



Female mating preferences for outbred versus inbred males are conditional upon the female's own inbreeding status



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Inbreeding occurs when relatives mate with each other, and it often has detrimental effects for the fitness of any resulting offspring. It is an important issue in ecology and evolutionary biology with profound implications for genetic variation and the evolution of mating systems and reproductive strategies. For example, inbreeding may shape mate choice through the avoidance of outbred, related individuals to prevent inbreeding, or through the avoidance of inbred, unrelated individuals that have been produced through inbreeding. Although the former has been studied extensively, little is known about mating preferences based on the inbreeding status of potential partners. It is also unclear whether these mating preferences are influenced by the inbreeding status of the choosing sex. Here, we examined female mating preferences for outbred versus inbred males using dichotomous choice tests in the burying beetle *Nicrophorus vespilloides*. We found that these mating preferences were conditional upon the female's own inbreeding status: inbred females preferentially mated with outbred males, whereas outbred females did not show such a preference. Our findings suggest that inbred males suffer reduced mating success only when interacting with inbred females. In species where this is the case, the fitness costs of inbreeding with respect to male mating success will therefore depend on the frequency of inbred females relative to outbred females, which depends on the rate of inbreeding in the population.

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Inbreeding refers to the mating between close relatives and is often associated with a reduction in the fitness of any resulting offspring, known as inbreeding depression (Charlesworth & Charlesworth, 1987). These fitness costs are due to a general loss of heterozygosity, which increases the likelihood that recessive, deleterious alleles are expressed (Charlesworth & Charlesworth, 1987). Given its detrimental effects for the fitness of inbred offspring, inbreeding may influence mate choice, which is the outcome of interactions between males and females, with females usually being the choosing sex and males the competing sex (Andersson, 1994).

Inbreeding can affect mating patterns at two distinct levels. First, the costs of inbreeding may lead to mating preferences for unrelated over related individuals. Active mate choice is a key mechanism for inbreeding avoidance, whereby individuals avoid mating with relatives to reduce the risk of producing inbred

offspring (Frommen & Bakker, 2006; Gerlach & Lysiak, 2006; Hansson et al., 2007). Second, females might avoid mating with inbred, unrelated partners if outbred, unrelated partners are of higher quality (Ilmonen, Stundner, Thoss, & Penn, 2009). Hence, inbreeding may shape mate choice through the avoidance of related individuals to prevent inbreeding and/or through the avoidance of low-quality individuals produced by inbreeding.

Inbreeding avoidance by active mate choice has been studied extensively across a wide range of taxa (Pusey & Wolf, 1996; Szulkin, Stopher, Pemberton, & Reid, 2013; Tregenza & Wedell, 2000). This work has focused on when and why animals may avoid, tolerate or in some cases prefer to mate with their relatives (Kokko & Ots, 2006; Szulkin et al., 2013). Relatively little is known about whether and when inbred individuals might be less preferred as potential mates, although a growing number of empirical studies in mammals, birds, fishes and insects have shown that outbred partners are typically preferred over inbred ones (Ala-Honkola et al., 2015; Bolund, Martin, Kempnaers, & Forstmeier, 2010; Ilmonen et al., 2009; McKee, Newton, & Carter, 2014; Okada, Blount, Sharma, Snook, & Hosken, 2011; Pölkki, Krams, Kangassalo, & Rantala, 2012; Zajitschek & Brooks, 2010; but see also Drayton, Milner, Hunt, & Jennions, 2010; Michalczyk, Martin,

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Millard, Emerson, & Gage, 2010). Theoretical work suggests that these preferences for outbred males are unlikely to be driven by indirect (genetic) benefits, because homozygosity is not heritable (Lehmann, Keller, & Kokko, 2007; Reinhold, 2002; but see Neff & Pitcher, 2008; Nietlisbach, Keller, & Postma, 2016). A more likely explanation is that inbreeding reduces overall male quality and condition such that females gain fewer direct benefits from mating with an inbred male (Fox, Xu, Wallin, & Curtis, 2012). Direct benefits that may be affected by inbreeding include sperm number and quality, nuptial gift size and parental care ability (Fox et al., 2012).

Traditionally, studies on female mate choice have focused only on the inbreeding status of males, giving outbred females a choice between outbred and inbred males. Nevertheless, the females' own inbreeding status might also influence their mating preferences. If low-quality females cannot afford the costs of being choosy (Burley & Foster, 2006; Cotton, Small, & Pomiankowski, 2006; Hunt, Brooks, & Jennions, 2005; Ilmonen et al., 2009; McKee et al., 2014), we might expect a stronger mating bias towards outbred males by outbred (high-quality) females than by inbred (low-quality) females. On the other hand, if the benefits gained from being choosy are inversely related to female quality, inbred females should have a stronger preference for outbred males to compensate for their own shortcomings (Ilmonen et al., 2009). It is important to better understand how inbreeding affects female choosiness since this may have important implications for sexual selection dynamics in inbred populations.

In this study, we used the burying beetle *Nicrophorus vespilloides*, to test whether females preferentially mate with outbred over inbred males and whether female choosiness is influenced by the female's own inbreeding status. Matthey and Smiseth (2015a) found no evidence for inbreeding avoidance in this species despite severe inbreeding depression in the offspring (Matthey, Strutt, & Smiseth, 2013; Pilakouta, Jamieson, Moorad, & Smiseth, 2015; Pilakouta, Sieber, Smiseth, 2016; Pilakouta & Smiseth, 2016) and heavy investment by both sexes in parental care (Pilakouta, Richardson, & Smiseth, 2015; Smiseth, Dawson, Varley, & Moore, 2005; Smiseth & Moore, 2004). Nevertheless, it is possible that females exhibit mating preferences based on the inbreeding status rather than the relatedness of potential partners. To test this, we conducted dichotomous choice tests during which we recorded the copulation rate of an outbred or inbred female presented with two potential mates, one outbred and one inbred. We predicted that females would avoid mating with inbred males, because they are low-quality mates (Matthey et al., 2013). We also expected that outbred and inbred females would differ in their choosiness, but we did not have an a priori prediction about the direction of this effect.

METHODS

Beetle Husbandry

We used virgin beetles from an outbred laboratory population maintained at the University of Edinburgh. The beetles used in this study comprised second- and third-generation beetles from lines originally collected in Edinburgh, U.K. They were housed individually in transparent plastic containers (12 × 8 cm and 2 cm high) filled with moist soil and kept at 22 °C and a 16:8 h light:dark cycle. All nonbreeding adults were fed small pieces of raw organic beef twice a week.

Generating Outbred and Inbred Beetles

In the first part of our experiment, we generated outbred and inbred males and females for use in the mate choice trials. To produce outbred individuals, we paired outbred beetles ($N = 25$)

that had no common ancestors for at least two generations. To produce inbred individuals, we paired outbred beetles ($N = 25$) that were full siblings. Each pair ($N = 50$) was placed in a transparent plastic container (17 × 12 cm and 6 cm high) filled with 1 cm of moist soil. Burying beetles use carcasses of small vertebrates as a breeding resource, so we provided each of these pairs with a freshly thawed mouse carcass (Livefoods Direct Ltd, Sheffield, U.K.). We did not disturb them until the larvae started dispersing from the carcass, which occurs approximately 5 days after hatching. At the dispersal stage, we placed five larvae from each brood into individual containers (12 × 8 cm and 2 cm high) filled with moist soil. The inbred and outbred offspring eclosed as adults about 20 days later, at which point they were sexed based on differences in the terminal segments of the abdomen (Trumbo, 1996). We only used one female and two males from each family. We also recorded the body size of all individuals by measuring their pronotum width using a digital calliper with a precision of 0.01 mm (Bartlett & Ashworth, 1988).

Dichotomous Choice Tests

In this species, adult beetles become sexually mature around 10 days after eclosion. For our mate choice trials, we only used virgin beetles aged between 10 and 20 days after eclosion to minimize variation in male and female age and to prevent variation due to previous mating experience. Each trial consisted of a single outbred or inbred female that was given a choice between an outbred and an inbred male. This design simulates a situation where a female encounters multiple males on a carcass in the wild (i.e. simultaneous mate choice). In half of the trials, we used an outbred female ($N = 15$) and in the other half we used an inbred female ($N = 15$). The two males used in each trial were size-matched based on their pronotum width (difference <0.10 mm) to exclude differences in female mating preferences due to male size. We always used unrelated individuals in each trial.

Mate choice trials took place in a transparent container (17 × 12 cm and 6 cm high) filled with 0.5 cm of moist soil and a freshly thawed mouse carcass (Livefoods Direct Ltd, Sheffield, U.K.) of a standardized size (27–30 g). We first tethered each male by tying one end of a piece of dental floss around the male's pronotum and taping the other end to the side of the box. The two males were tethered to opposite sides of the box to prevent competition, which otherwise would restrict the female's ability to choose between them (Otronen, 1988). We tied the dental floss such that there was about 3 cm of give to ensure that we did not limit the males' ability to mount and mate with the female (Matthey & Smiseth, 2015a). Both males could reach the carcass, which was placed in the middle of the box, but they could not come in direct contact with each other. We alternated between trials whether the outbred or inbred male was tethered on the side close to the front versus the back of the carcass (Matthey & Smiseth, 2015a).

At the start of the trial, we placed the female at the centre of the carcass such that she was equidistant from the two males. We recorded the time when the female first came into contact with the outbred and the inbred male and the number of copulations she had with each male over the next 45 min. Successful copulations occurred when the male inserted his aedeagus (intromittent organ) into the female's vagina (House et al., 2008). Given that each copulation typically lasts about 90 s and females do not have a refractory period (House et al., 2008), it was possible for females to mate repeatedly with the same male or both males. All outbred and inbred females mated at least once over the course of the 45 min mate choice trial. All trials ($N = 30$) were included in the analyses described below.

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