



Evidence of mate choice copying in Norway rats, *Rattus norvegicus*

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In the literature, nonindependent mate choice of females is frequently referred to as 'mate choice copying'. The label seems particularly appropriate when the probability that a focal female will mate with a male increases after she has watched him engage in sexual behaviour with another female. However, the classic definition of mate choice copying requires only that a male's attractiveness to a female change following his acceptance or rejection by another female regardless of whether such alteration in a female's response results from seeing him mate or from some other process. Here, we provide evidence that female Norway rats prefer to affiliate with a male that has recently engaged in sexual activity, even when they did not observe the male's previous mating. Furthermore, when we provided oestrous females with access to two males tethered some distance apart, the male that had recently copulated also mounted and achieved intromission and ejaculation sooner and more frequently than the male that had not recently copulated. We also provide evidence that increased attractiveness of male rats that had recently copulated was mediated by olfactory cues, and that female rats tended to affiliate with males that had engaged in sexual activity but not with males that had spent time with anoestrous females.

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The results of numerous studies in birds and fish suggest that females tend to prefer males that they have seen mating with other females. Visual cues play a major role in determining mate choice in many avian and piscine species, and it is therefore perhaps to be expected that, in fish and birds, direct observation of the prior sexual success of potential mates is important in their mate choice copying. However, the most frequently cited definition of mate choice copying (Pruett-Jones 1992, page 1000) does not require that a change in a female's preference for a male depends upon seeing him mate with another female, only that 'the conditional probability of choice of a given male by a female is either greater or less than the absolute probability of choice depending on whether that male mated previously or was avoided, respectively'.

Dugatkin (1996, page 87) has proposed amending Pruett-Jones's (1992) definition of mate choice copying by adding the sentence 'Further, the information about

a male's mating history (or some part of it) must be obtained by the female via observation'. Indeed, so far as we know, and as Dugatkin's (1996) amendment to Pruett-Jones's (1992) definition requires, all previous studies demonstrating nonindependent mate choice have been concerned with effects of visual observation of sexual behaviour of members of the opposite sex on the observed individual's subsequent attractiveness to its observer (e.g. Dugatkin & Godin 1992; Gibson & Høglund 1992; Grant & Green 1996; Galef & White 1998; Witte & Ryan 1998; reviewed in Galef & White 2000). For example, in Japanese quail, *Coturnix japonica* (1) females that had watched a male that they did not prefer in an initial test of affiliative preference while he courted and mated with another female subsequently significantly increased the time that they spent affiliating with him (Galef & White 1998), (2) a female's affiliative preference between males predicted her choice of sex partner (White & Galef 1999a) and (3) the probability that a nonpreferred male that mated with a female would fertilize her eggs increased significantly after she had seen him court and mate with another female (Persaud & Galef 2006). The change in affiliative preferences of female quail for nonpreferred males and the probability that nonpreferred males will fertilize

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a female's eggs require that females actually see the non-preferred male consorting with another female (White & Galef 1999b; Persaud & Galef 2006).

Kaveliers et al. (2006) reported that outbred female mice, *Mus domesticus*, showed greater interest in urine collected from males that had been exposed overnight to urine from an oestrous female than in urine collected from unstimulated males. Although Kaveliers et al. (2006) provide no evidence that preferences of female mice for urine odours predicted females' tendency to either affiliate or copulate with males, in discussing their findings, they (page 4296) suggest that female mice choosing a mate may use olfactory-based indicators of other females' interest in males when selecting a male with whom to mate. Thus, contrary to findings suggesting the importance of direct observation in mate choice copying in birds and fish, the results of Kaveliers et al.'s (2006) study suggest that rodents and the many other mammals whose choice of sexual partner is profoundly affected by olfactory rather than visual cues (Brown 1985) might use olfactory rather than visual information to learn about a potential partner's prior sexual success. If so, in some mammals, there might be mate choice copying even when females cannot directly observe the sexual activity of potential partners.

Here, we first determined whether a male Norway rat that had recently copulated with a conspecific female was more attractive to a focal female than a male that had not recently copulated, even when the focal female did not actually see the male engage in sexual behaviour with another female (experiment 1). In experiments 2 and 3, we determined whether the increased attractiveness of sexually active males that we observed in experiment 1 was mediated by olfactory cues resulting from either a male's interaction with an oestrous female or his ejaculation. In experiment 4, we determined whether females engaged in sexual activity sooner and more frequently with a male that had recently copulated with another female than with a male that had not, thus coming closer to providing evidence of true mate choice copying rather than of changes in affiliative behaviour.

EXPERIMENT 1

Experiment 1 was undertaken to determine whether female Norway rats prefer to affiliate with a male that has recently copulated with another female or with a male that has not recently engaged in sexual behaviour. We examined choices of focal females when they were both in oestrus and anoestrous to determine whether females' reproductive state affected their tendency to affiliate with sexually active males.

Methods

Subjects

All subjects were Long-Evans rats acquired at 7 weeks of age from Charles River Canada (St Constant, Quebec, Canada) and maintained until 4–6 months of age in the vivarium of the McMaster University Department of

Psychology, Neuroscience & Behaviour. While at McMaster University, the rats participated in a variety of studies of individual or social learning before participating in the present experiment, but none had sexual experience.

We maintained all subjects on ad libitum Teklad Rodent Diet 8640 (Harlan Teklad, Madison, WI, U.S.A.) and water in a room on a partially reversed day/night cycle, illuminated for 12 h/day, with light offset at 1330 hours. During the dark portion of the day/night cycle, three 20-W red incandescent bulbs illuminated the room in which subjects lived and in which we carried out experiments.

Males. To provide all males with sexual experience before the start of the experiment proper, each male resided for 1 week in a cage with two sexually mature females that played no further role in our studies. Four of these sexually experienced adult males served repeatedly as 'indicator males' that we used to determine whether female subjects were in oestrus. Twenty additional males served in 25 randomly composed pairs as 'target males' between which female subjects chose.

Females. Twelve 3–4-month-old virgin females in oestrus and 13 similar females not in oestrus served as subjects. An additional 25 females in oestrus served only as 'stimulus females' that interacted with one member of a pair of target males.

Apparatus

We used two types of apparatus in the experiment. To determine whether a female was in oestrus, we placed her together with an indicator male in a 20-gallon (76-litre) aquarium, measuring 60 × 30 × 40 cm. The floor of each aquarium was covered with wood-chip bedding, and, to prevent escape, the aquarium was closed with a wire-mesh lid.

We measured a female subject's preference between a pair of males in a floor enclosure, measuring, 1 m wide × 2 m long × 0.3 m high, constructed of angle iron and 0.5-inch (1.25-cm) screen, with a galvanized sheet-metal floor covered in wood-chip bedding. Barriers constructed of 0.5-inch (1.25-cm) screen and located 1.4 m apart and 0.3 m from each end of the floor enclosure prevented males from entering the 1.4-m long × 1.0-m wide central compartment in which we placed individual focal females.

Procedure

We initiated experiments immediately after light offset after determining whether female subjects were in oestrus. To determine females' reproductive condition, we placed the indicator males individually in four 20-gallon aquaria, gave the males 5 min to acclimate, and then introduced a female subject into each aquarium. For the next 5 min, we observed the pairs.

We considered a female to be in oestrus if she darted and consistently showed lordosis when mounted by the indicator male throughout the 5-min observation period, and we considered a female to be anoestrous if she refused

to let the indicator male mount her. If, as was usually the case, it proved necessary to examine a second or third group of females to find a sufficient number of females in oestrus for the experiment we had planned, we waited 5 min between removing four females from and introducing four new females into the aquaria containing indicator males.

Once we had determined which females were in oestrus and which were not, we removed the indicator males and females from the aquaria and cleaned two of the aquaria, replacing the bedding and wiping the aquarium walls with a 70% alcohol solution. We then placed one of a pair of randomly selected target males in a cleaned aquarium together with a female in oestrus and the other member of the pair of target males in an empty aquarium.

We waited until the target male placed with the female in oestrus had ejaculated, removed the female from the aquarium and placed the mated male behind the screen barrier at one end of the test enclosure and the unmated male behind the screen barrier at the other end of the test enclosure. Five minutes later, an experimenter unaware of which target male had recently engaged in sexual activity introduced a subject female either in oestrus or not in oestrus at the midpoint of the test enclosure and then videotaped the test enclosure for 10 min. At the end of the 10-min test session, the experimenter, still unaware of the location in which recently mated and unmated males had been placed, determined the percentage of the first 3 min and the full 10 min of testing that the female subject spent in the half of the enclosure where each male had been restrained. Although there is considerable controversy as to the relative merits in mate choice studies of using a 'forced-choice' procedure or a procedure in which 'no choice' is scored while a subject is in some neutral area of the test arena, we prefer the forced-choice procedure because it makes fewer untested assumptions about the distance that individuals maintain when attracted to one another.

Ethical note

The McMaster University Animal Research Board approved the experiments reported here (AUP No. 04-06-28). At the end of the experiment, we euthanized all subjects.

Results and Discussion

A 2 (reproductive state) \times 2 (time) repeated measures ANOVA showed no significant main effects of either duration of testing ($F_{1,23} = 1.11$, $P = 0.30$; Fig. 1) or reproductive state of female subjects ($F_{1,23} = 0.07$, $P = 0.79$) and no significant interaction between main effects ($F_{1,22} = 0.02$, $P = 0.88$).

During the first 3 min of testing, females, whether in oestrus (Student's t test: $t_{11} = 3.07$, $P < 0.02$; Fig. 1) or anoestrous ($t_{12} = 2.21$, $P < 0.05$; Fig. 1) spent more time in the half of the test enclosure closer to the recently mated male.

At the end of the 10-min test, anoestrous females had still spent significantly more than half of the test period on the side of the test enclosure containing a recently

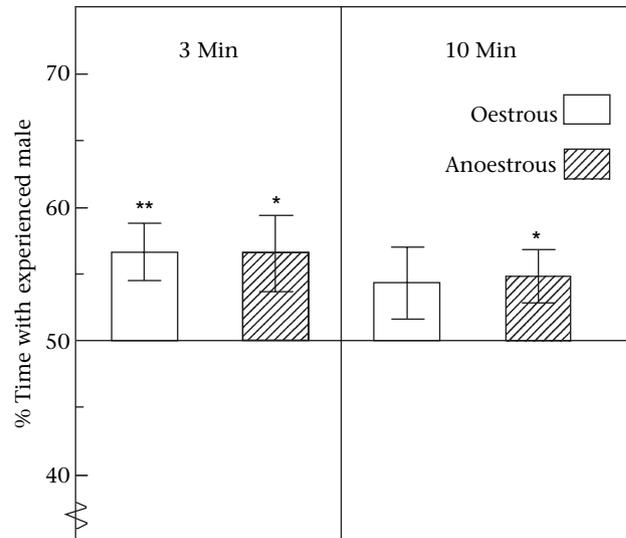


Figure 1. Mean \pm SE percentage of 3-min and 10-min intervals that anoestrous females and oestrous females spent closer to the male that had recently copulated with another female. * $P < 0.05$; ** $P < 0.02$.

mated male ($t_{12} = 2.38$, $P < 0.05$; Fig. 1), whereas oestrous females showed a nonsignificant tendency towards preferring mated males ($t_{11} = 1.59$, $P = 0.14$; Fig. 1). We do not know why the effects of previous mating of males on females' preferences appeared slightly more durable in anoestrous than in oestrous females, but a general decline as testing progressed in the attention that females paid to males that they could not contact was not unexpected.

In summary, although the effect of recent prior sexual experience on female affiliative preference was not large, both oestrous females and anoestrous females preferred to affiliate with males shortly after those males mated with other females.

EXPERIMENT 2

We undertook experiment 2 to determine whether olfactory cues associated with engaging in sexual behaviour mediated the increased attractiveness to females of males that had recently engaged in sexual activity. If so, females that were unable to sense olfactory information from males that had recently engaged in sexual activity should not be more attracted to such males than to unmated males.

Methods

Subjects

Eighteen pairs of males that had histories of acquisition and maintenance identical to those of subjects that participated in experiment 1 participated in experiment 2. Eighteen females whose reproductive state was unknown served as subjects, and 18 females in oestrus served as stimulus animals that interacted with one member of each pair of target males. During testing, female subjects

were either separated from males by Plexiglas barriers ($N = 10$) or rendered anosmic ($N = 8$).

Apparatus

We used the test enclosure that we had used in experiment 1. However, we separated 10 of the 18 female subjects from their target males using transparent Plexiglas partitions rather than screen partitions.

Procedure

We conducted testing in experiment 2 as in experiment 1. However, because we had found in experiment 1 that anoestrous females and oestrous females were equally likely to prefer to affiliate with recently mated males, we did not determine the reproductive state of focal female subjects before testing their preferences between recently mated and unmated males. Consequently, we used indicator males only to identify oestrous females to serve as stimulus females.

We used two methods to examine the role of olfactory cues in mediating females' choices between recently mated and unmated males. First, we examined the behaviour of females ($N = 10$) tested as in experiment 1, but with transparent Plexiglas partitions rather than screen partitions separating subject females from target males. Second, we repeated the procedure of experiment 1 with females ($N = 8$) that we had rendered anosmic 24 h before they chose between males restrained behind screen partitions. We induced anosmia by intranasal infusion of zinc-sulfate solution using the procedures described in Alberts & Galef (1971) with the exception that we anaesthetized subjects with Isoflurane (Baxter Co., Mississauga, ON, Canada), rather than with ether.

Results and Discussion

Unlike female subjects in experiment 1, neither the females that were separated from target males by Plexiglas partitions (3 min: $t_9 = 0.12$, $P = 0.90$; 10 min: $t_9 = 1.72$, $P = 0.12$; Fig. 2) nor the anosmic females (one-sample t tests: 3 min: $t_7 = 0.40$, $P = 0.70$; 10 min: $t_7 = 0.19$, $P = 0.85$; Fig. 2) preferred to affiliate with recently mated males. The results of the present experiment, like those of Kaveliers et al. (2006), implicate olfactory cues in the tendency of female rodents to affiliate with males that have recently mated with another female.

EXPERIMENT 3

We undertook experiment 3 to determine whether females in experiment 1 preferred to affiliate with males that had recently been in the company of a female even if no sexual activity had occurred. Our methods were identical to those of experiment 1, except that we placed one member of each pair of target males with an anoestrous female (rather than with an oestrous female) before we allowed an anoestrous focal female to choose between him and his pair mate.

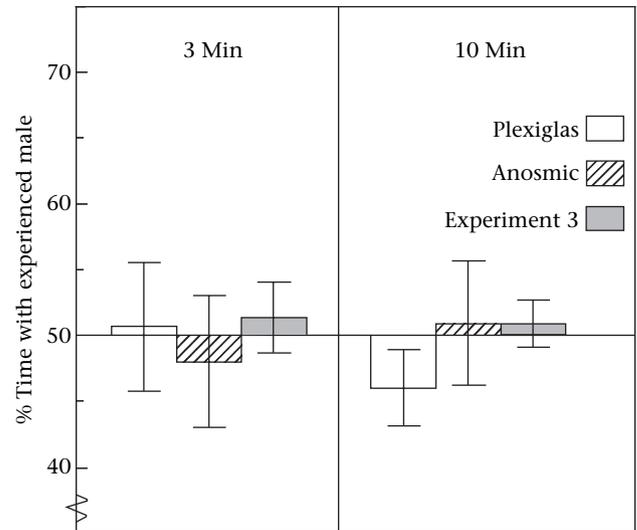


Figure 2. Mean \pm SE percentage of 3-min and 10-min intervals that females in experiments 2 and 3 spent closer to the male that had recently copulated with another female: female subjects were separated from males by Plexiglas partitions or were rendered anosmic and separated from males with screen partitions (experiment 2); one target male had been paired with an anoestrous female rather than with an oestrous female and females and males were separated by screen partitions (experiment 3).

Methods

Subjects

Twenty anoestrous female rats served as subjects, 10 as focal animals and 10 as stimulus animals that we paired with one randomly chosen member of each of 10 pairs of males.

Apparatus and procedure

The apparatus and procedure were identical to those of experiment 1, except that we paired one member of each pair of males with an anoestrous rather than an oestrous female and all females choosing between members of male pairs were anoestrous.

Results and Discussion

Focal female subjects showed no preference for target males that had been paired with an anoestrous female (3 min: $t_9 = 0.48$, $P = 0.64$; 10 min: $t_9 = 0.50$, $P = 0.63$; Fig. 2). Taken together with the results of experiments 1 and 2, the present finding suggests that the preference of focal females in experiment 1 for males that had recently copulated was a response to olfactory cues associated either with oestrous females or with ejaculation, and not a response to olfactory cues associated with females per se.

We have found only a single study comparing the attractiveness to sexually active female rats of the odour of sexually active and inactive conspecific females (Xiao et al. 2004). Subjects in that study were all gonadectomized and then either brought into oestrus by injection

with estradiol and progesterone or left sexually inactive. Such induced, sexually active female rats did not show differential attraction to air streams bearing the odour of sexually active and inactive female conspecifics (Xiao et al. 2004), suggesting that, in experiment 1, olfactory cues associated with male arousal or ejaculation attracted females to males that recently copulated.

EXPERIMENT 4

Although there are exceptions (e.g. White & Galef 1999a; Couldridge & Alexander 2001; Goncalves & Oliveira 2003), for practical reasons, most studies of mate choice copying use the tendency of a female subject to remain in the proximity of a male as a surrogate measure for her preferring him as a sexual partner. A female's tendency to remain near a male is obviously an important determinant of the male's probability of mating with her. However, and equally obviously, there is far more to mate choice and to mate choice copying than increased affiliation. On the hypothesis that female Norway rats prefer as sex partners those males with whom they prefer to affiliate, we predicted that a female Norway rat choosing between two potential sex partners, one a male that had recently copulated with another female and the other an unmated male, would be more likely to engage in sexual activity with the recently mated male.

Methods

Subjects

Fifteen virgin female rats in oestrus and 15 pairs of target males all with histories of acquisition and maintenance identical to those of subjects in previous experiments served as subjects. An additional 15 females in oestrus served as stimulus females with whom we mated one member of each pair of target males before placing the target males in the test enclosure.

Apparatus

We used the same apparatus that we had used in experiments 1, 2 and 3 except that we did not place barriers in the test enclosure. Rather, we used harnesses (Adjustable Harness and Lead Set for Hamsters, Rolf C. Hagen, Inc., Montreal, Quebec, Canada) and 61-cm-long chains to restrain the members of a pair of target males at opposite ends of the 2-m-long enclosure.

Procedure

The procedure was identical to that of experiment 1 except that, during the test phase of the experiment, instead of placing recently mated and unmated target males behind barriers, we secured each male in a harness to which we had habituated them for several hours per day for 3 days before they participated in the experiment.

Once one of a pair of males had mated with a female in oestrus and pair members had been tethered at opposite ends of the test enclosure, we left them undisturbed for 5 min before an experimenter who was unaware of which

of the tethered males had recently mated with a female placed a subject female at the midpoint of the test enclosure. We then videotaped each 10-min test session, and an experimenter, again blind as to which of the two target males had recently had previously mated with a female, subsequently determined which male was first (1) to mount, (2) to intermit and (3) to ejaculate and the number of times that each male (4) mounted, (5) achieved intromission and (6) achieved ejaculation during the 10-min test.

Data analysis

Because we had a directional hypothesis (i.e. that male rats that had copulated recently would be chosen as sexual partners by female rats more frequently than males that had not), we report one-tailed *P* values in Table 1.

Results and Discussion

During the 10-min test, males that had recently ejaculated were more likely than their unmated pair mate to first mount the subject female (binomial test; Table 1) and to first achieve both intromission and ejaculation (neither male in two pairs succeeded in ejaculating; Table 1). Males that had recently copulated also gained a higher percentage of mounts (one-sample *t* test; Table 1), intromissions (Table 1) and perhaps ejaculations (Table 1) than did males that had not had recent sexual experience. The results are consistent with the hypothesis that female rats tend to choose as sexual partners males that have recently had sexual contact with other females, although as discussed further in the General discussion, an alternative interpretation of the data cannot be excluded. Note also that the various dependent variables presented in Table 1 are not independent of one another and cannot, therefore, be treated as providing independent evidence in support of the hypothesis that female rats prefer recently mated males as sex partners.

GENERAL DISCUSSION

The results of experiment 1 indicate that female Norway rats, whether anoestrous or oestrous, preferred to affiliate with a conspecific male that had recently copulated with another female, even when the subject females did not

Table 1. Relative success of recently mated male Long–Evans rats in achieving mounts, intromissions and ejaculations during a 10-min test

	Relative success	<i>P</i> *
First mount†	12/15	0.018
First intromission†	14/15	0.001
First ejaculation†	11/13	0.011
% Mounts	61.3±6.0	0.029
% Intromissions	69.1±8.0	0.021
% Ejaculations	69.6±10.6	0.047

*All *P* values are one tailed.

†Number of recently mated males/total number of males.

directly observe males while they engaged in sexual behaviour. Similar evidence of socially induced enhanced affiliation with a member of the opposite sex has been generally accepted as demonstrating nonindependent mate choice in animals (e.g. Dugatkin 1992; Dugatkin & Godin 1992; Witte & Massmann 2003; Widemo 2006). Whether one wishes to refer to such nonindependent affiliative preference as 'mate choice copying' is a matter of taste. The results of experiment 1 fulfil the conditions of Pruett-Jones's (1992) definition of mate choice copying; they do not fulfil those of Dugatkin (1996).

The results of experiment 2 indicate that the tendency of female rats to affiliate with recently mated males is mediated by olfactory cues, and the results of experiment 3 suggest that those cues are produced either by females in oestrus or by males when they are sexually aroused, or when they copulate or ejaculate. Female Norway rats thus may be similar to female house mice in their attraction to odours associated with sexually stimulated conspecific males (Kaveliers et al. 2006).

The results of experiment 4 are consistent with the hypothesis that the increased attention to recently mated males shown by females in experiment 1 results in mate choice copying (sensu Pruett-Jones 1992). However, the methods of experiment 4 do not allow us to determine whether (1) females preferred recently mated males as sexual partners or (2) the heightened sexual arousal in recently mated males was responsible for the shorter latencies and increased frequencies with which recently mated males mounted, intromitted and, perhaps, ejaculated. If recent sexual experience increases male rats' motivation to pursue and mate with females, then males that have recently copulated might have enhanced mating success, even if females do not prefer them as sex partners.

Controlling for such priming effects on males' sexual prowess is considerably more difficult when nonindependent mate choice is mediated by olfactory rather than by visual cues. When mate choice copying is visually mediated, comparison of the sexual success of males that have mated either in view of or concealed from the view of subject females permits determination of the role, if any, of increased male arousal in males' success in acquiring access to females (e.g. Dugatkin 1992; White & Galef 1999b). However, when females use olfactory cues to detect a male's recent mating history, no noninvasive procedures can determine whether male arousal is important in determining apparent female preference for recently mated males as sex partners.

The biological significance of the results of experiment 4 is also open to question. In species such as Norway rats, where females may be inseminated by several males during a single oestrus (McClintock & Anisko 1982), the functional significance of previously mated males showing shorter latencies to ejaculation or more frequent mounts and intromissions during a relatively brief test period is uncertain. Female Norway rats can mate for hours (Gilbert et al. 1980), and the last male to mate with a female as well as the males that mated with her most frequently have an advantage in fertilizing her eggs (Dewsbury & Hartung 1980). Consequently, first

inseminations or frequent inseminations during a few minutes of a female's oestrus may not be particularly biologically relevant in that such inseminations may not predict a male's relative success in fertilizing a female's eggs. A species in which females' oestrus was relatively brief might provide subjects better suited to laboratory studies of biologically relevant, olfactory-based, nonindependent mate choice.

Despite these difficulties, the present results are useful in suggesting a more definitive experiment. For example, a female Norway rat coming into oestrus that either has been previously rendered anosmic or has an intact olfactory system could be placed throughout her fertile period in an enclosure with both a previously mated and a previously unmated male tethered some metres apart. Molecular techniques could then be used to establish the paternity of each female's offspring. If olfactory cues mediate females' preference for recently mated males as sex partners and as fathers for their young, then recently mated males should father the majority of the young of intact but not of anosmic females. Such an experiment would be demanding but may provide the only way to determine whether olfactorily mediated preferences of female Norway rats to affiliate and initiate mating with recently mated males predicts an increased probability that a recently mated male will father a female's offspring.

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