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ORIGINAL PAPER

Odor-based mate choice copying in deer mice is not affected by familiarity or kinship

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Abstract

Individuals pay attention to the social and mate decisions of others and use these to determine their own choices, displaying mate choice copying. The present study with deer mice, *Peromyscus maniculatus*, showed that females copied the odor preferences and appetitive components of the mate choice of other females. It was found that an association between male and female odors, which is indicative of the apparent interest expressed by a female in a male, enhanced the preference of another female for the odors of that male. This socially learned odor preference lasted for at least 24 h and extended to a preference for the actual male that was the odor source. Neither kinship nor prior familiarity with the female whose odor was presented had a significant influence on the degree of odor-based mate choice copying displayed. These findings show that female deer mice can engage in mate choice copying using the odor-based social interest and mate choice of other females.

Keywords Social learning · Social discrimination · Social information · Mate copying · Olfactory communication

Introduction

Social information guides decision-making in most animals and can be acquired either directly or indirectly through social learning from the behavior and products of others with similar requirements (Choleris et al. 2009; Danchin et al. 2004). Evidence from a range of taxa has shown that the mate choice decisions of one individual can be influenced by those of another, resulting in mate choice copying (e.g. Dugatkin 1992; Dugatkin and Godin 1992; Galef and White 1998; Little et al. 2011; White and Galef 2000; Witte and Ryan 2002). Although true mate choice copying was proposed to directly involve observing a sexual interaction (i.e. copulatory behavior), in the original formulation, it was indicated that females do not need to observe actual mating but only an apparent choice (Pruett-Jones 1992). Individuals pay attention to the sensory cues associated with the mate choices of others, thereby reducing the risks and uncertainties associated with their own choices. Odor cues, in particular, provide social information that can be utilized in mate choice copying. Olfactory cues are integral to the expression of the appetitive (pre-copulatory) components of rodent mate choice and sexual behavior (Hurst 2009). Odours guide the social behavior and mate responses of rodents, with females of various species using odors to determine the condition, health, and suitability of a male as a potential mate (e.g. Ferkin 2019; Hurst 2009; Kavaliers et al. 2019, 2020). Females attend to male odors, deposit scent marks in response to male odors, and investigate the odors of other females (Ferkin 2019; Ferkin and Li 2005; Zala et al. 2004).

There is suggestive evidence from rodents that females can have their mate choice influenced by the odors of conspecifics. Female laboratory mice, *Mus musculus*, preferred the odors of a specific male that had been associated with an estrous female and avoided and discriminated against the odors of a male associated with an infected female (Kavaliers et al. 2005, 2019). Similarly, female Norway rats, *Rattus norvegicus*, preferred the cues of recently mated males (Galef et al. 2008). It has been further speculated that female odors may similarly influence the mate choice of meadow voles, *Microtus pennsylvanicus*, and likely other species of rodents (Scauzillo and Ferkin 2019).

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Mate choice copying may be influenced by a range of environmental and social factors (Blanchet et al. 2010; Davies et al. 2020; Kavaliers et al. 2017; Scauzillo and Ferkin 2019; Vakirtzis 2011). A relatively common observation across studies of social learning is the enhancement of learning with increased familiarity or relatedness between subjects. Familiar/related individuals tend to share similar biological and environmental conditions, thus, likely increasing the salience of social information provided by conspecifics. In studies of socially acquired fear deer mice, *Peromyscus maniculatus*, laboratory mice, and laboratory rats observers displayed enhanced learning from demonstrators that were familiar and, or kin (Agee et al. 2019; Jeon et al. 2010; Jones and Monfils 2016; Jones et al. 2014; Kavaliers et al. 2005; Monfils and Agee, 2019). Similarly, familiarity and kinship enhanced social learning of food preferences in house mice and Mongolian gerbils, *Meriones unguiculatus*, though not of laboratory rats (Agee et al. 2019; Choleris et al. 1997; Valsecchi et al. 1996). Although there is evidence that mate-choice copying is influenced by various characteristics of the copied female [e.g. relative quality, experience (reviewed in Davies et al. 2020; Kavaliers et al. 2017; Scauzillo and Ferkin 2019)] whether or not familiarity and relatedness affect male choice copying is not clear.

Deer mice are a polygynous non-microtine (Cricetinae) widespread North American rodent whose natural history is well established (Bedford and Hoekstra 2018; King 1968; Wolff 1968). *Peromyscus* have been used as a model for studying natural variations and adaptations in a range of behavioral, ecological, and neurobiological functions, including those related to mate choice and olfaction (e.g. Bedford and Hoekstra 2015; Delaney and Hoekstra 2018; Galea et al. 1994; Innes and Kavaliers, 1987). Deer mice and related *Peromyscus* species exhibit odor-based familiarity/kin social recognition, including in social learning of fear (Dewsbury 1988, 1990; Grau 1982; Halpin and Hoffman 1987; Kavaliers et al. 2005; Keane 2000; Vestal and Hellack 1978). Accordingly, we examined mate choice copying and the effects of familiarity and kinship in deer mice.

Using an odor preference test, the results of which are consistent with social and sexual interest and preferences (Ehman and Scott 2002; Krackow and Matsuck 1991), we considered the effects of kinship (genetic relatedness) and familiarity (prior association) on odor-related mate choice copying by female deer mice. In view of the significant effects of familiarity and kinship on social learning of fear in deer mice, we hypothesised that these factors may influence other forms of social learning, such as that of mate copying. In addition, we tested whether or not odor-based copying translates into preference for the actual male that was the odor source.

Materials and methods

Animals

Adult deer mice of both sexes (20–25 g) were weaned at 20 days of age and then housed for 1–2 months as same sex pairs that were composed of either siblings (kin) or unrelated individuals (non-kin). Mice were held in transparent polyethylene cages with a wood-chip bedding under a reproductively stimulatory long 14 h light: 10 h dark cycle (light 0800–2200 h) at 20 °C with food (Mouse Breeder Blox, Wayne Laboratory Diets, Madison, WI) and water available ad libitum. Mice were 6–8 generations from a wild trapped population. Outbreeding was maintained with no sibling pairings. Different groups of female mice were used for each of the experiments.

Experimental apparatus

Both the odor and male preferences of individual female mice were determined in a translucent Plexiglas Y-maze apparatus (5 cm diameter) with 30 cm arms (illustrated in Coopersmith and Lenington 1992). Stimulus compartments in each of the two arms of the Y in which either the odors or individual male mice were placed, along with the start box in which a female mouse was placed, were 14 cm long. A solid Plexiglas barrier restricted the female mouse to the start box and perforated Plexiglas barriers at the two stimulus arms prevented contact and interaction with either the odor sources or the male mice. Removable solid Plexiglas barriers present at ‘seams’ 8 cm into each of the stimulus arms prevented exposure of the female mice to either the odors or male mice until the designated test times.

General experimental procedures

Habituation to apparatus

Individual female mice were placed in the apparatus and allowed to explore the various arms (after being held for 5 min in the start box) for 30 min on three consecutive days prior to the test day. Individual males were similarly habituated to the closed stimulus arms over three days. When both male and female urine were used samples were adjacently spotted on the same filter paper.

Urine collection

Urine was obtained by palpation from single males and females and frozen at -18° C until its use (Kavaliers et al. 2003). A fixed aliquot of male and female urine (2 μl) was thawed, diluted 1:5 with deionized water and spotted on filter paper (1.0 cm diameter spot, Whatman No.5 filter paper, London, UK) before each days testing.

Determination of odor preferences

In the odor preference tests, an individual female was placed in the start box of the apparatus for 1 min. Then, the solid barrier was removed and the mouse was allowed to access the two arms of the Y-maze. Approximately 1 min after the test, mouse had entered the stimulus arms and re-entered the neutral arm, the Plexiglas barriers in the arms were removed and the mouse too was exposed to the test odor combinations. During the subsequent 5 min tests, the time a female spent in each stimulus arm within 8 cm of the odors relative to the seam in each arm of the apparatus was recorded. This distance was chosen on the basis of the results of prior studies that took into account the odor constituents and diffusion (Kavaliers et al. 2003).

Odor preference was defined as the time each test female spent in the one stimulus arm of interest divided by the total time spent in the two stimulus arms. Odor and control arms were randomized between trials and subjects for both the Day 1 and Day 2 tests. Trials were stopped and an alternate mouse was used if the test female spent less than 30 s of the 5 min test period in the distal end of the two arms (2–5% of trials). Females generally spent between 100 and 200 s in at least one of the stimulus arms of the Y-maze, with no evidence of systematic differences between the various trials and odor combinations. Between trials, the Y-maze was washed thoroughly with hot water and unscented soap. The results of previous studies established that the results obtained in the 5 min test were comparable to those obtained with longer tests of 15–30 min.

Experiment 1: Effects of kinship and familiarity on preferences for male odors

The odor choices ($n = 8$, in all cases) provided to estrous female mice on Day 1 were: (1) Male B + no female (blank filter paper) vs Male A; (2) Male B + familiar and kin (sibling) female vs Male A; (3) Male B + familiar/non-kin female vs Male A; (4) Male B + unfamiliar/non-kin female vs Male A. Twenty-four hours later (Day 2), odor preferences were again determined, without any accompanying female odor in the stimulus odor pairs. On Day 1, the male odor sources “A” and “B” came from equivalent non-kin unfamiliar males. On Day 2, Male “B” odor was the same as on Day 1, while Male “A” odor was from a male different from that used on Day 1. The unfamiliar Male A was used to increase the power of discrimination, in that estrous female mice show an enhanced discrimination of, and preference for unfamiliar males (Kavaliers et al. 2003). Female mice that were defined as unfamiliar were never housed together and encountered one another for the first time in the experiment. Mice considered as familiar were housed together since weaning (30+ days) or since birth if kin. Daily wet vaginal smears were used to determine the estrous state (estrous characterized by cornified squamous epithelial cells) during the test period.

Experiment 2 and 3: Effects of anestrous and own odors on preference for male odors

The odor choices ($n = 8$ in all cases) provided on Day 1 for Experiment 2 were: (1) Male B + familiar/non-kin anestrous female vs male A; and (2) Male B + familiar/non-kin estrous female vs Male A. For Experiment 3, the Day 1 choice was Male B + female’s own estrous odour vs Male A. Twenty-four hours later (Day 2), odor preferences were again determined, without any accompanying female odor in the stimulus odor pairs. The male odor sources “A” and “B” came from equivalent non-kin unfamiliar males. On Day 2, Male “B” odor was the same as on Day 1, while Male “A” odor was from a male different from that used on Day 1.

Experiment 4: Male odor preferences and actual male preferences

The odor choices ($n = 8$, in all cases) provided to females on Day 1 were: (1) Male B + no female odor (blank filter paper) vs Male A; (2) Male B odor + unfamiliar/non-kin female odor vs Male A odor. Twenty-four hours later on Day 2, females were provided a choice of Actual Male B vs Male A. On Day 2, Male “B” was the male whose odor was presented on Day 1 while Male “A” was different from the male A whose odor was presented on Day 1.

Data analysis

Preferences for a male odor on Day 1 (Experiments 1–4) and Day 2 (Experiments 1–3) were calculated by the time spent investigating the male odor of interest in the Y-maze by the time spent investigating both odors (i.e. Male B/ Male A + Male B). For experiment 4, preference for the actual male that was associated with the female odor on Day 1 was calculated on Day 2. One sample t-tests were used to test whether or not the odor and male preferences differed from random (0.5). The effects of various female odors associated with the male odors were assessed in general linear models and separate one-way repeated measures analyses of variance (ANOVA). The Greenhouse–Geisser test was used to evaluate normality and all of the data found to be normally distributed. Post hoc tests were performed using Tukey’s Honestly Significant Difference test, and all tests used a significance criterion of $\alpha = 0.05$. Eta squared (ϵ^2) was used to measure effect size. All statistical analyses were performed in IBM SPSS statistics 2.0.

Results

Experiment 1: Effects of kinship and familiarity on preferences for male odors

The repeated measures ANOVA revealed a significant effect of the presence of a female odor on the preferences for the odor of a male ($F_{7,\,49} = 10.999$, $p < 0.001$, $\epsilon^2 = 0.611$). When given a choice between the odors of two males without any accompanying female odors (blank filter paper), the test females displayed no significant odor preference on either Day 1 or Day 2 (Day 1 $t_7 = 0.61$, $p = 0.615$; Day 2 $t_7 = 0.50$, $p = 0.628$) (Fig. 1). In all cases, females showed a significant preference for the odor of the male (Male B) that was associated with that of an estrous female odor (Day1: familiar kin $t_7 = 7.079$, $p < 0.001$; familiar non-kin $t_7 = 6.768$, $p < 0.001$; unfamiliar non-kin $t_7 = 6.545$, $p < 0.001$). There were no significant differences ($ps > 0.10$) between these Day 1 odor preferences which were all significantly different ($ps < 0.01$) from those shown for the no odor condition. Subsequently on Day 2 when only male odors were provided, females continued to show a significant preference for the odors of the male (Male B) that had been associated with that of the female (familiar kin $t_7 = 6.326$, $p < 0.001$; familiar non-kin $t_7 = 8.428$, $p < 0.001$; unfamiliar non-kin $t_7 = 6.53$, $p < 0.001$). There were no significant differences ($ps > 0.10$) between any of the Day 2 preferences. There were significantly greater Day 1 than Day 2 preferences for familiar kin ($p = 0.04$) and unfamiliar non-kin ($p = 0.04$), with no significant difference ($p = 0.20$) for the familiar non-kin female odor associations.

Experiment 2–3: Effects of anestrous and own odors on preferences for male odors

The repeated measures ANOVA revealed a significant effect of the estrous state of the female odor on subsequent preference for male odor ($F_{3,21} = 21.888$, $p < 0.001$, $\epsilon^2 = 0.758$) (Fig. 2). On both Day 1 and Day 2, females displayed a significant preference for the odors of males (Male B) associated with the odors of an estrous female (Day 1 $t_7 = 7.898$, $p < 0.001$; Day 2 $t_7 = 6.522$, $p < 0.001$). There were no significant differences between the Day 1 and Day 2 preferences ($ps > 0.20$). Females provided with odors of anestrous females displayed no significant male odor preferences (Day 1 $t_7 = 1.284$, $p = 0.24$; Day 2 $t_7 = 1.361$, $p = 0.216$). On both Day 1 and Day 2, females displayed a significantly greater preference ($ps < 0.01$) for the odor of the male associated with an estrous than an anestrous female odor. Females displayed no significant preference for the odors of males associated with their own odor (Day 1 $t_7 = 0.524$, $p = 0.617$; Day 2 $t_7 = 0.547$, $p = 0.601$).

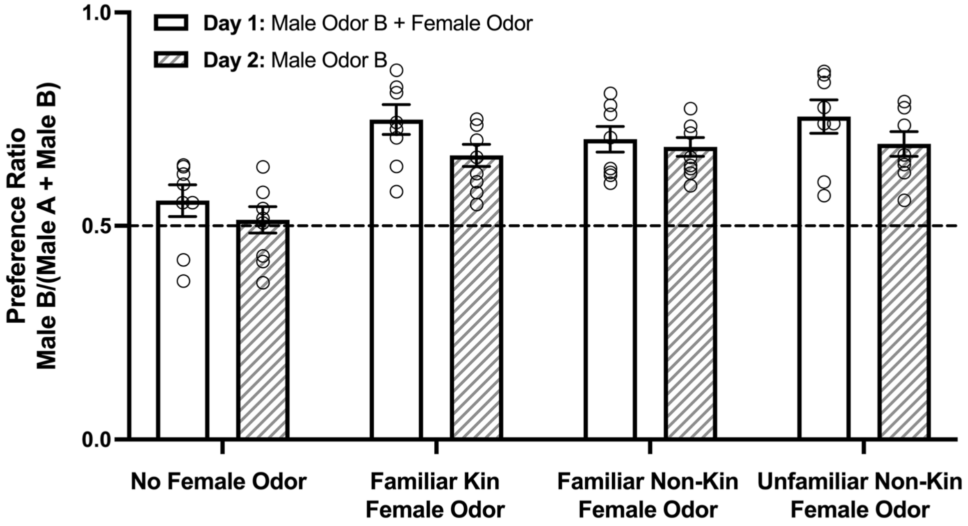

Fig. 1 Y-maze odor response of female deer mice to the odors of a male (Male B) provided either with or without the odor of another female. On Day 1, male odor B was associated with the odor of a female (Familiar Kin; Familiar Non-Kin; Unfamiliar Non-kin; or No Female Odor (Control Blank)). On Day 2, male odor B was provided just by itself. Responses are given as preference ratios (i.e. Time spent in the vicinity of the odor of Male B/Time spent in the vicinity of the odor of Male B + Time spent in the vicinity of the odor of Male A). Dashed line (0.50) indicates no preference. Preferences were determined over a 5 min period. $N = 8$ in all cases. Vertical lines denote a standard error of the mean

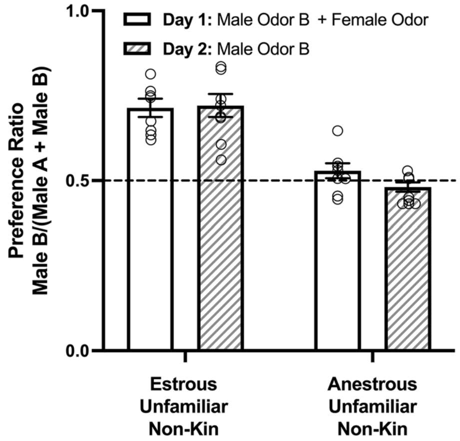

Fig. 2 Y-maze odor response of female deer mice to the odors of a male (Male B) provided either with or without the odor of another female. On Day 1, male odor B was associated with the odor of either an Estrous or Anestrous Unfamiliar - Non-Kin female odor. On Day 2, male odor B was provided by itself. Responses are given as preference ratios (i.e. Time spent in the vicinity of the odor of Male B/ Time spent in the vicinity of the odor of Male B + Time spent in the vicinity of the odor of Male A). Dashed line (0.50) indicates no preference. Preferences were determined over a 5 min period. $N = 8$ in all cases. Vertical lines denote a standard error of the mean

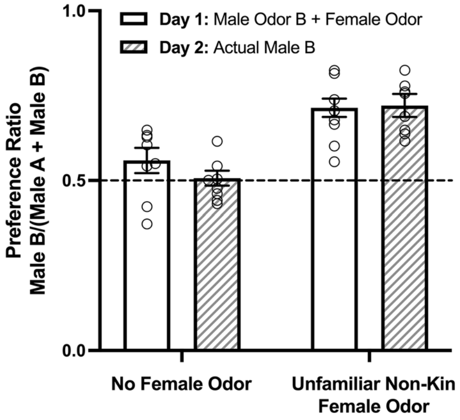

Fig. 3 Y-maze response of female deer mice to male (Male B). On Day 1, male odor B was associated with the odor of an oestrous Unfamiliar -Non-Kin female or no female odor (blank, control odor). On Day 2, actual male B was provided. Responses are given as preference ratios (i.e. Time spent in the vicinity of Male B/ Time spent in the vicinity of Male B + Time spent in the vicinity of Male A (odors on Day 1 and actual males on Day 2)). Dashed line (0.50) indicates no preference. Preferences were determined over a 5 min period. $N = 8$ in all cases. Vertical lines denote a standard error of the mean

Experiment 4: Male odor preferences and actual male preferences

The repeated measures ANOVA revealed a significant effect of prior male (B) and female odor association of the subsequent preference for an actual male ($F_{3,21} = 11.226$, $p = 001$; $\epsilon^2 = 0.61$) (Fig. 3). Females exposed to a male odor (B) with no prior female association (blank filter paper) (Day 1) and subsequently (Day 2) the male (B) by itself displayed no significant odor or male preference, respectively (Day 1 $t_7 = 1.28$, $p = 0.24$; Day 2 $t_7 = 1.31$, $p = 0.21$). There were no significant differences ($ps > 0.20$) between the Day 1 and Day 2 preferences. In contrast, females displayed a significant preference for the male odor (B) associated with an estrous unfamiliar non-kin female odor (Day 1 $t_7 = 7.89$, $p < 0.001$). Subsequently females displayed a significant preference for the actual male (B) (Day 2 $t_7 = 6.522$, $p < 0.001$). There were no significant differences between the Day1 and 2 preferences.

Discussion

Social and mate responses are context-dependent and sensitive to ongoing social information. Individuals pay attention to the cues associated with the mate choice decisions of others and utilize these to determine their own choices, engaging in mate choice copying (Danchin et al. 2004; Galef et al. 2008; Kavaliers et al. 2017). Here, we showed that the association between male and female odors (i.e. apparent interest expressed by another female in a male) influences the subsequent responses of female deer mice to male odors and, as such, the appetitive components of mate choice. Neither kinship nor familiarity with the female that was the odor source had a significant influence on the degree of mate choice copying displayed. This socially acquired odor preference lasted for at least 24 h and extended to a preference for the "actual" male that was the odor source. Thus, female deer mice utilize the odor-based mate choices and interests of other females in a manner similar to the visually based mate choice copying reported in birds, fishes, and humans (e.g. Dugatkin 1992; Dugatkin and Godin 1992; Galef and White 1998; Little et al. 2016; White and Galef 2000; Witte and Ryan 2002).

The odor preference tests used here do not directly test mating preferences. Rather they assess sociability, affiliation, and social selection. However, as shown here and previously with laboratory rats (Galef et al. 2008), results from olfactory cues extend to preferences for actual males and are consistent with the appetitive components of mate choice. In this regard, many studies of mate choice copying use the tendency of a female to be in the proximity of and, or affiliate with a male, as a surrogate measure for her preferences for him as a sexual partner (Davies et al. 2020).

There is mounting evidence for a very quick detection and neurohumoral mediation of the behavioral responses to conspecifics through a variety of volatile and non-volatile odor cues (Baum and Kelliher 2008; Hurst 2009). Individuals in the wild are more likely to detect an indirect proxy of mate choice (i.e. odor interest) rather than to observe very briefly performed actual mating. This includes scent over-marking of male odors by females whereby a female expresses her interest in that male (Ferkin 2019). As such, the odors of a female that are associated with that of a male can be used to guide the mate choice and sexual interests of another female (Kavaliers et al. 2017, 2019). Estrous female deer mice recognized and preferred the urinary odors of males that were associated with the odors of another estrous female over those of males that either had no association, or were associated with either the odors of an anestrous female, or her own odors. This shows that females were neither displaying a significant choice for the odors of females per se nor simply responding to an enhanced olfactory stimulus. This is reinforced by the findings that when given a choice between two males of equivalent condition, females prefer the male that had been previously associated with an estrous female odour. Whether or not this involves true individual recognition or just category recognition (i.e. familiar versus novel) remains to be determined.

These results extend prior findings of olfactory-mediated mate choice copying in laboratory mice and Norway rats (Galef et al. 2008; Kavaliers et al. 2006, 2017). Non-visual cues such as odors are likely to provide social information of importance for mate choice and mate choice copying in a variety of species of rodents (e.g. meadow voles). Odours provide recognition at a number of levels including: sex, age, reproductive status (i.e. estrous state), social hierarchy, genetic relatedness, familiarity, condition and quality, through to true individual recognition (Cherry and Baum 2020; Choleris et al. 2009). Investigations with species from a various mating systems, condition and status are required to further examine mate choice copying in rodents and other vertebrates.

The nature of the female odor (i.e. whether it was from a familiar and, or kin female) did not significantly influence the extent of mate-choice copying displayed. This is consistent with a recent meta-analysis which reported that mate choice copying was not affected by the type of social information available to the observer female (Davies et al. 2020). There is, however, evidence from various species, including humans that demonstrator type (e.g. age, prior experience) does matter in mate choice copying (Kavaliers et al. 2017; Scauzillo and Ferkin 2019). Moreover, female laboratory mice have been shown to display an avoidance of, and discrimination against, male mice whose odor had been associated with that of an infected female (Kavaliers et al. 2019). These findings suggest that the nature of, and information provided by, female odors may be important in determining subsequent responses to males.

Other forms of social learning, such as social learning of fear, social transmission of food preferences, though not in all cases, are affected by familiarity and kinship (Agee et al. 2019; Choleris et al. 1997; Jeon et al. 2010; Jones and Monfils 2016; Jones et al. 2014; Valsecchi et al. 1996). Prior social relationships affected social learning of defensive responses to micro-predators in male deer mice from the same population (Kavaliers et al. 2005). Observers whose demonstrators were either kin (siblings), or members of a familiar pair (kin or non-kin) displayed enhanced social learning of defensive responses to biting flies. In addition, various *Peromyscus* species have been shown to exhibit sibling recognition and a preference to associate with siblings (Dewsbury 1988, 1990; Grau 1982; Halpin and Hoffman 1987). This raises the possibility that although females may be able to discriminate between familiar and kin individuals, that information does not necessarily influence their responsiveness and the degree of mate choice copying displayed, at least in a laboratory setting. Mate choice is multifaceted with at least three key components—sexual arousal and motivation (proceptivity), preferences, and choosiness (Jennions and Petrie 1997) that may be differentially affected by familiarity and kinship.

Disparities in social information use could be due to a number of factors including levels of arousal and attention, salience, as well as sex differences in the expression of social learning (Choleris and Kavaliers 1999; Davies et al. 2020; Kavaliers et al. 2017; Scauzillo and Ferkin 2019). In the case of social learning of fear, familiar and kin individuals are likely to be exposed to a similar environment and threats. For mate choice copying, responding to a diversity of males associated with both familiar and unfamiliar individuals is likely to be more adaptive. Females are likely to encounter cues associated with familiar/kin in natal areas and unfamiliar individuals upon dispersal.

Male condition and health incentive value, availability of males, as well as a female's prior sexual experience also need to be considered. Poorer-quality males may be more salient when they are associated with familiar and or kin females. Consummatory sexual responses that involve multiple sensory inputs may be differently regulated and influenced by social information and familiarity/kinship. In addition to the preceding, for a fuller understanding how mate choice copying may affect mate preferences, determinations under natural conditions are needed.

Author contributions MK designed the experiments and collected the data. EC, IRB, MK, and KPO interpreted the data, contributed to the writing, and approved the final version of this manuscript. We thank Dr. Doug Colwell and Terry Seely, Joan Ingoldsby and Dawn Grey for their assistance.

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Data accessibility The data sets generated and analyzed during the current study will be deposited in the Western University Data Repository and are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest We have no competing interests.

Ethical approval All procedures were conducted in accordance with the Institutional Animal Care Committees (University of Western Ontario (Western University) protocol number 20008-058-05; Agriculture and Agri-Food Canada (Lethbridge) protocol no. LRC 172) and the guidelines of the Canadian Council for Animal Care).

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