Physiology & Behavior, Vol. 49, pp. 239–243. © Pergamon Press plc, 1991. Printed in the U.S.A. 0031-9384/91 $3.00 + .00

Concentrations of Sex Steroid Hormones in Pregnant and Fetal Mongolian Gerbils

M. M. CLARK,*[1] D. CREWS AND B. G. GALEF, JR.*

**Department of Psychology, McMaster University, Hamilton, Ontario L8S 4K1, Canada*
Institute of Reproductive Biology, Department of Zoology, University of Texas, Austin, TX 78712

Received 6 June 1990

CLARK, M. M., D. CREWS AND B. G. GALEF, JR. *Concentrations of sex steroid hormones in pregnant and fetal Mongolian gerbils.* PHYSIOL BEHAV **49**(2) 239–243, 1991.—Sex steroid concentrations in the plasma of 24-day pregnant Mongolian gerbils (*Meriones unguiculatus*) and their male and female fetuses were measured using radioimmunoassays. It was found that, on Day 24 of gestation: (a) androgen levels were higher in those male fetuses developing adjacent to no female fetuses than in those male fetuses developing between two female fetuses and (b) androgen levels were higher in those female fetuses developing between two male fetuses than in those female fetuses with no immediate, male neighbours. Further, plasma taken from 24-day pregnant dams that had exhibited vaginal opening at a relatively early age had significantly lower androgen levels and significantly higher estradiol levels than did plasma taken from 24-day pregnant dams that had exhibited relatively late vaginal opening. The data provide direct evidence of hormonal mediation of previously described differences both in the morphology and reproductive biology of male and female adult gerbils as a function both of their fetal intrauterine locations relative to members of the other sex and of the age at vaginal introitus of their respective dams.

Fetal sex steroids Intrauterine position Maternal sex steroids Sex ratio Sexual maturation Mongolian gerbils

IN all litter-bearing rodent species examined to date (e.g., mice, rats, and gerbils), the intrauterine locations of male and female fetuses, relative to fetuses of same or different sex, have been found to correlate with their adult morphological and behavioral characteristics (1, 3, 5, 7, 9–14, 19, 24–27, 29–31). Such effects of intrauterine location on adult phenotype are, presumably, the result of the direct or indirect action of steroids that are excreted by fetuses, cross fetal membranes, and alter the internal hormonal milieu of co-residents of a uterine horn during a prenatal sensitive period (9, 25, 26, 28).

Intrauterine location relative to members of the other sex has been found to have substantial effects on the morphological and behavioral phenotypes of adult Mongolian gerbils (*Meriones unguiculatus*), the subject species in the experiment reported below (2, 3, 5). Most relevant to the present enquiry, adult female Mongolian gerbils that, as fetuses, occupied intrauterine locations adjacent to no males (0M females) are 1.4 to 4.0 times as likely to exhibit vaginal opening before weaning at 25 days of age than are female gerbils that resided as fetuses in intrauterine locations adjacent to one or two males (respectively, 1M and 2M females) (3). Effects of intrauterine location on age at vaginal introitus are of importance in understanding gerbil biology because the intrauterine location of female gerbils relative to males has profound effects on females' later reproductive life histories. Early-maturing (E-M) female gerbils have twice the lifetime fecundity of late-maturing (L-M) female gerbils (6); E-M female gerbils give birth to both a greater percentage of female offspring and a greater proportion of early-maturing daughters than do L-M female gerbils (6).

The reproductive performance of adult male gerbils is also affected by their intrauterine locations relative to members of the other sex. Those adult male gerbils that resided next to no females in utero (0F males) mount estrous females with shorter latencies and ejaculate after fewer intromissions than do adult male gerbils that resided between two females in utero (2F males) (5). Preliminary data indicate that 2F males are significantly less likely to impregnate females during a two-month period of interaction with them than are 0F males (unpublished authors' observation).

While effects of intrauterine location relative to members of the other sex similar to those seen in Mongolian gerbils have also been reported in house mice (26, 29, 30), in general, the intrauterine locations of fetal gerbils seem to have more profound effects on their future reproductive behavior than the intrauterine locations of house mice have on their future reproductive behavior. Consequently, Mongolian gerbils may provide a more useful preparation than house mice for examining effects of intrauterine location on reproductive biology at both individual and population levels of analysis.

Use of Mongolian gerbils to study effects of intrauterine location on adult reproductive behavior would be facilitated if something were known of the hormonal mediation of effects of intrauterine location on development in gerbils. Unfortunately, no direct measurements have yet been made of plasma hormone levels of fetal gerbils from known intrauterine locations. Several

[1]Requests for reprints should be addressed to Dr. Mertice M. Clark, Department of Psychology, McMaster University, Hamilton, Ontario L8S 4K1, Canada.

morphological and behavioral characteristics of adult gerbils, known to result from prenatal or neonatal exposure to androgens [increased anogenital distance (16), increased scent gland size (16), and increased scent-marking behavior (18, 20–22)] are associated both with increased uterine contact with male fetuses and decreased uterine contact with female fetuses. For example, 0F male gerbils have larger ventral scent glands, scent mark more frequently, and have larger anogenital distances than do 2F male gerbils (5); 0M female gerbils have significantly shorter anogenital distances than 1M or 2M female gerbils (unpublished author's observation). While such observations suggest that the effects of intrauterine location on development in gerbils may be androgen mediated, they provide only indirect evidence of differential prenatal exposure to steroids as a result of development in different intrauterine locations relative to members of the other sex.

The present experiment was undertaken to measure directly circulating concentrations of sex steroid hormones of fetal gerbils from known intrauterine locations. Because we were also interested in the possibility that the differences in the reproductive life histories of female gerbils born to E-M and L-M dams (6) briefly described above are associated with differences in the uterine hormonal environment provided for young by E-M and L-M dams, we also measured sex steroid levels in the blood of gerbil dams and statistically analyzed separately the hormone levels of male and female fetuses carried by E-M and L-M dams.

METHOD

Subjects

Thirty-three adult, female Mongolian gerbils (*Meriones unguiculatus*), born in the McMaster vivarium to stock acquired from Tumblebrook Farm (Brookfield, MA), and 144 of their fetuses at Day 24 of gestation served as subjects. Sixteen of the adult females had exhibited vaginal opening by 25 days of age [i.e., were early-maturing (E-M) females (6)] and 17 had exhibited vaginal opening after reaching 25 days of age [i.e., were late-maturing (L-M) females (6)]. All subjects participated in the experiment during the months of December, January, or February of 1988–1989.

Procedure

Mating. At 90 days of age, each of the 33 adult female subjects was placed with a sexually proven adult male from the McMaster colony in a $15 \times 30 \times 15$-cm polypropylene shoebox cage with a hardware cloth lid and a layer of wood-chip bedding (Beta-chip, Northeastern Products, Warrensburg, NY) on its floor. The date on which each pair mated was determined using time-lapse video recording. It was expected that a female would give birth 25 days following an observed copulatory episode.

All pairs were left undisturbed in a humidity- and temperature-controlled colony room, illuminated on a 12-h light/dark cycle, until the female in a pair was conspicuously pregnant (i.e., late in the second or early in the third week of pregnancy), when each male was removed from his mate's cage. Following removal of males, females were again left undisturbed until Day 24 of gestation.

Collection of blood samples. Twenty-four days following observed copulation, each female that had gained weight at a rate consistent with her impregnation on the day of observed copulation was anesthetized with ether, her uterus externalized, and her pups removed singly. The experimenter recorded the position and sex of each fetus. Fetal sex was determined on the basis of anogential distance, a method that has proven more than 99% accurate with gerbil fetuses on Day 24 of gestation (4).

Immediately following caesarian delivery, fetuses were anesthetized by hypothermia. Blood from fetuses and dams was collected by cardiac puncture, collected in heparinized capillary tubes, centrifuged for 20 min at -4°C, and the plasma stored at -110°C for later assay.

Classification of intrauterine position. The intrauterine position of each male and female fetus was classified with respect to the number of adjacent fetuses of the other sex using a method similar to that employed by vom Saal to describe the intrauterine position of mouse fetuses (24). Those female fetuses adjacent to no male fetuses were classified as 0M females, those between two male fetuses as 2M females, and those adjacent to only one male fetus as 1M females. Conversely, those male fetuses adjacent to no females were classified as 0F males, those adjacent to one female as 1F males, and those between two females as 2F males. For practical reasons, we classified our male fetuses with respect to their location relative to female fetuses rather than with respect to their location relative to male fetuses, as vom Saal (24) had done in mice. The median number of gerbil fetuses/intrauterine horn (3.0) is far smaller than the median number of mouse fetuses/intrauterine horn (6.0) and the frequency of 2M male gerbil fetuses was too low to provide sufficient numbers of 2M males for statistical analyses.

Radioimmunoassay of blood samples. Blood samples from both dams and their fetuses were analyzed using the radioimmunological technique described in detail in (15) with the following modifications: 1) the ratio of celite to propylene glycol to ethylene glycol in columns was 6:2:1 (w:v:v); 2) the antibodies used in assays were: for DHT and testosterone, Anti-T No. T3003 (Wien Laboratories, Succasunna, NJ) at 1:15,000 dilution and for estradiol No. ED17–94 (Endocrine Sciences, Tarzana, CA) at 1:5,200 dilution; and 3) the tracers used for DHT (No. NET-544), testosterone (No. NET-553) and estradiol (No. ENET-517) were supplied by New England Nuclear (Boston, MA).

Data analysis. Differences in plasma hormone levels were identified by matched *t*-tests, Student's *t*-tests, and one-way analyses of variance, as appropriate. In cases of significant nonhomogenity of variance, Mann-Whitney U-tests or median tests were employed.

RESULTS

Data Selection

More than 85% of fetal blood samples had both DHT and estradiol levels lower than the sensitivity of the assay (approximately 0.03 ng/ml). Consequently, fetal DHT and estradiol levels could not be examined. As a result, we discuss below only the testosterone assays of fetal plasma and the testosterone, DHT and estradiol assays of maternal plasma.

Data were discarded from: (a) 23 fetuses from which insufficient plasma (25 ml) was recovered for testosterone assay, (b) 4 fetuses and 11 adults with intraassay coefficients of variability (cvs) for testosterone >10% and (c) 26 fetuses in a single testosterone assay with an intraassay cv for the control sample of testosterone of 30.5%. Testosterone levels of 39 male fetuses, 35 female fetuses and 22 dams remained to be examined. Data were also discarded from 11 DHT and 10 estradiol assays of maternal plasma with intraassay cvs >10%. The intra- and interassay cvs of retained data were as follows: for testosterone: 6.9 and 1.4%, for DHT: 6.6 and 2.4%, and for estradiol: 3.9 and 15.7%.

Effects of Fetal Sex on Fetal Plasma Androgen Levels

Figure 1 presents data describing the levels of testosterone

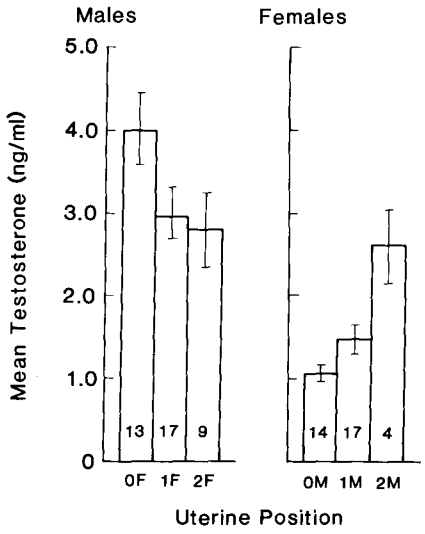

FIG. 1. Circulating concentrations (ng/ml) of testosterone in the plasma of male (left-hand panel) and female (right-hand panel) fetuses developing adjacent to 0, 1, or 2 fetuses of the opposite sex. Vertical bars indicate ±1 SE. Numbers within histograms refer to the number of fetuses in each group.

found in male and female fetuses as a function of their respective intrauterine positions relative to fetuses of the other sex. Within-litter analyses revealed that, on Day 24 of gestation, male gerbil fetuses had circulating levels of androgens (mean ± SE = 2.56 ± 0.21 ng/ml) almost twice as high as those of their female siblings [mean ± SE = 1.54 ± 0.16 ng/ml; matched *t*-test, $t(14) = 3.80$, $p<0.002$].

Effects of Intrauterine Location on Fetal Plasma Androgen Levels

As can also be seen in Fig. 1, intrauterine positions of both male and female fetuses, relative to fetuses of the other sex, had significant effects on plasma androgen levels in the fetus. Androgen concentrations in the plasma of male fetuses (left-hand panel of Fig. 1) decreased as the number of female fetuses adjacent to male fetuses increased, $F(2,37) = 3.68$, $p<0.05$, and 2F males had significantly lower androgen levels than did 0F males (Newman-Keuls test, $p<0.05$). Plasma androgen levels of female fetuses (right-hand panel of Fig. 1) increased as the number of male fetuses to which female fetuses were adjacent increased, $F(2,32) = 15.3$, $p<0.001$, and 2M females had significantly higher plasma androgen levels than did 0M females fetuses (Newman-Keuls test, $p<0.02$).

Effects of Litter Sex Ratios and Number of Males in Litters on Fetal Plasma Androgen Levels

As the proportion of males in a litter increased, the a priori probability that a female fetus would develop adjacent to one or more males increased, while the a priori probability that a male fetus would develop adjacent to one or more females decreased. Consequently, 2M females and 0F males tended to come from more male-biased litters than did 0M females and 2F males. It is, therefore, possible that the elevated plasma androgen levels observed in 2M females (relative to 0M females) reflected the higher proportion of males in litters containing 2M females (relative to litters containing 0M females), rather than differences in the intrauterine locations of 2M and 0M females per se. Similarly, it is also possible that the elevated plasma androgen levels observed in 0F males (relative to 2F males) reflected the higher proportion of males in litters containing 0F males than in litters containing 2F males, rather than differences in the intrauterine locations of 0F and 2F males. Plasma androgen levels in both 1M females and 1F males were, in fact, positively correlated with the proportion of males in the litters from which they were taken (1M females: Spearman's $r = .62$, $p<0.01$; 1F males: Spearman's $r = .45$, $p<0.05$).

The number of males per litter was also significantly positively correlated with the plasma androgen levels of both 1M females (Pearson's $r = .45$, $p<0.05$) and 1F males (Pearson's $r = .52$, $p<0.025$). In sum, with intrauterine location relative to fetuses of the other sex held constant at one member of the opposite sex, both the sex ratios of litters and number of males/litter were positively correlated with fetal androgen levels.

Effects of Intrauterine Position on Plasma Androgen Levels Independent of Number of Males/Litter or Sex Ratios of Litters

In 10 of 12 litters in which males were found in two intrauterine locations relative to females, the male located adjacent to fewer females had higher plasma androgen levels than did the male located adjacent to a greater number of females (Sign Test, $p<0.02$). Similarly, in 9 of 13 litters in which female fetuses were found in two intrauterine locations relative to males, the female fetus adjacent to a greater number of males had higher plasma androgen levels than did the female fetus adjacent to fewer males (Sign Test, $p<0.05$). Thus with both the sex ratios of litters and number of males/litter held constant, intrauterine position relative to fetuses of the opposite sex was correlated with androgen levels in fetal plasma. Taken together, the results described in the present and preceding sections indicate that fetal androgen levels were correlated both with fetal positions and with the sex compositions of litters.

Levels of Testosterone, DHT, and Estradiol in Plasma From Early- and Late-Maturing Gerbil Dams

As can be seen in Fig. 2, on Day 24 of gestation those dams that had exhibited vaginal opening before reaching 25 days of age (E-M dams) exhibited a different hormonal profile than did those gerbil dams that had exhibited vaginal opening after reaching 25 days of age (L-M dams). Plasma of L-M dams contained both significantly higher concentrations of androgens [testosterone: $t(20) = 2.01$, $p<0.05$; DHT: Mann-Whitney U-test, $U = 25$, $p<0.04$] and significantly lower levels of estradiol (Mann-Whitney U-test, $U = 33$, $p<0.05$) than did plasma of E-M dams.

Relationship of Maternal Age at Vaginal Opening to Levels of Fetal Androgens

As can be seen in Fig. 3, the plasma androgen levels of both 1F male fetuses and 1M female fetuses carried by E-M dams were lower than the plasma androgen levels of 1F male and 1M female fetuses carried by L-M dams [both t's(15)>2.15, both p's<0.05]. Thus, with intrauterine location held constant, the ages at vaginal opening of dams of both male and female fetuses were correlated with their respective fetuses' plasma androgen levels at Day 24 of gestation.

The relationship between age at vaginal introitus of dams and androgen levels of fetuses is complicated by the fact that litters carried by L-M dams were more male-biased than were litters

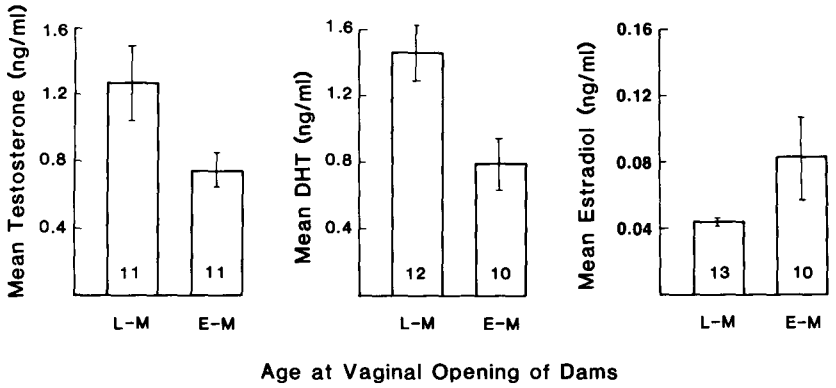

FIG. 2. Circulating concentrations (ng/ml) of testosterone (left-hand panel), dihydrotestosterone (middle panel) and 17-β estradiol (right-hand panel) in the plasma of E-M and L-M dams on Day 24 of gestation. Vertical bars indicate ± 1 SE. Numbers within histograms refer to the number of dams in each group.

carried by E-M dams (6). In the present experiment, L-M dams had litters with both significantly more male fetuses (mean ± SE = 4.2 ± 0.4 male fetuses) and a significantly higher proportion of male fetuses (mean ± SE = 0.60 ± 0.04) than did E-M dams [mean ± SE = 2.6 ± 0.3 male fetuses and 0.37 ± 0.03 male fetuses; both t's(15)>3.35, both p's<0.02]. Thus the differences observed in plasma androgen levels of fetuses carried by E-M and L-M dams might reflect differences in the number or proportion of males carried by E-M as compared with L-M dams. Consistent with such an interpretation were significant positive correlations between both the number and percentage of males in a litter and circulating levels of testosterone in maternal plasma (number of males/litter: Pearson's r = .55, p<0.025; proportion of males/litter: Spearman's r = .38, p<0.05).

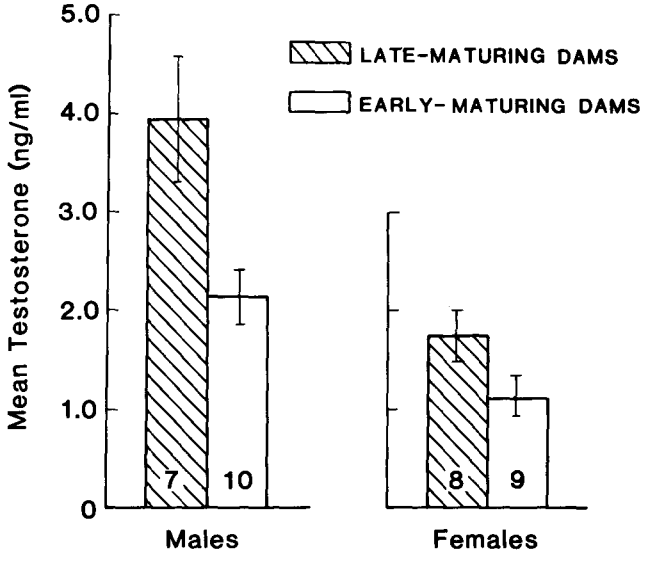

FIG. 3. Circulating concentrations of testosterone (ng/ml) in the plasma of male (left-hand panel) and female (right-hand panel) fetuses developing adjacent to one fetus of the opposite sex whose dams were either early-maturing (E-M) or late-maturing (L-M). Vertical bars indicate ± 1 SE. Numbers within histograms are the number of fetuses in each group.

Relationship of Plasma Androgen Levels in the Fetus and in the Dam

Maternal androgen levels were significantly positively correlated with the androgen levels of their sons (Pearson's r = .35, p<0.05), but not of their daughters (Pearson's r = −.10, p>0.10).

DISCUSSION

The present study was undertaken: first, to determine whether the intrauterine positions of fetal gerbil pups relative to fetuses of the other sex were correlated with their respective androgen levels and, second, to determine whether there were differences in the internal hormonal milieu of gerbil pups gestated by early- and late-maturing dams. The data show that intrauterine positions of both male and female gerbil fetuses, independent of the sex ratio or number of males in their respective litters, were correlated with fetal androgen levels: (a) Female gerbil fetuses, like female mouse fetuses, developing in intrauterine locations adjacent to males had higher concentrations of androgens in their plasma than did female gerbil fetuses developing in intrauterine locations without immediate male neighbors. (b) Male gerbil fetuses developing adjacent to females had lower plasma concentrations of androgen than did male fetuses developing without immediate female neighbours. On the other hand, with intrauterine location relative to members of the opposite sex held constant, we found (a) significant positive correlations between both the number and proportion of male fetuses in a litter and fetal androgen levels of that litter and (b) a significant positive correlation between circulating concentrations of androgens in dams and their respective male fetuses, findings not reported in mice (27).

Data from studies of rodent species other than mice are consistent with the conclusion that factors other than number of adjacent males may influence fetal androgen levels. Both in hamsters, where the number of males caudal rather than adjacent to a given fetus affects its androgen levels (23), and in rats, where both the number of males caudal to a fetus (14) and the number of males present in utero (8,19) affect the degree of masculinization of females, the sex ratio of litters or the number of males in a litter seem to affect fetal androgen levels.

Our data also clearly indicated that the age at vaginal opening of a dam was correlated with both sex steroid levels in her plasma (Fig. 2) and androgen levels in her male and female fetuses (Fig.

3) on Day 24 of gestation. However, significant correlations among numbers of males in litters, proportions of males in litters, age at vaginal opening of dams, and plasma steroid levels of both dams and fetuses will make unravelling of the causal nexus responsible for the observed interrelationships particularly difficult. It is, for example, possible that in gerbils, as in monkeys (17), male fetuses are an important source of maternal androgens and that maternal androgen levels affect the androgen levels of female fetuses.

Regardless of its cause, the fact that those female fetuses gestated by L-M mothers are exposed to higher levels of maternal androgens (and lower levels of maternal estradiol) than are those female fetuses gestated by E-M mothers suggests that differences in rate of sexual maturation exhibited by daughters of E-M and L-M dams (3,6) may be mediated by their dams respective sex steroid hormone levels. Further, the finding of higher androgen levels in female fetuses developing adjacent to two males than in female fetuses developing adjacent to no males suggests that the greater frequency of E-M females developing in 0M than in 2M intrauterine locations (3) may also be mediated by sex steroid hormones.

ACKNOWLEDGEMENTS

This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada to both M.M.C. and B.B.G., Jr. and by a National Institute of Mental Health (MH41770) and a Research Scientist Award to D.C. We wish to express our thanks to Yuki Morris for performing the radioimmunoassays and to Fred vom Saal for his helpful comments on an earlier draft of the manuscript.

REFERENCES

1. Brown, M. J.; Schultz, G. S.; Hilton, F. K. Intrauterine proximity to male fetuses predetermines level of epidermal growth factor in submandibular glands of adult female mice. Endocrinology 115: 2318–2323; 1984.
2. Clark, M. M.; Bone, S.; Galef, B. G., Jr. Intrauterine positions and schedules of urination: Correlates of differential maternal anogenital stimulation. Dev. Psychobiol. 22:389–400; 1989.
3. Clark, M. M.; Galef, B. G., Jr. Effects of intrauterine position on rate of sexual development in female Mongolian gerbils. Physiol. Behav. 42:15–18; 1988.
4. Clark, M. M.; Galef, B. G., Jr. Sexual segregation in the left and right horns of the gerbil uterus: 'The male embryo is usually on the right, the female on the left' (Hippocrates). Dev. Psychobiol. 23:29–37; 1990.
5. Clark, M. M.; Malenfant, S. A.; Winter, D. A.; Galef, B. G., Jr. Fetal intrauterine position affects copulation and scent marking by adult male gerbils. Physiol. Behav. 47:301–305; 1990.
6. Clark, M. M.; Spencer, C. A.; Galef, B. G., Jr. Reproductive life history correlates of early and late sexual maturation in female Mongolian gerbils (*Meriones unguiculatus*). Anim. Behav. 34:551–560; 1986.
7. Clemens, L. G. The neurohormonal control of male sexual behavior. In: Montagna, W.; Sadler, W. A., eds. Reproductive behavior. New York: Plenum Press; 1974:25–53.
8. Clemens, L. G.; Coniglio, L. P. Influence of prenatal litter composition on mounting behavior of female rats. Am. Zool. 11:617–618; 1971.
9. Clemens, L. G.; Gladue, B. A.; Coniglio, L. P. Prenatal endogenous androgenic influences on masculine sexual behavior and genital morphology in female rats. Horm. Behav. 10:40–53; 1978.
10. Gandelman, R.; vom Saal, F. S.; Reinisch, J. M. Contiguity to male foetuses affects morphology and behavior of female mice. Nature 266:722–724; 1977.
11. Kinsley, C.; Konen, C.; Miele, J.; Ghiraldi, L.; Svare, B. Intrauterine position modulates maternal behaviors in female mice. Physiol. Behav. 36:793–799; 1986.
12. Kinsley, C.; Mield, J.; Konen, C.; Ghiraldi, L.; Svare, B. Intrauterine contiguity influences regulatory activity in adult female and male mice. Horm. Behav. 20:7–12; 1986.
13. Kinsley, C.; Mield, J.; Wagner, C. K.; Ghiraldi, L.; Broida, J.; Svare, B. Prior intrauterine position influences body weight in male and female mice. Horm. Behav. 20:201–211; 1986.
14. Meisel, R. L.; Ward, I. Fetal female rats are masculinized by male littermates located caudally in the uterus. Science 213:239–241; 1981.
15. Moore, M. C.; Whittier, J. M.; Crews, D. Sex steroid hormones during the ovarian cycle of an all-female parthenogenetic lizard and their correlation with pseudosexual behaviour. Gen. Comp. Endocrinol. 60:140–153; 1985.
16. Raible, L. H.; Gorzalka, B. B. Neonatal testosterone propionate treatment in the female gerbil: Morphological and behavioral effects. Behav. Neurosci. 101:215–218; 1987.
17. Resko, J. A. Androgen secretion by the fetal and neonatal rhesus monkey. Endocrinology 87:680–687; 1970.
18. Thiessen, D. D.; Friend, H. C.; Lindzey, G. Androgen control of territorial marking in the Mongolian gerbil. Science 160:432–435; 1968.
19. Tobet, S. A.; Dunlap, J. L.; Gerall, A. A. Influence of fetal position on neonatal androgen-induced sterility and sexual behavior in female rats. Horm. Behav. 16:251–258; 1982.
20. Turner, J. W., Jr. Influence of neonatal androgen on the display of territorial marking in the gerbil. Physiol. Behav. 15:265–270; 1975.
21. Turner, J. W., Jr. Sex differences in the response to neonatal steroid treatment in the Mongolian gerbil. Physiol. Behav. 33:173–177; 1984.
22. Turner, J. W., Jr.; Carbonell, C. Effect of perinatal antisteroid treatment on territorial marking behavior in the Mongolian gerbil. Neuroendocrinology 41:207–212; 1985.
23. Vomachka, A. J.; Lisk, R. D. Androgen and estradiol levels in plasma and amniotic fluid of late gestational male and female hamsters: intrauterine position effects. Horm. Behav. 20:181–193; 1986.
24. vom Saal, F. S. Variation in phenotype due to random intrauterine positioning of male and female fetuses in rodents. J. Reprod. Fertil. 62:633–650; 1981.
25. vom Saal, F. S. Sexual differentiation in litter-bearing mammals: Influence of sex of adjacent fetuses in utero. J. Anim. Sci. 67:1824–1840; 1989.
26. vom Saal, F. S.; Bronson, F. H. In utero proximity of female mouse fetuses to males: Effects on reproductive performance during late life. Biol. Reprod. 19:842–853; 1978.
27. vom Saal, F. S.; Bronson, F. H. Sexual characteristics of adult female mice are correlated with their blood testosterone levels during prenatal development. Science 208:597–599; 1980.
28. vom Saal, F. S.; Dhar, M.; Even, M. Intrauterine blood flow, intrauterine transport of steroids, and the intraintrauterine position phenomenon in rats. Paper presented at the Conference on Reproductive Behavior, Saratoga Springs, NY; June, 1989.
29. vom Saal, F. S.; Grant, W. M.; McMullen, C. W.; Laves, K. S. High fetal estrogen concentrations: Correlation with increased adult sexual activity and decreased aggression in male mice. Science 220: 1306–1309; 1983.
30. vom Saal, F. S.; Moyer, C. L. Prenatal effects on reproductive capacity during aging in female mice. Biol. Reprod. 32:1116–1126; 1985.
31. Wechman, R., Jr.; Brown, M.; Hilton, F. Intrauterine position affects sex-accessory biochemistry in adult female mice. Biol. Reprod. 33:803–807; 1985.