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Effects of space on the copulatory behavior of deer mice (*Peromyscus maniculatus*)

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The copulatory behavior of deer mice, *Peromyscus maniculatus*, was tested in two enclosures that differed in area by a factor of approximately 20. The latency for animals to come into close proximity was significantly longer in the larger enclosure. Once such proximity was achieved, copulation was very similar in the two enclosures. Only the mean interintromission interval in the first ejaculatory series varied significantly with cage size. Thus, the practice of testing these mice in small cages appears to have little effect on the parameters measured, as compared with behavior in larger enclosures.

The information gained from well controlled laboratory experiments in animal behavior provides an indispensable part of our understanding of many species. However, work in the laboratory usually involves gross departures from the natural environment of an animal. In many cases, it may be informative to investigate possible effects of parameters that obviously vary from field to laboratory.

One such parameter is the amount of available space. In most laboratory studies, the experimental space provided is much smaller than that available to the animal in the field. Although most investigators utilizing rodent species are sensitive to the possible behavioral effects of limited cage size, few studies explicitly examine the effects of space on behavior. There are, however, notable exceptions. Using two *Peromyscus* species, Hill (1977) found increases in ingestion and activity with a doubling of cage size, whereas Vestal and Hellack (1977) showed that the frequency of agonistic interactions did not vary with cage size. On the basis of these results, it appears that the effects of space may be behavior and species specific.

Typical investigations of rodent copulatory behavior are conducted in cages that provide only a small fraction of the space potentially usable by a pair in the field. No studies were located that directly measured copulatory behavior as a function of cage size uncontaminated by other variables. McClintock and Adler (1978) found changes in the copulatory behavior of *Rattus norvegicus* correlated with changes in cage size. However, interpretation of these data is complicated by several factors that varied in addition to cage size (e.g., several females were present in large-cage tests and tests were not conducted using hormone-induced estrus). McGill (1977) reported differences in the copulatory behavior of *Mus musculus* with cage size, but he provided only partial data. The present study was designed to investigate the effects of cage size, uncontaminated by other variables, on the copulatory pattern of a single species, deer mice, *Peromyscus maniculatus*.

P. maniculatus is a largely nocturnal muroid rodent that is widely distributed in North America and is found in a variety of habitats. Given the cryptic, nocturnal habits of this species, field observations of their sexual behavior would necessarily be difficult. Electrophoretic evidence suggests that at least some litters conceived in the field are of multiple paternity (Birdsall & Nash, 1973). The copulatory pattern of this species is characterized by multiple intromissions prerequisite to ejaculation, no intravaginal thrusting, multiple ejaculations, and no lock. This corresponds to Pattern 13 in Dewsbury's (1972) classification (Clemens, 1969; Dewsbury, 1979a).

METHOD

The animals used were 12 pairs of reproductively mature (i.e., 90-120 days old at start of experiment) *P. maniculatus* from the colony maintained at the University of Florida. They were laboratory-bred descendents of a group originally trapped near East Lansing, Michigan. The colony was maintained on a 16:8 photoperiod, with lights out at 0930 h. All animals were housed in 29 x 19 x 13 cm clear plastic cages.

The large enclosure was built on a plywood base measuring 4 x 8 ft. Three sides were plywood and the front was clear Plexiglas. The effective space usable by the animals measured 238 x 117 x 64 cm. A layer of San-I-Cel bedding approximately 2 cm deep covered the floor of the enclosure. Two 25-W red bulbs mounted on the top of the front panel of the enclosure provided illumination during testing. The small cages used were 48 x 27 x 13 cm of clear plastic. The floor space available in the large cage was approximately 20 times greater than in the small cages. San-I-Cel was used as bedding, and illumination was provided by two 25-W red bulbs placed behind the cage.

All testing began after the midpoint of the dark phase (1430 to 1530 h). Behavioral estrus was induced by an intramuscular injection of .06 mg estradiol benzoate approximately 72 h prior to testing, followed by an injection of .6 mg progesterone 4-6 h prior to testing.

All pairs were pretested in 48 x 27 x 13 cm clear plastic cages with San-I-Cel bedding. No animals were paired with siblings. Pretests were initiated by placing a female into the

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neutral cage, in which a male had been placed 30-60 min before. Pretests were terminated after no more than two ejaculations in an effort to minimize exposure to the small-cage situation before actual testing began. Only pairs that copulated in a pretest were used for testing. Several days prior to testing, mice were introduced individually into the large enclosure and allowed to explore it for approximately 1 h. Each pair was then tested twice in each cage size. Six pairs were tested in the large enclosure first, and six pairs were tested in the small cage first. After the first test for a pair, cage size alternated. All tests for an individual pair were separated by at least 2 weeks. Tests were initiated in the same manner as pretests; females were placed into a cage in which a male had been placed 30-60 min before. One hour was permitted for initiation of copulation. If a pair failed to copulate, they were tested in the same cage size approximately 2 weeks later. Tests were terminated when a pair reached a satiety criterion of 30 min with no intromissions or at 1730 h, when the lights went on.

The copulatory behavior of *P. maniculatus* consists of groups or "series" of mounts (with pelvic thrusting but no vaginal penetration), intromissions (with extravaginal thrusting and penetration, but no sperm transfer), and ejaculations (with extravaginal thrusting, penetration, and the emission of semen). Each complete series includes several intromissions, culminates in ejaculation, and is separated from other series by discernible intervals.

The following standard copulatory measures were recorded: mount latency (ML), the time (in seconds) from introduction of the female to the first mount or intromission; intromission latency (IL), the time (in seconds) from introduction of the female to the first intromission; ejaculation latency (EL), the time (in seconds) from the first intromission of a series to ejaculation; intromission frequency (IF), the number of intromissions to ejaculation; mount frequency (MF), the number of mounts preceding ejaculation; mean interintromission interval (MIII), the mean interval (in seconds) separating the intromissions of a series, including the interval between the last intromission and ejaculation; and postejaculatory interval (PEI), the time (in seconds) from ejaculation to the next intromission. An abbreviation followed by a hyphen and a number signifies the ejaculatory series to which it refers (e.g., MF-2). Ejaculation frequency (EF) refers to the number of ejaculations per satiety test. In addition to the standard copulatory measures, the latency for animals to come into close proximity (approximately one body length) was recorded (proximity latency, PL). All measures were recorded using an Esterline-Angus operations recorder.

RESULTS

Copulatory behavior in the two test situations was very similar. The basic pattern of behavior remained unchanged by cage size. In the large enclosure, pairs frequently utilized a small corner of the apparatus for a large proportion of their sexual behavior. Often this area was no larger than that available in the 48 x 27 x 13 cm cages, the standard cage size for observing copulatory behavior of this species in this laboratory. Typically, females run in a series of roughly concentric circles during copulation. A bout of circling usually ended with a mount, intromission, or ejaculation. In both size cages, the diameters of these circles were approximately equivalent.

An analysis of variance was used to assess differences in the copulatory measures due to cage size, run order (large vs. small cage first), and test number (first vs. second in a given cage size). (See Table 1.) Only EF and measures for the first two ejaculatory series were considered for the purposes of this analysis, as some pairs failed to achieve a third ejaculation on some tests. There were no significant effects due to either testing order or test number.

Table 1
Copulatory Measures in Large and Small Cages

Measure	Small Cage	Large Cage	F
EF	4.5	4.0	3.27
PL	46.0	448.7	24.60†
ML	660.2	1034.5	4.63
IL	685.8	1047.0	4.20
EL-1	275.7	391.7	2.85
IF-1	12.3	9.7	4.78
MF-1	1.5	1.0	1.03
MIII-1	35.1	59.6	5.50*
PEI-1	362.5	343.9	1.29
EL-2	133.7	117.4	1.02
IF-2	11.9	9.3	2.22
MF-2	1.0	.7	1.11
MIII-2	15.0	14.5	.19
PEI-2	410.2	428.9	.26

*$p < .05$. †$p < .001$.

The latency of animals to come into close proximity (PL) was significantly longer in the large cage. PL was on the average about 400 sec longer in the large cage. Both ML and IL were also approximately 400 sec longer in the large cage, although these differences were not significant ($F = 4.63$, $p < .06$; $F = 4.20$, $p < .07$). IF in the first series was larger in the small cage, and this difference also approached significance ($F = 4.78$, $p < .06$). The MIII in the first series was longer in the large cage than in the small cage. EF was similar in both size cages, and the values obtained were comparable to those found in other small cage studies (Dewsbury, 1979a).

In addition, the Test by Cage Size by Test Order interactions for ML, IL, and PL were significant. The longest latencies occurred in the first test, with those first tests occurring in large cages showing longer latencies than those occurring in small cages.

DISCUSSION

The copulatory behavior of *P. maniculatus* in small laboratory cages is very similar to that seen in enclosures approximately 20 times as large. Once the members of a pair have come into close proximity, copulation is often indistinguishable in the two environments, although the duration of MIII-1 was significantly longer in the large enclosure and the corresponding difference for IF-1 approached significance.

The longer MIIIs of the large-cage group were due, at least in part, to the behavior of those females that initially resisted the efforts of the male. These females often utilized a much greater portion of the large apparatus than did more receptive females. Resistant females in the small cages had no more area available than was typically used by their nonresistant counterparts and, as a result, presumably were able to exercise less control over the copulatory pattern.

In the large cages, by running from the male for longer periods of time, these females created, in effect, an "enforced interval" for the male (Larsson, 1956). Larsson demonstrated

that when male rats were separated from the female between intromissions for periods longer than the MIIIs usually seen in the laboratory, IF-1 decreased (the enforced interval effect). Similar results have been found in deer mice through the use of correlational techniques (Dewsbury, 1979b). This effect was not found in the second ejaculatory series, presumably because initially resistant females often become less resistant as copulation progresses.

McClintock and Adler (1978) found that wild and domestic *Rattus norvegicus* in large seminatural enclosures had MIIIs for first series that were two to three times those in small cages. The difference they found, with its correspondingly large difference in intromission frequency, is much greater than that found in this study. Several factors may be responsible for that difference. First, McClintock and Adler found that females were more likely to be resistant early in estrus (i.e., there were longer chases and more fights). Their large-enclosure animals were continuously videotaped for at least 1 week; copulations that occurred at any point in the estrous cycle were recorded. On the other hand, females for the small-enclosure comparison were selected on the basis of a cornified vaginal smear and the presence of lordosis in response to manual stimulation. Thus, copulations early in estrus, with the associated increase in MIIIs, were more likely to be seen in the large enclosure than in the small enclosure. Another factor contributing to the different findings of the studies under consideration here is that different species were involved. Although both *P. maniculatus* and *R. norvegicus* show copulatory Pattern 13 in Dewsbury's (1972) classification, their copulatory patterns were affected differently by space manipulations. As McClintock and Adler mention, their small cages were only about two body lengths in diameter. By comparison, the small cages used in this study for *P. maniculatus* were about six or seven body lengths long. While the relatively small cages used by McClintock and Adler did not allow for typical female solicitation, the small cages in this study apparently provided sufficient space for copulation to proceed more like it does in a larger area.

McGill (1977), using *Mus musculus* in cages differing in area by a factor of about six, also found longer MIIIs and lower IFs in large cages. It is not apparent from his data whether all pairs showed the effect or the effect was mainly due to a few resistant animals. McGill suggests that wild females may space intromissions further apart than in typical laboratory cages, thus decreasing time spent mating. Although in the present study we did not find such a decrease in EL, our data also suggest that an "enforced interval" may sometimes occur in the wild. The possible effects on physiology and relations to the social situation in the field remain to be investigated.

Although some quantitative measures of copulatory behavior may be significantly altered as a function of cage size, the overwhelming impression is that the course of the copulatory interaction is minimally altered once initial contact is made.

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