higher levels of testosterone and significantly increasing frequencies of scent marking late in gestation.

The fact that the number of males that females delivered was significantly positively correlated with their ventral gland sizes for the entire sample of 48 dams, but not for litters of either 7 or 8 pups, suggests that ventral gland size may vary with the number of pups/litter as well as with the number of males/litter. Indeed, for the entire sample of 48 dams we found a significant positive correlation between litter size and ventral gland size, Spearman's $r = 0.32$, $p < .0.05$, almost as large as the correlation between the number of males/litter and the ventral gland sizes of females, Spearman's $r = 0.36$, reported in Table 1.

General Discussion

The results of both Experiments 1 and 2 are consistent with the hypothesis that male gerbil fetuses do, in fact, increase the testosterone levels of their dams and, consequently, affect both the behavior and morphology of their dams during gestation.

In Experiment 1, changes in gender composition of successive litters born by individual female gerbils were correlated with changes in their frequencies of scent marking. Others have shown that frequency of scent marking by female gerbils is affected by the levels of androgen to which females are exposed (Thiessen & Lindzey, 1970; Yahr, 1976). In Experiment 2, we found that the number of males that females carried was correlated with their plasma testosterone levels. Taken together, these findings suggest strongly that changes in dams' plasma testosterone levels, the result of testosterone secretion by male fetuses, resulted in changes in dams' frequencies of scent marking in successive pregnancies.

Of course, our results are all correlations and, as has been noted countless times before, correlation does not imply causality. Experimental studies are needed to investigate directly causal relationships between the gender composition of litters and the hormone levels, behavior, and morphology of pregnant females. Further experimental studies are also required to determine whether male fetuses actually secrete androgens directly into their dam's circulation or, in some fashion, stimulate their dams to produce androgens. Mongolian gerbils provide a model system in which such experiments can be undertaken without difficulty.

Notes

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