

Pregnancy and copulatory behavior in random-bred house mice mated in postpartum estrus

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Sixteen male-female pairs of random-bred house mice were studied in a total of 61 matings in postpartum estrus. An array of behavioral measures and measures related to resulting pregnancies were determined. Measures of copulatory behavior were comparable to those in hormone-induced estrus. There was no evidence that the number of preejaculatory intromissions, the total number of intravaginal thrusts, or any other behavioral measure was related to any aspect of pregnancy measured. Thus, the paradox of a considerable amount of male copulatory behavior coupled with a low stimulus requirement for pregnancy in female house mice reported in earlier studies appears unattributable to effects of domestication, mode of estrus, or failure to permit females to carry litters to term.

In both laboratory rats and house mice a functional luteal phase occurs only if the animal mates or receives similar vaginal stimulation. In both species the occurrence of ejaculation is usually preceded by a series of vaginal intromissions without sperm transfer (Beach & Jordan, 1956; McGill, 1962). In laboratory rats these preejaculatory intromissions have been demonstrated to be critical for pregnancy initiation (Adler, 1969; Wilson, Adler, & LeBoeuf, 1965). By contrast, although female mice receive much more stimulation than do female rats because of the male pattern of intravaginal thrusting (McGill, 1962), preejaculatory intromissions appear unnecessary for the initiation of a luteal phase (Land & McGill, 1967; McGill, 1972). The mere occurrence of the ejaculatory reflex appears sufficient for pregnancy initiation (McGill, 1970; McGill & Coughlin, 1970). Thus, house mice appear to be an exception to the otherwise orderly correlation between the amount of copulatory behavior delivered by the males and the stimulus requirements for pregnancy initiation in the females of different species (Dewsbury, 1978).

Studies of house mice have generally been conducted with domesticated mouse strains mating in cycling estrus following a sterile cycle and have emphasized the induction of luteal activity as a dependent variable. Several explanations have been proposed for the paradoxically low stimulus requirements of female mice (Dewsbury, 1978; McGill, 1977). Three will be considered here. First, because vaginal stimulation affects sperm transport (Adler, 1969), parturition (Diamond, 1972), and litter size (Davis, Gray, & Dewsbury, 1977)

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in other species, the possibility that preejaculatory stimulation may affect these aspects of pregnancy initiation in mice needs testing. Second, because stimulus requirements for pregnancy differ in postpartum vs. cycling estrus in other species (Dewsbury, in press; Davis & Connor, Note 1), the effects of postpartum estrus need study. Third, because domesticated strains have undergone considerable artificial selection for good breeding performance, it is possible that stimulus requirements for pregnancy have been lowered as a corollary response. Thus, nondomesticated mice should be studied. In the present study, nondomesticated mice were studied in tests that continued to parturition after mating in postpartum estrus.

METHOD

Subjects were 16 male-female pairs of house mice, *Mus musculus* of the random-bred WRL line. This line was bred via a true random-breeding program from the time of their trapping in a factory in Philadelphia, Pennsylvania (Connor, 1975, 1978). All mice were at least 90 days of age at the time of testing. Mice were housed in clear plastic cages 29 x 19 x 13 cm with wood shavings as bedding. Food and water were available at all times. The colony room was maintained on a reversed 14:10 photoperiod with light onset at 1800 h.

The original design called for experimental manipulation of the number of preejaculatory intromissions. However, variability among different pairs and tests was so great that the original design was dropped and a correlational design adopted. Each pair was permitted to produce at least one litter. An attempt was then made to conduct four tests of each pair in subsequent periods of postpartum estrus. In fact, 13 pairs completed all four tests, while 3 pairs completed three tests each, for a total of 61 successful tests.

At the time of the weaning of a previous litter (21 days), the male and female were separated by a hardware cloth barrier placed in the center of the cage. Cages were checked daily for the birth of new litters. At approximately 1600 h on the afternoon of the day on which a litter was found, the barrier was removed and the mice permitted to copulate for one complete

ejaculatory series (see McGill, 1962). The barrier was then re-introduced. Twelve behavioral measures, defined as in McGill (1962), were recorded for each test. Cages were checked each morning for the birth of a new litter; the occurrence or non-occurrence of a litter, litter size, and gestation period were determined. If a litter was born, the next test was conducted on the afternoon of the birth of that litter; the barrier remained in place except for the period of the test. If no litter was born, the barrier was removed and the mice permitted to breed until another postpartum estrus occurred. Similarly, the barrier was left out if a pair failed to copulate when tested.

RESULTS

The 61 tests produced a total of 42 pregnancies and 19 failures to deliver a litter. It is unlikely that any litters were missed, as in the 19 failures females showed no increase in body size, nor were any remnants of pups found. The mean litter size was 5.8 (range = 2-9) and the mean gestation period was 27.9 days (range = 23-33).

Measures of copulatory behavior, defined as in McGill (1962), are presented in Table 1. Also presented are values for mice of the same genotype tested in hormone-induced estrus, taken from Dewsbury, Oglesby, Shea, and Connor (in press). Measures were not greatly affected by mode of estrus induction. Whereas males delivered a mean of 11.5 intromissions and 182.2 thrusts in hormone-induced estrus, they delivered a mean of 12.3 intromissions (range = 1-73) and 126.3 thrusts (range = 20-555) in the present study.

Using *t* tests, behavioral data from the 42 tests resulting in pregnancy were compared with those from the 19 tests resulting in no pregnancy. There were no significant differences. For example, the mean numbers of intromissions in tests with and without pregnancies were 12.2 and 12.6, respectively ($t = .09$). The mean total numbers of thrusts were 126 and 127, respectively ($t = .04$).

The pregnancy rates for females receiving relatively few intromissions were comparable to the overall rate of 69% (42/61). For example, 16 of the 22 tests in which males ejaculated after three or fewer intromissions

resulted in pregnancies (73%). All three tests in which the male ejaculated on the first intromission resulted in pregnancies.

For the 61 tests there were no significant correlations between the number of offspring produced and any behavioral measure. For example, the correlation of the number of offspring with the number of intromissions was $+0.04$; that with the total number of thrusts was $+0.03$. Similarly, when just the 42 tests with litters were considered, correlations between litter size and behavioral measures lacked statistical significance (e.g., for number of intromissions, $r = +.10$; for number of thrusts, $r = +.08$).

DISCUSSION

Behavioral data obtained in the present study were generally of the same order of magnitude as those obtained for this strain in hormone-induced estrus (Dewsbury et al., in press). This suggests that these modes of estrus induction produce only relatively small quantitative differences in copulatory behavior.

The data on pregnancy initiation are fully consistent with the earlier data of McGill and his associates. There is no evidence of a role of amount of vaginal stimulation or other behavioral parameters in the initiation of any aspect of pregnancy measured in these tests. Although earlier research was conducted on domesticated strains tested in cycling estrus with only the occurrence of the luteal phase as a dependent variable, the present research used mice random bred from wild-trapped mice, postpartum estrus, and permitted females to carry litters to term. Thus, domestication, mode of estrus, and effects on sperm transport, parturition, and litter size provide no explanation for the paradoxically low stimulus requirements for pregnancy initiation in house mice.

The best available explanation for the low stimulus requirement of female house mice is that it is an adaptation to ensure pregnancy initiation on occasions in which males ejaculate quickly (Dewsbury, 1978; McGill, 1977). Such occasions occur with some frequency in some strains (as in the present study), may be particularly characteristic of dominant males, may be facilitated by pauses within ejaculatory series, and may be a function of a lack of full recovery from previous copulatory activity (Dewsbury, 1978; McGill, 1977; Mosig & Dewsbury, 1976). However, while this may explain the low stimulus requirements of the females, it leaves unexplained the substantial

Table 1
Measures of Copulatory Behavior in Postpartum and Hormone-Induced Estrus

| Measure | Postpartum Estrus | | Hormone-Induced Estrus* | |
|---------------------------------|-------------------|-------|-------------------------|-------|
| | Mean | SE | Mean | SD |
| Mount Latency | 434.0 | 67.0 | 291.6 | 55.4 |
| Intromission Latency | 530.8 | 77.4 | 373.4 | 69.6 |
| Ejaculation Latency | 824.3 | 129.9 | 699.4 | 117.4 |
| Mean Interintromission Interval | 78.1 | 13.9 | 58.2 | 6.8 |
| Time of Intromission | 12.9 | .7 | 15.6 | 2.6 |
| Time of Mounts | 2.4 | .2 | 2.3 | .4 |
| Ejaculation Duration | 19.6 | .9 | 16.1 | 1.2 |
| Preintromission Mount Duration | 1.4 | .1 | 1.6 | .2 |
| Total Number of Thrusts | 126.3 | 15.4 | 182.2 | 25.1 |
| Number of Intromissions | 12.3 | 2.0 | 11.5 | 1.9 |
| Thrusts per Intromission | 14.1 | .8 | 21.8 | 1.6 |
| Number of Mounts | 2.5 | .5 | 3.7 | 1.0 |

*From Dewsbury, Oglesby, Shea, and Connor (in press).

amount of preejaculatory behavior displayed by the male. In one strain there is a mean of 2 h, 132 intromissions, and 1,578 thrusts before ejaculation (Mosig & Dewsbury, 1976). The available literature provides no convincing indication of a biological function for this prolonged sexual activity. One anonymous reviewer of a previous manuscript suggested, "Perhaps domestication has emancipated mice from environmental constraints, and the species [sic.] which take two hours, 132 intromissions and 1578 thrusts to achieve ejaculation have simply become hedonists!" More likely, future research will reveal some, as yet undetermined, function for this behavior.

REFERENCE NOTE

1. Davis, H. N., & Connor, J. R. *Male modulation of female reproductive physiology during postpartum mating in Norway rats*. Paper presented at the Eastern Conference on Reproductive Behavior, Storrs, Connecticut, June 1977.

REFERENCES

- ADLER, N. T. Effects of the male's copulatory behavior on successful pregnancy of the female rat. *Journal of Comparative and Physiological Psychology*, 1969, **69**, 613-622.
- BEACH, F. A., & JORDAN, L. Sexual exhaustion and recovery in the male rat. *Quarterly Journal of Experimental Psychology*, 1956, **8**, 121-133.
- CONNOR, J. L. Genetic mechanisms controlling the domestication of a wild house mouse population (*Mus musculus* L.). *Journal of Comparative and Physiological Psychology*, 1975, **89**, 118-130.
- CONNOR, J. L. Development of inbred and random bred stocks of wild mice. *Mouse News Letter*, 1978, **58**, 61-62.
- DAVIS, H. N., GRAY, G. D., & DEWSBURY, D. A. Maternal age and male behavior in relation to successful reproduction by female rats (*Rattus norvegicus*). *Journal of Comparative and Physiological Psychology*, 1977, **91**, 281-289.
- DEWSBURY, D. A. The comparative method in studies of reproductive behavior. In T. E. McGill, D. A. Dewsbury, & B. D. Sachs (Eds.), *Sex and behavior: Status and prospectus*. New York: Plenum, 1978. Pp. 83-112.
- DEWSBURY, D. A. Copulatory behavior of deermice (*Peromyscus maniculatus*): III. Effects on pregnancy initiation. *Journal of Comparative and Physiological Psychology*, in press.
- DEWSBURY, D. A., OGLESBY, J. M., SHEA, S. L., & CONNOR, J. L. Inbreeding and copulatory behavior in house mice: A further consideration. *Behavior Genetics*, in press.
- DIAMOND, M. Vaginal stimulation and progesterone in relation to pregnancy and parturition. *Biology of Reproduction*, 1972, **6**, 281-287.
- LAND, R. B., & MCGILL, T. E. The effects of the mating pattern of the mouse on the formation of corpora lutea. *Journal of Reproduction & Fertility*, 1967, **13**, 121-125.
- MCGILL, T. E. Sexual behavior in three inbred strains of mice. *Behaviour*, 1962, **19**, 341-350.
- MCGILL, T. E. Induction of luteal activity in female house mice. *Hormones and Behavior*, 1970, **1**, 211-222.
- MCGILL, T. E. Preejaculatory stimulation does not induce luteal activity in the mouse *Mus musculus*. *Hormones and Behavior*, 1972, **3**, 83-85.
- MCGILL, T. E. Reproductive isolation, behavioral genetics, and functions of sexual behavior in rodents. In J. S. Rosenblatt & B. R. Komisaruk (Eds.), *Reproductive behavior and evolution*. New York: Plenum, 1977. Pp. 73-109.
- MCGILL, T. E., & COUGHLIN, R. C. Ejaculatory reflex and luteal activity induction in *Mus musculus*. *Journal of Reproduction and Fertility*, 1970, **21**, 215-220.
- MOSIG, D. W., & DEWSBURY, D. A. Studies of the copulatory behavior of house mice (*Mus musculus*). *Behavioral Biology*, 1976, **16**, 463-473.
- WILSON, J. R., ADLER, N., & LEBŒUF, B. The effects of intromission frequency on successful pregnancy in the female rat. *Proceedings of the National Academy of Sciences*, 1965, **52**, 1392-1395.

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