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Mate preference for dominant vs. subordinate males in young female Syrian hamsters (*Mesocricetus auratus*) following chemically-accelerated ovarian follicle depletion

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HIGHLIGHTS

- 4-Vinlcyclohexene diepoxide (VCD) accelerated ovarian aging in young female hamsters.
- VCD-treated and control females showed preference for dominant over subordinate males.
- Accelerated ovarian aging did not influence mate preference of young females.

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ABSTRACT

Life history theory predicts that selectivity for mates generally declines as females age. We previously demonstrated this phenomenon in Syrian hamsters (*Mesocricetus auratus*), in that older females showed reduced preference for dominant over subordinate males. To test the hypothesis that decreased reproductive quality due to aging reduces mate preference, we decoupled reproductive and chronological age by treating young female hamsters with 4-vinylcyclohexene diepoxide (VCD), which destroys ovarian follicles and functionally accelerates ovarian follicle depletion without compromising the general health of rodents. In this study, VCD effectively reduced follicle numbers in young Syrian hamsters. VCD-treated and control females were allowed to choose between a dominant and a subordinate male in a Y-maze on the day of proestrus. Both VCD-treated and control females demonstrated preference for the dominant male by leaving a greater proportion of vaginal scent marks near him, which is a behavior that females display when soliciting prospective mates. However, there was no effect of treatment on the proportion of vaginal scent marks left for the dominant male. Furthermore, ovarian follicle numbers were not significantly correlated with any behaviors in either group. We conclude that accelerated ovarian follicle depletion does not reduce mate preference in young female hamsters.

1. Introduction

In mate selection, females must weigh the benefits of being choosy (e.g. fertility and genetic quality of mate) against the costs (e.g. time, energy and predation risk). Life history theory predicts that females of advanced age should be less choosy than younger females, given the age-associated decline in fertility/fecundity and increased cost of remaining selective. Indeed, old age is associated with reduced selectivity [1–4] and greater variability in mate preference in several species (e.g. guppy, cricket, cockroach, and moth) [1,4]. While studies on age and mate choice in mammals are limited, recent evidence suggests that old (15 months old) female Syrian hamsters (*Mesocricetus auratus*) have reduced preference for dominant males as compared to young females [5]. Young females of this species generally show strong preference for dominant over subordinate males [6–9].

There are several physiological factors that might explain why older females demonstrate reduced mate selectivity, including the age-related decline in reproductive potential. Moore and Moore [2] found that older female cockroaches (*Nauphoeta cinerea*) are less choosy than young females, and they indicated that this decrease in choosiness was correlated with the age-related decline in reproductive quality, as determined by the number of offspring produced. However, the relative importance of reproductive age in female mate choice has yet to be explicitly tested. Like the cockroach, the age at which female hamsters show reduced mate preference (15 months) is also an age at which fertility has significantly declined [10]. Reproductive aging in female mammals occurs at a more rapid rate than other physiological systems, and it is due in part to a progressive decrease in the size and quality of the ovarian follicular pool [11]. Additionally, the rate of ovarian senescence is variable among individual females depending on their life history (i.e.

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season of birth, parity) [12] and genetic background [13]. Therefore, reproductive aging can vary among individuals and it is not always correlated with chronological age.

The purpose of this study was to determine if ovarian follicle depletion contributes to reduced female mate preference and selectivity for a mate, as we previously observed in chronologically old Syrian hamsters [5]. In the previous study we compared mate preferences of 6- and 15-month-old female hamsters, and we found that young females left a significant proportion of vaginal scent marks in the vicinity of the dominant male, whereas 15-month-old females did not. For the present study, we decoupled ovarian and chronological age by treating young (8-week-old) female hamsters with 4-vinylcyclohexene diepoxide (VCD), a toxicant that accelerates ovarian follicle loss. VCD is specifically lethal to preantral follicles in rodents, which accelerates ovarian senescence [14] without compromising brain function [15] or other body systems [16,17]. Accordingly, VCD is often used in rodents as a tool to study the transition period and physiological consequences of age-related reproductive failure in females [18–20], and it is increasingly used to study female behavior associated with ovarian senescence [15,16,21,22]. To determine if ovarian age influences selectivity for potential mates, VCD-treated females were allowed to choose between a dominant and a subordinate male on the day of proestrus. We inferred mate preferences from scent marking behavior and the amount of time that females spent near each prospective mate [5], and compared the behaviors of VCD- and vehicle-treated females.

2. Materials and methods

2.1. Animals

Eight-week-old Syrian hamsters were purchased from Charles River Laboratories (Wilmington, MA). Upon arrival at our facility, animals were housed individually in polycarbonate cages. Food (Prolab 1000, Syracuse, NY) and water were available ad libitum. Hamsters were maintained on 14 h of light/day with lights on between 20:00 and 10:00 EST. Ambient temperature and relative humidity were held constant at 21 ± 5 °C and 50 ± 10% respectively. Males and females were housed in one room, and individuals were transported to a separate empty room for behavioral observation. Ovaries from five 15-month-old female hamsters were obtained from a breeding colony maintained at Cornell University. All experimental procedures were approved by Cornell University's Institutional Animal Care and Use Committee.

2.2. VCD treatment

Eight-week-old female hamsters were treated with 400 mg/kg VCD (Sigma Aldrich, St. Louis, MO) once daily for 10 days by i.p. injection. This dose was based on a pilot experiment in which 8-week-old hamsters treated with 400 mg/kg had follicle numbers comparable to those counted in the ovaries of 15-month-old females. Control females were given daily vehicle (1:1 mixture of 0.9% saline and DMSO) injections. Injections were administered under isoflurane anesthesia (3%) during the light phase of the light–dark cycle (between 08:00 and 10:00 EST).

2.3. Behavioral tests and observations

Behavioral testing was conducted between 1 and 9 weeks after the final VCD injection, over a period of three days. This included the metestrus, diestrus, and proestrus phases of the 4-day estrous cycle. Mate preference was observed on the day of proestrus, a time at which females actively solicit mates [23]. Females were tested in pairs, which included one VCD-treated and one control female of the same age with synchronous estrous cycles. Behavioral observations were made between 10:15 and 12:00 under dim white light to facilitate video recording. No more than two pairs of females were tested per week. The day before testing began each female was confirmed to be in estrus by placing a non-experimental male into the cage and monitoring for lordosis, evident by the arching of back and tail up posture that is characteristic of receptive females in estrus [23]. The same male was used throughout the experiment, and he was not allowed to mount the females. All animals were sexually naïve at the time of behavioral testing.

2.3.1. Days 1 and 2 (metestrus and diestrus): establishment of male dominance relationships

The first day of testing occurred on the day of metestrus. Females observed the formation of a dominant–subordinate relationship between two unrelated males in a three-compartment Plexiglas arena, as described previously [5]. Males within a dyad were of the same age (mean age across all dyads: 18.5 ± 0.7 weeks) and were matched for body mass (<7.5% difference within a dyad). Test females (one VCD-treated and one control) were placed in separate enclosures (50 cm × 23 cm × 31 cm) at opposite ends of the arena. Males were placed in the central enclosure (50 cm × 44 cm × 31 cm), where they were separated from the females by coarse wire mesh framed with Plexiglas. Each male was marked by placing a small piece of green or yellow tape on the dorsum. Males were placed in the central compartment of the arena one by one and covered with an open-ended Plexiglas container to isolate them from each other and the females before the observations began. The isolation containers were removed and the males were observed for 5 min.

The males were monitored for signs that a dominant–subordinate relationship had been established. Males of this species enter into rolling fights and bite and kick until one has established dominance [8]. Subordinance is easily recognized when a male displays the tail up posture following one of these rolling fights [8,23].

The first observation period was immediately followed by a 10-minute rest period in which the males were returned to their home cages. Females remained in their enclosures in the arena. The first day of observation concluded with a second 5-minute observation period identical to the first. The tape was removed from each male, and all animals were returned to their home cages. The same procedure was conducted on day two of testing (diestrus). The side of the arena in which the VCD-treated female was placed was alternated with each pair of females tested. The arena was cleaned with 50% ethanol between groups.

Twelve pairs of females were tested. Mean age at the time of behavioral testing was 16.7 ± 0.5 weeks. Eleven individual females were exposed to more than one dyad of males because eight dyads failed to establish a clear dominant–subordinate relationship during the first two days of observation. These trials were terminated at the end of testing on day 2. Six females were exposed to a second dyad on the next consecutive estrous cycle. The dominant–subordinate relationships remained stable over the four-day testing period in all dyads that formed such a relationship. Males from dyads that failed to establish a dominant–subordinate relationship on the first two days of testing were re-paired with another male for future testing with a different pair of VCD- and vehicle-treated females.

2.3.2. Day 3 (proestrus): Y-maze tests

The third day of testing (proestrus) began with a 5-minute observation of the male dyad, identical to those performed on days 1 and 2, except that only one of the two females (the focal female) was placed in her enclosure in the arena. Thereafter, all three animals were then returned to their home cages for a 10-minute rest period.

Female mate preference was observed in a Plexiglas Y maze after the male–male dyad observation. First, the focal female was allowed to explore the empty Y maze for 5 min, where she had access to the entire maze except the male enclosures at the distal ends of the arms. The female was then placed in an enclosure at the base of the Y maze while each male was placed in an enclosure at the end of the Y, where they were separated from the female by a coarse wire mesh. The female was released from her enclosure and allowed to move freely throughout