ISSN 0340-5443, Volume 64, Number 8

Behav Ecol Sociobiol (2010) 64:1247–1253
DOI 10.1007/s00265-010-0939-7

ORIGINAL PAPER

Adult female hamsters avoid interspecific mating after exposure to heterospecific males

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Received: 24 November 2009 / Revised: 8 February 2010 / Accepted: 15 February 2010 / Published online: 5 March 2010

Abstract When females mate with a heterospecific male, they do not usually produce viable offspring. Thus, there is a selective pressure for females to avoid interspecific mating. In many species, females innately avoid heterospecific males; females can also imprint on their parents to avoid later sexual interactions with heterospecific males. However, it was previously unknown whether adult females can learn to discriminate against heterospecific males. We tested the hypothesis that adult females previously unable to avoid interspecific mating learn to avoid such mating after being exposed to heterospecific males. Syrian hamster (*Mesocricetus auratus*) females not previously exposed to Turkish hamster (*Mesocricetus brandti*) males can discriminate between odors of conspecific and heterospecific males, but they mate with either type of male. However, when we exposed adult females to both a conspecific male and a heterospecific male through wire-mesh barriers for 8 days, and then paired them sequentially with the two males, females were more receptive to conspecific males and more aggressive to heterospecific males. When females were paired with the heterospecific male first and the conspecific male second, no female was receptive and all were aggressive to heterospecific males. When females were paired with the conspecific male first, only 43% of females were then aggressive toward the heterospecific male. That is, interactions with conspecific males may decrease a female's ability to properly avoid heterospecific males. Our study clearly shows for the first time that females can learn during adulthood to avoid interspecific mating just by being exposed to stimuli from heterospecific males.

Keywords Heterospecific · Interspecific mating · Species discrimination · Learning · Lordosis · Aggression

Communicated by: A. Schulte-Hostedde

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Introduction

Interspecific mating (i.e., involving mates of two different species) normally leads to no or unfit offspring (Gröning and Hochkirch 2008). Thus, there is strong selective pressure on females to avoid interspecific mating, and, indeed, there are many reported cases in which females are not sexually receptive and are even aggressive toward males of closely related species (Andersson 1994). This type of discriminative behavior against heterospecifics may evolve rapidly during the contact period between two species after allopatry (Andersson 1994; Servedio et al. 2009). The resulting avoidance of interspecific mating, once in place, can be an innate behavior (Hebets 2007). However, individuals of some species may have a more variable response to heterospecifics that involves learning (Irwin and Price 1999; Servedio et al. 2009). Learning during early development (imprinting) has been reported in several species (Irwin and Price 1999). Learning to discriminate between conspecific and heterospecific individuals during adulthood, however, has only been shown in males of fruit flies and guppies (Dukas 2004; Magurran and Ramnarine 2004; Dukas 2008). Female guppies, contrary to males, are unable to learn to discriminate against heterospecific males (Haskins and Haskins 1949). We are not aware of any study showing that adult females learn to discriminate against heterospecific males. Here, we investigated for the first time this question in two hamster species (*Mesocricetus* spp.).

Estrous female Syrian hamsters, *Mesocricetus auratus*, show a preference for the odors of conspecific males over those of heterospecific Turkish hamster males, *Mesocricetus brandti* (delBarco-Trillo et al. 2009b). Brain activity in the posterior medial amygdala of estrous female Syrian hamsters is also higher after being exposed to odors of conspecific males than to odors of heterospecific males (delBarco-Trillo et al. 2009a). These observations indicate that female Syrian hamsters can discriminate between conspecific males and heterospecific males. However, Syrian hamster females do not innately avoid mating with heterospecific males (delBarco-Trillo et al. 2009b); even though, if Turkish and Syrian hamsters do mate, they do not produce viable offspring (Todd et al. 1972; Murphy 1977). That is, when Syrian hamster females without any prior experience with heterospecific males were paired with a conspecific male and then with a heterospecific male (or vice versa), we found that all females were receptive to both conspecific and heterospecific males, allowed both types of male to mate with them, and did not show any sign of aggression toward any male (delBarco-Trillo et al. 2009b). This inability to avoid interspecific mating may exist in the wild or it could be a result of captivity (delBarco-Trillo et al. 2009b). In either case, the laboratory Syrian hamster is clearly not innately prepared to avoid interspecific mating. However, learning to avoid interspecific mating may be important in this species. The current distribution of the Syrian hamster is highly restricted and, thus, does not overlap with the distribution of the Turkish hamster to the North (Neumann et al. 2006). However, phylogenetic information indicates that current distributions of these two species and the Caucasian hamster, *Mesocricetus raddei*, were different in the recent past and may have overlapped: the Syrian hamster is more related to the Caucasian hamster than to the Turkish hamster, but the Turkish hamster distribution separates the distribution of the Syrian hamster to the South and the distribution of the Caucasian hamster to the North (Neumann et al. 2006).

In the previous studies in which we paired Syrian hamster females with Turkish male hamsters, female subjects had never had any previous contact with heterospecific males (delBarco-Trillo et al. 2009b). Here, we tested the hypothesis that a previous contact with a heterospecific male and a conspecific male may be sufficient for adult females to develop the ability to avoid interspecific mating. To test this hypothesis, we exposed females for 8 days to a conspecific and a heterospecific male behind wire-mesh partitions, and then paired each female sequentially with the two males she had been exposed to. We measured sexual receptivity and aggression toward each one of the two males. Similar behavior toward the conspecific and heterospecific males would suggest that Syrian hamster females did not learn to avoid interspecific mating. Alternatively, if females were less sexually receptive and/or more aggressive toward heterospecific males, this would indicate that adult females can learn to avoid mating with heterospecific males simply by being exposed to them for an extended period of time and without requiring unsuccessful mating.

Methods

Animals

All animals were born and raised in captivity at Cornell University, Ithaca, NY. Hamsters were weaned at 30 days of age and housed individually in solid-bottom polycarbonate cages (45×24×14.5 cm) with sani-chip bedding material and constant access to water and food (Prolab 1000, Agway, Syracuse, NY, USA). Turkish and Syrian hamsters were maintained in separate rooms with independent air intake and exhaust. It must be noted that females were exposed to conspecific stimuli during rearing. Turkish hamsters were maintained on a 16L:8D light–dark schedule with lights off between 10:00 and 18:00 hours (Eastern Standard Time). Syrian hamsters were maintained on a 14L:10D light–dark schedule with lights off between 09:00 and 19:00 hours. Experiments were run between 10:00 and 13:00 hours. We used dim and indirect light to allow videotaping and observations. The video camera was located approximately 1 m from the cage.

To determine that a female was in estrus on a specific day, a conspecific male hamster was placed inside the female's home cage. If lordosis occurred within 15 s, the female was considered in estrus (no mounting occurred during estrous testing). Lordosis is a stereotypical position in *Mesocricetus* spp. in which the female arches her back (down in the center), spreads her legs, raises her tail, and remains immobile from seconds to minutes. If no lordosis was observed, the female was retested on the following days (up to 3 days) until lordosis occurred. Given the 4-day estrous cycle in Syrian hamsters (Lisk 1985), once the day of estrus was determined, we could always determine the subsequent estrous days. In this study, females were always tested 4 days after determining their estrous day.

Experimental design

We used an arena (90×50×30 cm) divided in three similarly-sized sections (29.7×50×30 cm) by two wire-mesh partitions with 1-cm^2 openings. We started a test by placing one male in one of the two lateral sections, and a second male in the other lateral section. The two males were either two Syrian hamster males (*N*=10) or one Syrian and one Turkish hamster male (*N*=15). We then placed an estrous Syrian hamster female in the middle section. The female could perceive and interact in a limited manner with both males through the wire-mesh partitions. We used soiled bedding from each animal's home cage as substrate for its respective section of the arena. Each animal had constant access to its own water and food. Animals lived undisturbed in this arena during two full estrous cycles (i.e., 8 days), always in a room different from the colony and testing rooms. The light cycle in this room was the same as in the females' rooms (i.e., 14L:10D light–dark). No more than four arenas were used at the same time. Arenas with two conspecific males and arenas with one conspecific male and one heterospecific male were never carried out concurrently to avoid the cross-over of stimuli between arenas. After 8 days living in the three-sectioned arena, the female and the two males were transferred to individual cages lined with clean bedding and the three animals were moved to the testing room. The first trial started 10 min after the animals had been transferred to their individual cages. For the first trial, one of the two males was placed in the estrous female's cage for 5 min. Then, we transferred the first male to its cage, and 5 min later, we started the second trial by placing the second male in the female's cage for 5 min. We videotaped all trials. We did not interfere with the behavior of animals during these trials.

In those tests in which the female was tested with a conspecific male and a heterospecific male (*N*=15), the conspecific (or preferable) male was tested first in seven tests and the heterospecific (or non-preferable) male was tested first in the other eight tests. The 10 tests in which females were tested with two conspecific males functioned as an additional control. In these control tests, the female was exposed for 8 days and then paired with both a conspecific male that she should prefer (preferable male) and a conspecific male that she should not prefer (non-preferable male). In five of the 10 tests, females were tested with a brother (non-preferable male) and an unrelated male (preferable male). In the other five tests, females were tested with a loser in a recent fight (non-preferable male) and the winner of that same fight (preferable male). Then it was determined whether any sexual preference for either type of conspecific male (preferable against non-preferable) was of the same magnitude as the preference toward a conspecific male over a heterospecific male. Since there were no differences between the brother/unfamiliar condition and the loser/winner condition, we pooled data from these two conditions into a more general preferable/non-preferable conspecific male condition (*N*=10).

In all tests, females were tested with the two males that they had been exposed to during 8 days (either two conspecific males or one conspecific male and one heterospecific male). An additional control treatment would have entailed exposing females to two conspecific males and then pairing those females with a conspecific male and a heterospecific male. However, such females would have been paired with an unfamiliar heterospecific male, which would have introduced the confounding factor of familiar vs unfamiliar heterospecific males. We have shown previously that when Syrian hamster females without previous interactions with heterospecific males are paired with an unfamiliar Turkish hamster male, they behave as if they had been paired with a conspecific male (delBarco-Trillo et al. 2009b).

We scored the recorded videos to determine the latency to lordosis, the duration of lordosis, and whether the female showed any type of aggressive behavior. If a female did not show lordosis during a test, we scored the latency as 300 s. We considered that an aggressive behavior occurred if we observed any attempted biting or tumbling fights.

Statistics

Tests with two conspecific males and tests with one conspecific male and one heterospecific male were analyzed separately. We used SPSS 11.5 for Windows for all statistical analyses. We used the GLM Repeated Measures option in SPSS, selecting a full factorial model with Type III sum of squares. For each lordosis variable (latency or duration), we had two levels, one being the variable when the female was tested with the preferable male and the other level being the variable when the female was tested with the non-preferable male. The between-subject factor was order (i.e., whether the female was tested first with the preferable male or with the non-preferable male). For aggressive behavior, because the data were nominal (i.e., presence or absence of aggression), we used the McNemar test.

Results

When females were tested with two conspecific males, latency to lordosis did not differ between trials with the preferable conspecific male (24.6±11.37 s; mean ± SD) and trials with the non-preferable conspecific male (17.7±5.23 s; $F_{1,8}$=1.63, P=0.24; Fig. 1a). In addition, lordosis duration did not differ between trials with the preferable

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conspecific male (269.22±14.42 s) and trials with the non-preferable conspecific male (274.88±9.66 s; $F_{1,8}$=0.34, P=0.58; Fig. 1b). There was no female aggression toward any conspecific male (Fig. 2). For all of the variables considered, there was no significant interaction between type of male (preferable or non-preferable) and testing order (whether the preferable conspecific male was tested first or second; P>0.05).

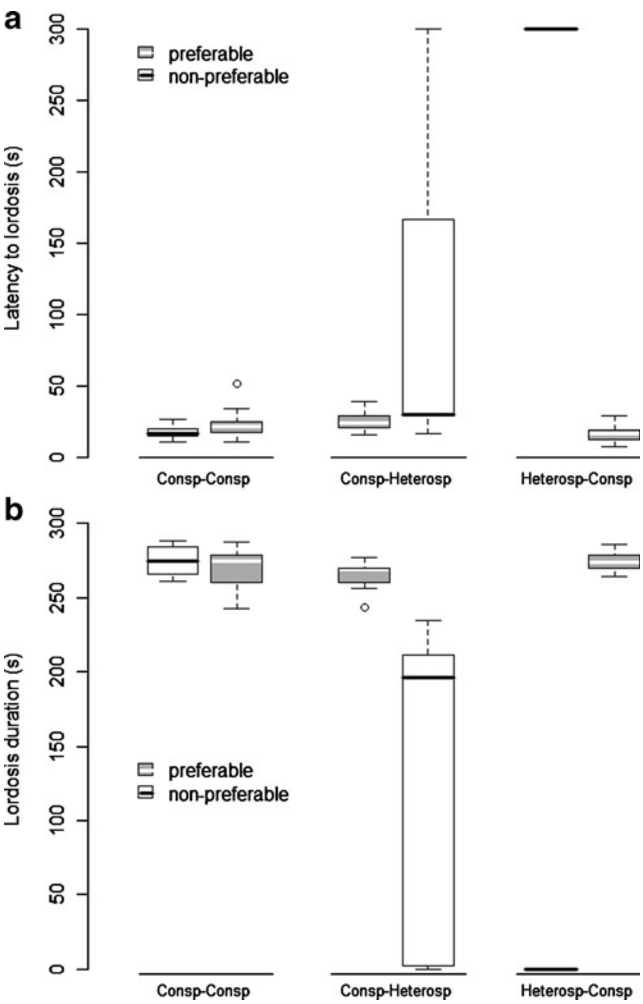

Fig. 1 Latency to lordosis (**a**) and lordosis duration (**b**). *Consp-Consp* denotes tests in which the female was tested in two consecutive trials with two different conspecific males; the presumably preferable male was a non-kin male or a winner in a recent fight, whereas the non-preferable male was either a brother or a loser in a recent fight. *Consp-Heterosp* denotes tests in which the female was tested first with a conspecific male and then with a heterospecific male in two successive trials. *Heterosp-Consp* denotes tests in which the female was tested first with a heterospecific male and then with a conspecific male. In Consp-Heterosp and Heteosp-Consp tests, the preferable male was the conspecific male whereas the non-preferable male was the heterospecific male. The *bar* within each *box* represents the sample median, each *box* represents 50% of the data around the median, and the two *whiskers* around each *box* represent the 95% confidence interval. *Circles* represent outliers

When females were tested with a conspecific and a heterospecific male, latency to lordosis was significantly shorter with the conspecific (or preferable) male (21±8.19 s) than with the heterospecific (or non-preferable) male (209.27±132.86 s; $F_{1,13}$=57.1, P<0.0005). There was a significant effect of testing order ($F_{1,13}$=16.5, P=0.001), as well as a significant interaction between type of male and testing order ($F_{1,13}$=17.91, P=0.001; Fig. 1a). That is, latency to lordosis did not differ statistically when the conspecific males were tested either first (25.71±7.74 s) or second (16.88±6.4 s), but testing order did affect latency to lordosis in the presence of the heterospecific male (heterospecific males in the first trial: 300 s, i.e., no lordosis in any trial; heterospecific males in the second trial: 105.57±132.92 s).

Lordosis duration was longer with the conspecific male (269.51±10.33 s) than with the heterospecific male (57.11±97.73 s; $F_{1,13}$=99.31, P<0.0005). Testing order had a significant effect on lordosis duration ($F_{1,13}$=8.34, P=0.013), and there was also a significant interaction between type of male and testing order ($F_{1,13}$=10.09, P=0.007; Fig. 1b). That is, lordosis duration did not differ statistically when conspecific males where tested either first (264.09±11.17 s) or second (274.26±7.16 s), but testing order did affect lordosis duration in the presence of the heterospecific male (heterospecific males in the first trial: 0 s; heterospecific males in the second trial: 122.39±113.87 s).

Females were not aggressive toward conspecific males in any trial. When the female was paired with the heterospecific male in the second trial, females were aggressive toward the heterospecific males in 42.86% of the cases (3/7 trials), which was not significantly different from the 0% aggression toward conspecific males (McNemar test: N=7, P=0.25). When females were paired with the heterospecific male in the first trial, they were aggressive in all instances (8/8 trials), which was significantly higher than the 0% aggression toward the conspecific males (N=8, P=0.008; Fig. 2).

Discussion

We have previously found that Syrian hamster females without prior interactions with heterospecific, Turkish hamster males mate with and are not aggressive toward such males (delBarco-Trillo et al. 2009b). In this study, we show that, after being exposed to a conspecific male and a heterospecific male across a wire-mesh barrier for two estrous cycles (i.e., 8 days), females behaved differently toward conspecific and heterospecific males in both sexual and aggressive behavior. This was especially the case when females were first paired with the heterospecific male. In all such trials, females were not sexually receptive and were highly aggressive toward the heterospecific males. These results indicate that female Syrian hamsters learned to avoid mating with heterospecific males.

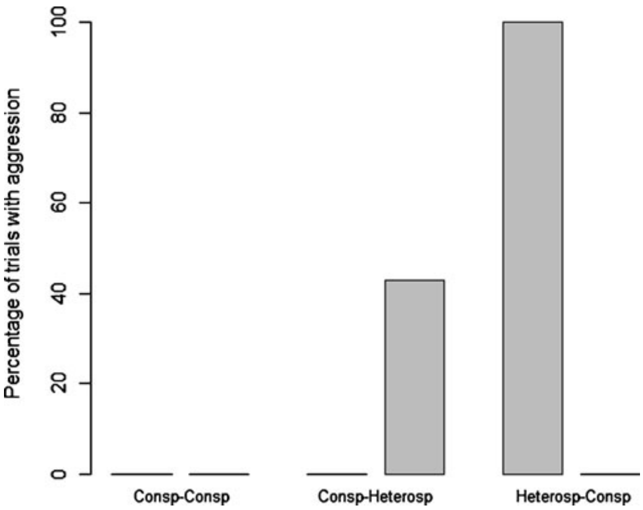

Fig. 2 Percentage of trials in which females were aggressive toward males. *Consp-Consp* denotes tests in which the female was tested in two consecutive trials with two different conspecific males. *Consp-Heterosp* denotes tests in which the female was tested first with a conspecific male and then with a heterospecific male in two successive trials. *Heterosp-Consp* denotes tests in which the female was tested first with a heterospecific male and then with a conspecific male

Our study clearly shows that exposure to heterospecific individuals during adulthood can influence subsequent behavior toward heterospecifics. Previous studies in other taxa have shown that learning before sexual maturity (e.g., imprinting) may regulate later interactions with heterospecific individuals (Huck and Banks 1980; Kendrick et al. 1998; Irwin and Price 1999; Vasilieva et al. 2001; Slagsvold et al. 2002; Verzijden and ten Cate 2007). Most of these studies used a cross-fostering experimental design and usually reported that, when individuals were raised by a heterospecific foster parent, they treated heterospecifics more like conspecifics when they were adults. These results are contrary to what we show here, i.e., exposure to heterospecifics increases avoidance toward them. Imprinting studies show, however, that species discrimination may not be present at birth and that it may need to be learned. Interactions with either conspecifics or heterospecifics may be sufficient for early development of the ability to discriminate against heterospecific mates. For example, in a series of experiments with *Drosophila paulistorum*, contact with conspecifics or heterospecifics during early development enhanced discriminatory abilities, whereas social isolation during early development resulted in decreased discriminatory abilities (Kim et al. 2004).

In comparison to studies on early development, there have been relatively few studies showing that adults may learn to avoid interspecific mating. This may be due to the general assumption that most learning happens during early development and not during adulthood. These few studies, however, have been conducted on very diverse taxa, suggesting that learning to avoid mating with heterospecific individuals during adulthood may be more prevalent than previously thought. For example, males of one *Drosophila* species, after initially courting (and being rejected by) a female of another species, later showed less courtship toward heterospecific females than inexperienced males did, while no differences were observed between experienced and inexperienced males toward conspecific females (Dukas 2004, 2008; but see Kandul et al. 2006). Learning to avoid interspecific mating in *Drosophila* species seems to be related to unsuccessful interactions with heterospecific individuals. For instance, male *Drosophila persimilis* that had previous mating experience with female *Drosophila pseudoobscura* were as likely to mate with other heterospecific females as were virgin males (Kujtan and Dukas 2009). That is, when males are rejected by heterospecific females, they will be subsequently less attracted to other heterospecific females (Dukas 2004, 2008, 2009), but if they mate with heterospecific females, they do not learn to avoid other heterospecific females (Kujtan and Dukas 2009). This is in contrast to our study in which females did not have full access to the males during the exposure phase.

Studies on learning to avoid interspecific mating during adulthood have also been conducted in Trinidadian guppies (*Poecilia* spp). *Poecilia reticulata* males living allopatrically with *Poecilia picta* will mate with conspecific and heterospecific females at random, but after 1 week of exposure to *P. picta* females, males learn to avoid mating with heterospecific females (Magurran and Ramnarine 2004). Interestingly, females seem unable to learn in the same way that males do, and even after several days of exposure, they do not behave differently toward conspecific and heterospecific males (Haskins and Haskins 1949). *Poecilia reticulata* males are also able to learn to avoid mating with females of a distantly related species (*Skiffia bilineata*) if they are exposed to them for 14 days, but they do not generalize this learning to unfamiliar females of this species; they just avoid the females to which they were exposed (Valero et al. 2009).

The function of learning to avoid heterospecific males is clearly the avoidance of interspecific mating. Innate avoidance may be advantageous when two species live in sympatry and interspecific mating is possible, but it may not be advantageous when they live in allopatry. For instance, male Trinidadian guppies living allopatrically do not innately discriminate heterospecific from conspecific females, but instead, they require learning to do so, whereas males in locations where species are sympatric discriminate against heterospecific females innately (Magurran and Ramnarine 2004; Magurran and Ramnarine 2005). It has been hypothesized that selection for efficient avoidance of interspecific mating may cause a shift from learning to avoid such mating to innate avoidance (Irwin and Price 1999). If this hypothesis is generally correct, our results indicate that *Mesocricetus* spp. are still in the learning stage and that they have not yet reached the innate avoidance stage. This may be because the different species have evolved recently, and/or because the different species have been allopatric for most of their existence and, thus, there has not been strong selection for innate heterospecific avoidance (Neumann et al. 2006).

Interestingly, female hamsters were less discriminative toward heterospecific males after a short interaction with a conspecific mate. This is the first study reporting that interactions with conspecific males may hinder a females' ability to discriminate against heterospecific males. At the physiological level, this indicates that mating with a conspecific male may increase the hormonal and/or neural milieu of a female over a threshold beyond which the necessary sexual receptivity and non-aggressiveness toward conspecific males may hinder sexual avoidance and agonism against heterospecific males. This may be important at the functional level, because there may be a trade-off between sexual receptivity toward conspecific males and avoidance of heterospecific males, especially when the differences between the two types of males are small (i.e., when the two species are very closely related). Too much effort in the avoidance of heterospecific males may reduce a female's ability to accept conspecific males as mates, whereas a high receptivity toward conspecific males may reduce a female's ability to reject heterospecific males. This trade-off implies that females in the wild may be less successful at avoiding interspecific mating than laboratory experiments might suggest.

The present study does not show whether females that were exposed to both a heterospecific male and a conspecific male learned to avoid interspecific mating simply because they were exposed to the heterospecific male or because they were concurrently exposed to both types of male. However, when Syrian hamster females are exposed for 8 days only to a heterospecific male, these females also learn to avoid heterospecific mating (unpublished data). Therefore, females do not seem to require concurrent stimuli from both types of males; exposure to the heterospecific male seems to be sufficient.

In conclusion, we show for the first time that females can learn during adulthood to avoid interspecific mating just by being exposed to heterospecific males. We also show for the first time that interactions with conspecific males may decrease a female's ability to properly avoid heterospecific males.

Acknowledgements This work was supported by NIMH grant NIMH 5 R01 MHO58001-08 to R. E. Johnston. We thank two anonymous reviewers. The experiments here described comply with the current laws of the USA. All research was conducted with approval from Cornell University's Institutional Animal Care and Use Committee (protocol #1993-0120). The authors declare that they have no conflicts of interest.

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