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Interactions with heterospecific males do not affect how female *Mesocricetus* hamsters respond to conspecific males

Javier delBarco-Trillo^{a,b,*} and Robert E. Johnston^a

^aCornell University, Department of Psychology, Ithaca, NY, U.S.A

^bMuseo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas (CSIC), Madrid, Spain

Abstract

Reproductive interference includes any interspecific interaction that reduces the fitness of one or both species involved. There are several types of reproductive interference, but they normally involve the direct cost of interacting or mating with heterospecifics. An indirect cost of interacting with heterospecific individuals is a consequent reduction in successful interactions with conspecifics. We tested the hypothesis that being aggressive towards a heterospecific individual will diminish sexual responses towards conspecifics in later encounters. We used two species of *Mesocricetus* hamsters (Syrian and Turkish hamsters), whose interspecific interactions have previously been determined. We exposed or both exposed and paired Syrian hamster females with a conspecific or a heterospecific male. Five minutes later, we paired all females with a conspecific male and measured the latency to lordosis, the duration of lordosis and any incidence of aggression. We found that (1) interactions with heterospecific males did not affect how females responded to conspecific males in later encounters and (2) previous pairing of female subjects with either conspecific or heterospecific males promoted a faster sexual response by females in subsequent interactions with conspecific males. Thus, aggressive interactions of Syrian hamster females with heterospecific males, contrary to our initial hypothesis, had a positive effect on subsequent interactions with conspecific males.

Keywords

aggression; hamster; interspecific mating; lordosis; *Mesocricetus*; reproductive interference

Mating by females with heterospecific males can entail costs, such as the production of nonviable or infertile offspring. Consequently, many species have developed behavioural responses to avoid mating with heterospecifics (Liou & Price 1994; Coyne & Orr 2004). Such responses may include aggressive responses, or a lack of sexual response, towards heterospecific males (Andersson 1994; Coyne & Orr 2004). Such responses can be innate (Hebets 2007), learned during development (Irwin & Price 1999; ten Cate & Vos 1999; Servedio et al. 2009) or learned during adulthood (Dukas 2004; Magurran & Ramnarine

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*Correspondence: J. delBarco-Trillo, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas (CSIC), José Gutiérrez Abascal 2, Madrid, Spain., delbarcotrillo@gmail.com (J. delBarco-Trillo).

We declare that we have no conflict of interest.

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2004; Dukas 2008; delBarco-Trillo et al. 2010). Intense aggressive responses towards heterospecifics, either innate or learned, could hamper how individuals respond to conspecifics, which could be seen as a form of indirect reproductive interference (Gröning & Hochkirch 2008). Reproductive interference involves any interspecific interaction that reduces the fitness of at least one of the species involved (Gröning & Hochkirch 2008; Burdfield-Steel & Shuker 2011). Gröning & Hochkirch (2008) distinguished seven types of reproductive interference, including misdirected courtship (Verrell 1994), interspecific mating (Magurran & Ramnarine 2004) and hybridization (Rhymer & Simberloff 1996). A type of reproductive interference that was not directly discussed by Gröning & Hochkirch (2008) is how interactions with heterospecifics may adversely affect how individuals later respond to opposite-sex conspecifics.

How interactions with heterospecific males may negatively influence the behaviour of females towards conspecific males has been shown, for example, in *Gryllus* crickets (Izzo & Gray 2011). *Gryllus texensis* females show an innate preference for conspecific males over *G. rubens* males; however, after interacting with a heterospecific male, *G. texensis* females were as likely to mate with a conspecific as with a heterospecific male (Izzo & Gray 2011). Izzo & Gray (2011) argued that when females encounter a low-quality male (heterospecific) they reduce their choosiness and start accepting heterospecific males as well as conspecific males as mates. In another study, *Drosophila pseudoobscura* females that rejected heterospecific males (*Drosophila persimilis*) were later more likely to reject conspecific males compared to naïve females (Kutjan & Dukas 2009). Although this study seems to support the hypothesis that interactions with heterospecific males may negatively affect interactions with conspecific males, Kutjan & Dukas (2009) concluded that those females that rejected heterospecific males were choosier than naïve females and thus would be more likely to reject low-quality conspecific males compared to naïve females that are presumably less choosy.

The two alternative scenarios, that interactions with heterospecifics may have positive or no consequences for later interactions with conspecifics, have also been supported in other species. First, the hypothesis that interactions with heterospecifics will improve further interactions with conspecifics has been partially supported in *Drosophila yakuba* and *Drosophila santomea* (Chang 2004). Females of these species were paired with a conspecific or a heterospecific male and 8 days later they were paired again. *Drosophila yakuba* females that were paired with a heterospecific male were more likely to remate than females that were first paired with a conspecific male, although this may have been because heterospecific males transfer fewer sperm (Chang 2004). Second, the hypothesis that interactions with heterospecifics will not affect subsequent behaviour towards conspecifics has been supported in *Drosophila* flies (Dukas 2004, 2008) and birds (Baker 1994). For example, females of *Passerina cyanea* and *Passerina amoena*, after being exposed to heterospecifics, maintained their preference for conspecific males over heterospecific males (Baker 1994).

Interactions with heterospecifics may have a negative impact on later interactions with conspecifics especially when aggression towards heterospecifics takes place. The aggressive response towards heterospecifics may be carried on towards conspecifics or may decrease the normal display of sexual receptivity towards conspecifics. We tested the hypothesis that female aggression towards heterospecific males may later increase their aggression or decrease their sexual interest towards conspecific males. We tested this hypothesis using two species of *Mesocricetus* hamsters, the Syrian hamster, *Mesocricetus auratus*, and the Turkish hamster, *Mesocricetus brandti*. Although these two *Mesocricetus* species at present have nonoverlapping geographical distributions (Neumann et al. 2006), current distributions and phylogenetic relationships indicate that their distributions have fluctuated and possibly come

into contact over time (Neumann et al. 2006). For example, even though *M. auratus* is more closely related to *Mesocricetus raddei* than to *M. brandti*, the distribution of *M. brandti* is between those of *M. auratus* (to the south) and *M. raddei* (to the northeast; Neumann et al. 2006). The distribution of *M. auratus* has not yet been fully clarified (Hamar & Schutowa 1966; Gattermann et al. 2001) and has severely declined very recently (in evolutionary terms) owing to loss of habitat caused by agriculture and deliberate destruction by humans (Gattermann et al. 2001). Although we do not know how many episodes of overlapping distributions have occurred between these two species since their inception as separate species, approximately 2.7 million years ago (Neumann et al. 2006), a sophisticated form of behavioural isolation involving learning exists between these two species. Syrian hamster females show a preference for odours of conspecific males over those of Turkish hamster males (delBarco-Trillo et al. 2009a, b). Despite this olfactory discrimination and preference, Syrian hamster females that have never interacted with heterospecific males are equally sexually receptive to conspecific and heterospecific males (delBarco-Trillo et al. 2009b; delBarco-Trillo & Johnston 2010), although mating between Turkish and Syrian hamsters does not produce viable offspring (Todd et al. 1972; Murphy 1977). However, after Syrian hamster females are exposed to heterospecific hamsters through a wire mesh for several days, they are then aggressive and less sexually receptive towards heterospecific males (delBarco-Trillo et al. 2010; delBarco-Trillo & Johnston 2011a, b). The existence of this learned, aggressive discrimination makes these two *Mesocricetus* species an ideal model system to address how aggression of females against heterospecific males may have a negative impact on subsequent interactions with conspecific males.

METHODS

Animals

All animals were born and raised in captivity at Cornell University, Ithaca, NY, U.S.A. Hamsters were weaned at 30 days of age and housed individually in solid bottom polycarbonate cages (45 × 24 cm and 14.5 cm high) with sani-chip bedding material and constant access to water and food (Prolab 1000, Agway, Syracuse, NY, U.S.A.). A new square of compacted cotton was added during cage cleaning for animals to build a nest and was the only type of enrichment. Turkish and Syrian hamsters were maintained in separate rooms with independent air intake and exhaust. Turkish hamsters were maintained on a 16:8 h light:dark schedule with lights off between 1000 and 1800 hours (Eastern Standard Time). Syrian hamsters were maintained on a 14:10 h light:dark schedule with lights off between 0900 and 1900 hours. We used different light cycles because Turkish hamsters seem to require longer light cycles to reproduce successfully in captivity. All rooms were kept at temperatures of 21–25 °C. Experiments were run between 1000 and 1300 hours. We used dim, indirect white light to allow videotaping and observations.

There is a 4-day oestrous cycle in both Turkish and Syrian hamsters (Orsini 1961; Lisk 1985). To determine whether a female was in oestrus 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 oestrus (no mounting occurred during any oestrous testing). Lordosis is a stereotypical position in *Mesocricetus* spp. in which the female arches her back (down in the centre), spreads her legs, raises her tail, and remains immobile from seconds to minutes (Carter 1985). If no lordosis was observed, the female was retested on the following days (up to 3 days) until lordosis occurred. A different stimulus male was used each day. Females were always tested 4 days after determining the timing of their oestrous cycles (i.e. on their next oestrous day). Average age of females when tested was 204 days (range 101–313 days).

Procedures

We used four different treatments.

1. 'Exposed to but not paired with conspecific': each Syrian hamster female was exposed continuously to two conspecifics for 8 consecutive days and then allowed to mate with one of those conspecifics ($N=8$). That is, before a mating trial, the female had not been allowed to mate with any other male. For the initial 8-day exposure phase, we used an arena (90×50 cm and 30 cm high) divided into three similarly sized sections (29.7×50 cm and 30 cm high) by wire-mesh partitions with 1 cm^2 openings. This type of barrier is sufficient for hamsters to learn the individual identity of other individuals (Johnston & Peng 2008). We started the 8-day exposure on day 0 by placing two Syrian hamster males in the two lateral sections of the arena. We then placed an oestrous 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 the 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 oestrous cycles (i.e. 8 days), always in a room different from the colony and test rooms. The light cycle in this room was the same as in the females' housing rooms (i.e. 14:10 h light:dark). After 8 days living in the three-sectioned arena, the female and the two males were transferred to individual cages lined with clean bedding. The female and one of the two males were moved to a test room. Ten minutes later, the male was placed in the oestrous female's cage for 5 min. We videotaped the 5 min trial and scored the recorded videos to determine the latency to lordosis, the duration of lordosis, and whether the female showed any type of aggressive behaviour. We considered that aggressive behaviour occurred if we observed any attempted biting or tumbling fights (Siegel 1985).
2. 'Exposed to but not paired with heterospecific': procedures were similar to those in the 'Exposed to but not paired with conspecific' treatment, except that during the 8-day exposure phase, one conspecific male was placed in a lateral section of the arena and one heterospecific male was placed in the other lateral section. Each sexually naïve female was thus exposed to one conspecific male and one heterospecific male for 8 days. On day 8, the oestrous female was then paired with the familiar conspecific male ($N=7$).
3. 'Exposed to and paired with conspecific': procedures were similar to those in the 'Exposed to but not paired with conspecific' treatment, except that 5 min after the trial with the first conspecific male, the same female was paired for 5 min with the focal male. That is, each female was first exposed to two conspecific males for 8 days. On day 8, the oestrous female was allowed to mate with one of those two conspecific males, then she was paired with the other conspecific male (the focal male; $N=7$), that is, the female had previously mated with a conspecific male before being paired with the conspecific focal male.
4. 'Exposed to and paired with heterospecific': females were first exposed for 8 days to one conspecific male and one heterospecific male ($N=8$) or to only one heterospecific male ($N=7$). Then they were paired with first the heterospecific male and, second, a conspecific male (the focal male). Procedures for the eight trials in which females were exposed to both a conspecific male and a heterospecific male were similar to those in the 'Exposed to but not paired with heterospecific' treatment, except that the female was first paired for 5 min with the heterospecific male and 5 min later she was paired with the conspecific male (the focal male). For the seven trials in which females were exposed only to a

heterospecific male, we used arenas (50×38.1 cm and 21.5 cm high; Allentown, model no. PCT4SHT) divided into two, similarly sized sections (24.9×38.1 cm and 21.5 cm high) by a wire-mesh partition with 1 cm^2 openings. We placed the subject female on one side and a heterospecific male on the other side. After 8 days, the female and the male in the same arena were transferred to individual cages lined with clean bedding and the cages were moved to the test room. After 10 min, the heterospecific male was transferred to the female's cage for 5 min. We did not interfere with the behaviour of animals during this 5 min trial. Five minutes after the trial with the heterospecific male, the same female was paired for 5 min with an unfamiliar conspecific male in her own cage.

There were no differences between the condition in which the female was exposed during 8 days to a conspecific male and a heterospecific male and the condition in which the female was exposed during 8 days only to a heterospecific male, either for the latency to lordosis ($t_{13} = -0.32$, $P = 0.75$) or the duration of lordosis ($t_{13} = -0.09$, $P = 0.93$), so we pooled these two conditions in an overall 'Exposed to and paired with heterospecific' treatment. In none of these 15 trials did the females show any lordosis towards the heterospecific male. Females were, however, aggressive towards the heterospecific male (Siegel 1985) prior to being paired with the conspecific, focal male.

In summary, by comparing the behaviour of the females in the first two conditions ('Exposed to but not paired with conspecific' versus 'Exposed to but not paired with heterospecific'), we could determine whether the behaviour of a female towards a conspecific male was negatively affected by exposure to a heterospecific male. Similarly, by comparing the last two conditions ('Exposed to and paired with conspecific' versus 'Exposed to and paired with heterospecific'), we could determine whether the behaviour of a female towards a conspecific male was negatively affected by having recently being paired with a heterospecific male.

Ethical Note

Aggression of Syrian hamster females towards Turkish hamster males involved a preliminary interaction in which females normally attempted to bite the sides of the male. It was not possible to determine whether a female's attack ended in a bite. Afterwards, females chased the male away but biting did not occur. Chased males could not leave the cage during the 5 min trial but the size of the cage allowed them to stay away from the aggressor. Aggression from males towards females was not observed. We planned to stop a trial if blood was observed; however, this did not happen in any trial. At the end of each trial, males were checked for wounds, but none was observed. After each trial, animals were returned to their animal rooms to be used in other experiments. The experiments comply with the current laws of the U.S.A. All research was conducted with approval from Cornell University's Institutional Animal Care and Use Committee (protocol no. 1993-0120).

Statistical Analyses

We used IBM SPSS Statistics version 19 (SPSS Inc., Chicago, IL, U.S.A.) for all statistical analyses. Normality was assessed with the Shapiro–Wilk test. After we log-transformed the latency data, both latency to lordosis and duration of lordosis met the assumption of normality (Shapiro–Wilk test: $P > 0.05$ for all groups). The variances were homogeneous (Levene test: $P > 0.05$ for both latency and duration of lordosis). To compare latency to lordosis and duration of lordosis across the four treatments, we used two-way ANOVAs, the two factors being male type (conspecific or heterospecific) and pairing status before the trial (paired or not paired). Results are given as mean $\pm$ SE.

RESULTS

The longest latencies to lordosis occurred when the female had not been paired with a male prior to the test trial ('Exposed to but not paired with conspecific': 26.38 ± 4.1 s; 'Exposed to but not paired with heterospecific': 25.71 ± 2.93 s) whereas the shortest latencies to lordosis occurred when the females had been previously paired with another male ('Exposed to and paired with conspecific': 17.4 ± 1.69 s; 'Exposed to and paired with heterospecific': 16.71 ± 2.34 s; Fig. 1a). Accordingly, there was no significant effect of male type ($F_{1,33} = 0.02$, $P = 0.88$), but having been paired or not paired before the trial had a significant effect on the latency to lordosis ($F_{1,33} = 12.28$, $P = 0.001$). There was no significant interaction between male type and pairing status prior to the trial ($F_{1,33} = 0.014$, $P = 0.91$).

The shortest duration of lordosis occurred when the female had not been paired with a male prior to the trial ('Exposed to but not paired with conspecific': 264.2 ± 4.88 s; 'Exposed to but not paired with heterospecific': 264.09 ± 4.22 s) whereas longer durations of lordosis occurred when the female was previously paired with another male ('Exposed to and paired with conspecific': 274.44 ± 2.15 s; 'Exposed to and paired with heterospecific': 277.91 ± 3.28 s; Fig. 1b). Accordingly, there was no significant effect of male type ($F_{1,33} = 0.25$, $P = 0.62$), but having been paired or not paired before the trial had a significant effect on the duration of lordosis ($F_{1,33} = 11.44$, $P = 0.002$). There was no significant interaction between male type and pairing status prior to the trial ($F_{1,33} = 0.22$, $P = 0.64$).

Females were not aggressive towards any conspecific male, and mounting by the conspecific male took place in all tests.

DISCUSSION

We tested the hypothesis that interactions between females and heterospecific males may not only be negative per se (e.g. by producing nonviable offspring), but may also negatively affect how females respond to conspecific males. We have previously observed that Syrian hamster females can be extremely aggressive towards Turkish hamster males under some circumstances. This occurs, for example, after females are exposed to a heterospecific male during 8 days prior to being paired with that male (delBarco-Trillo et al. 2010). In this situation, a heterospecific male will trigger high levels of aggressive behaviour by the female and a lack of sexual receptivity in Syrian hamster females. This negative disposition in a female may be continued towards other males (including conspecific males) to which the female is later exposed. However, our results did not support this hypothesis. Instead we found that females behaved similarly towards all conspecific males, regardless of whether females had previously interacted or not with heterospecific males. Even when a female was aggressive towards a heterospecific male and then paired with a conspecific male, no aggression towards the conspecific male was observed. Therefore, negative interactions with heterospecific males do not seem to affect later interactions with conspecific males, even if the delay between such interactions is brief.

Females showed lordosis and maintained lordosis for a longer time when they had first been primed with a stimulus male 5 min before a test. It did not matter whether the primer male was a conspecific male or a heterospecific male. A priori, one would have expected a different response by the female to each type of male, given that we found that females were sexually receptive and not aggressive towards the conspecific males but were aggressive and not sexually receptive towards the heterospecific males. A faster sexual response towards a conspecific male after briefly mating with another conspecific male can be understood in terms of increased sexual arousal during mating with the first conspecific male. However, it is not clear why females would mate faster after being aggressive and not sexually receptive

towards a heterospecific male. One possibility is that after a negative interaction with a heterospecific male, the presence of a conspecific male may sexually arouse the female more than if the female had not been exposed to the heterospecific male. If so, this would indicate that aggressive interactions with a heterospecific male may further improve interactions with conspecific males. This scenario, however, may not be applicable to all taxa. For example, in crickets (*G. rubens* and *G. texensis*), after *G. texensis* females were exposed to a heterospecific male, they stopped showing a preference for conspecific males over heterospecific males (Izzo & Gray 2011). Another possibility is that conspecific males can detect whether the female has recently mated with another male (either a conspecific or a heterospecific male), and through a more vigorous pursuit and copulatory behaviour they could elicit lordosis faster and for a longer duration (Carter 1985); however, male behaviour appeared similar across treatments.

As shown in cross-fostering studies, exposure to heterospecifics during development may impair later interactions with conspecifics in some species (McDonald & Forslund 1978; Huck & Banks 1980) but not in others (Kirchhof-Glazier 1979). For example, when two species of sympatric lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) were cross-fostered and then paired during adulthood, cross-fostered females of both species showed less lordosis towards conspecific males than females that had not been cross-fostered (Huck & Banks 1980). Cross-fostered *Dicrostonyx* females were also more aggressive towards conspecific males than were females that had not been cross-fostered (Huck & Banks 1980). Our results do not agree with those of Huck & Banks's (1980) study. These cross-fostering studies, however, are not directly comparable to ours, since in cross-fostering studies the response of adults towards conspecifics or heterospecifics depends on the type of preadult experiences, whereas we investigated how experiences during adulthood can affect adults. Although cross-fostering studies in mammals show that female responsiveness to conspecific and heterospecific males can be altered before puberty (Quadagno & Banks 1970; Huck & Banks 1980), such experiences are artificial conditions that do not occur in nature and thus may not be considered very helpful in understanding the topic of reproductive interference in mammals.

It is not clear how often individuals of two sympatric species living in the wild encounter members of another species and, if so, how much experience they have with members of a closely related species. More research is needed to determine how the type of results reported in this paper relate to interspecific interactions in the wild and how such interspecific interactions may later affect intraspecific interactions.

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Female interactions with a heterospecific male do not affect conspecific behaviour
Across treatments, females were not aggressive towards conspecific males
Pairing with any male type promotes faster sexual response with conspecific males

Figure 1.

(a) Latency to lordosis and (b) duration of lordosis in trials in which females were paired with a conspecific male after being exposed to but not paired with another conspecific male ('C+/C-'), after being exposed to but not paired with a heterospecific male ('H+/H-'), after being exposed to and then paired with another conspecific male ('C+/C+'), or after being exposed to and then paired with a heterospecific male ('H+/H+'). Different letters denote a statistically significant difference. Values represent mean $\pm$ SEM.