



On the role of individual differences in female odor and ultrasonic vocalizations for male's choice of partner[☆]



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HIGHLIGHTS

- Male rats spent more time with the female of first entry compared to the other females.
- Females' ultrasonic vocalizations have no role in male mate choice.
- Females' odor has no role in male mate choice.
- Male rat mate choice could just be random.

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ABSTRACT

Intrasexual competition for access to a female mate is believed to be unusual in wild male rats, which suggests that female choosiness could be important. Even if competition is unusual, males still have to inevitably approach one partner first for copulation. In females, it has been shown that females spend longer time with one male compared to the others when tested in a multiple partner paradigm. The male mate preference was investigated in this study. In addition, the role of ultrasonic vocalizations (USVs) and female odors in the male's initial choice to approach one female instead of another was studied in this experiment. Male rats could choose between three different sexually receptive females. The experiment started with a 15-minute period with inaccessible females followed by a 15-minute period with accessible females in which the males could copulate with the females of his choice. The results showed that male rats spent more time with the female of 1st entry over the second or third females visited. No differences were found in USV subtype patterns emitted by the different females or the number of sniff episodes towards the different female chambers. Thus, the present experiments did not offer any evidence suggesting that USVs or individual differences in female odors play any role in male mate choice. Other factors that were not investigated in this study might be involved in male mate selection, but it should also be considered that mate selection could be random.

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1. Introduction

While intrasexual competition for access to a mate is believed to be common among mammals, competition is unusual in wild rats [1,2]. In species where males do not compete for females, female choosiness can become important. In laboratory studies, it was shown that female rats spend most time with one particular male, when two or more males were simultaneously available [3–8]. However, it is extremely unlikely that a particular female would spend exactly the same amount of time with each of the males, making the fact that she spends more time with one male than with others quite uninteresting. Therefore, a better

way of investigating mate preferences might be to look at the partner approached first of several partners. It was shown in females that the male of first choice is also the male with whom the longest time was spent and most sexual interactions occurred [8,9]. Furthermore, this male is frequently the only one achieving ejaculation [9]. As a consequence, the male of first choice has a considerable reproductive advantage over the males visited later.

No similar studies are available for male mate choice. Even if intrasexual competition was unusual and female choosiness was important, males will inevitably approach a partner for copulation, and someone will be approached first. If male rats show similar preferences for copulating with the female first approached and ejaculate more with this female, these females would have a considerable reproductive advantage over other females. In this study we tried to determine the causes of the male's initial choice to approach one female instead of another, and if males, like females, copulate more with the first chosen than with the others. Since approach to a conspecific must depend on

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distant stimuli, the modalities involved can be vision, olfaction or audition. Visual stimuli are probably not important, since males approach females even in complete darkness [10,11]. To the contrary, female olfactory stimuli are powerful attractants, since male rats approach the odor of sexually receptive females [12–16]. Anosmic males, on the other hand, do not immediately distinguish between females in estrus and in non-estrus, and show a sustained reduction in social investigation [17]. Together, this suggests that olfactory stimuli are important for the incentive value of females. Individual differences in the odors emitted by the females could determine the male's initial approach towards one female in relation to the others. This possibility was investigated in this study by exposing male rats to three inaccessible females and then allowing the males to copulate with the female or females of his choice.

Another powerful attractant at distance can be the auditory stimuli. Rats emit 50 kHz ultrasonic vocalizations (USVs) in the presence of a sexual partner and during copulation [18–20]. It has also been reported that males approach the playback of 50 kHz USVs [21,22]. Therefore, it could be suggested that USVs may contribute to the incentive value of female rats and that USVs emitted shortly before the male's mate choice could affect the male's behavior. The second purpose of the current study was to test this hypothesis.

2. Material and methods

2.1. Subjects

Twelve male rats and eleven female Wistar rats (250–300 g at the start of the experiments) were obtained from Charles River (Sulzfeld, Germany). The rats were housed in same sex pairs in Makrolon IV® cages on a reversed 12 h light/dark cycle (lights off between 11 am and 11 pm), in a room with controlled temperature (21 ± 1 °C) and relative humidity ($55 \pm 10\%$). Standard rodent food and tap water were available ad libitum. All experimentation was conducted in agreement with the European Union council directive 86/609/EEC and approved by the National Animal Research Authority in Norway.

All females were ovariectomized under isoflurane anesthesia and implanted subcutaneously with a 5 mm long Silastic capsule (medical grade Silastic tubing, 0.0625 in. inner diameter, 0.125 in outer diameter, Degania Silicone, Degania Bet, Israel) containing 10% 17 β -estradiol in cholesterol (both from Sigma, St. Louis, MO, USA) two weeks before the experiments. The ends of the capsules were sealed with medical grade adhesive silicone (Nusil Silicone Technology, Carpinteria, CA, USA). Progesterone was dissolved in peanut oil (Apteksproduksjon, Oslo, Norway) and was given to the females subcutaneously in a dose of 1 mg/rat and volume of 0.2 ml/rat approximately 4 h before the start of the experiments. This hormonal treatment assures maximal receptivity and proceptivity [23,24].

2.2. Apparatus

The experiments were conducted in a multiple chamber set-up (Fig. 1a), consisting of a middle large chamber (50 cm diameter) surrounded by three other small chambers (30 cm). The chambers were connected with openings of 5 cm diameter that were large enough for the males to move freely through the cage. The females, on the other hand, were tied in harnesses to keep them in the small chamber they were placed in.

The wall of the cage consisted of metal sheet covered with a black plastic surface. Sound absorbing isolation material of extruded polyethylene foam was used as cover for the inside of the chambers. Microphones that were sensible for high frequencies (obtained from Metris, Hoofddorp, The Netherlands) were placed above each chamber and adjusted so that all sounds from within the chamber were registered, while sounds from adjacent chambers were not. The microphones were connected to a computer with the Sonotrack® (sound analysis) system. In addition, video cameras located above each chamber were used to record the multiple partner tests on video. Event recording software Observer XT 10 (obtained from Noldus, Wageningen, The Netherlands) was used to score the rat behavior during the multiple partner test. The chambers were illuminated with dim lights, which resulted in approximately 5 lx at the bottom of the cage.

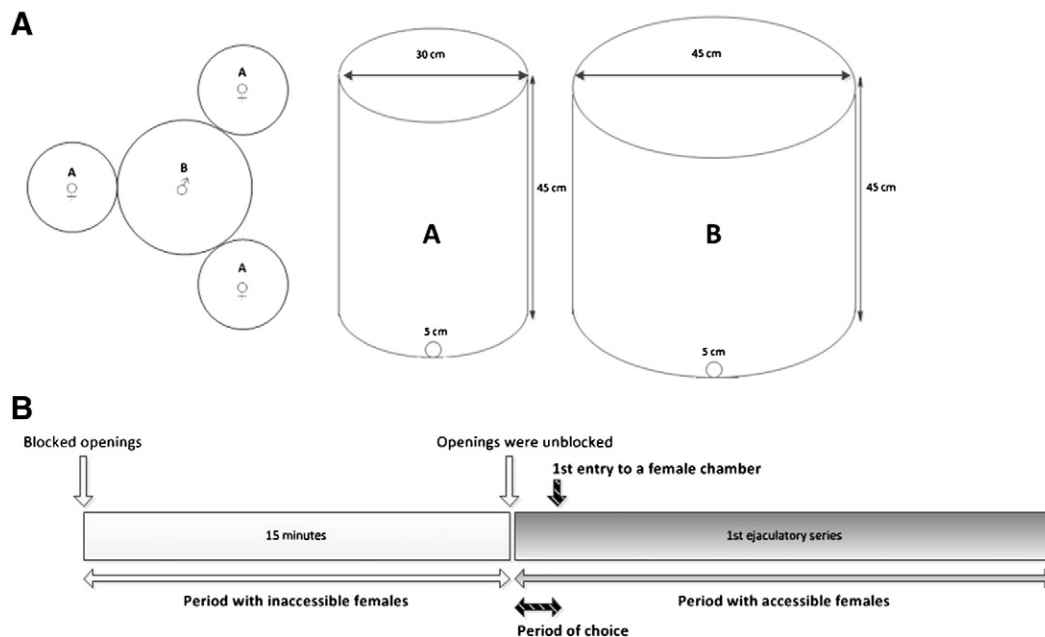


Fig. 1. Schematic drawing of the multiple partner choice test consisting of a middle large chamber (B, 50 cm diameter) surrounded by three other small chambers (A, 30 cm). The chambers were connected with openings of 5 cm diameter that were large enough for the males to move freely through the cage, while the females were tied in harnesses to keep them in the small chambers (A). And schematic overview of the experimental design. First there is a 15-minute period with inaccessible females in which the male was able to hear, smell and see the females without the possibility of physical contact. After the period with inaccessible females, the openings were unblocked and the males were allowed to copulate with the different females until the first postejaculatory intromission (period with accessible females) (B).

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