



Multiple paternity does not depend on male genetic diversity



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Polyandry is common in many species and it has been suggested that females engage in multiple mating to increase the genetic diversity of their offspring (genetic diversity hypothesis). Multiple paternity occurs in 30% of litters in wild populations of house mice, *Mus musculus musculus*, and multiple-sired litters are genetically more diverse than single-sired ones. Here, we aimed to test whether female house mice produce multiple-sired litters when they have the opportunity to produce genetically diverse litters. We assessed the rates of multiple paternity when females could choose to mate with two males that were genetically dissimilar to each other (i.e. nonsiblings and MHC dissimilar) compared with when females could choose to mate with two males that were genetically similar to each other (i.e. siblings and shared MHC alleles). Multiple mating may depend upon a female's own condition, and, therefore, we also tested whether inbred (from full-sibling matings) females were more likely to produce multiple-sired progeny than outbred controls. Overall we found that 29% of litters had multiple sires, but we found no evidence that females were more likely to produce multiple-sired litters when they had the opportunity to mate with genetically dissimilar males compared with controls, regardless of whether females were inbred or outbred. Thus, our findings do not support the idea that female mice increase multiple paternity when they have the opportunity to increase the genetic diversity of their offspring, as expected from the genetic diversity hypothesis.

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Polyandry or multiple mating is common in many species and females can increase the number or quality of offspring produced when mating with multiple males (Firman and Simmons, 2008b; Fisher, Double, Blomberg, Jennions, & Cockburn, 2006; García-González & Simmons, 2005; Hoogland, 1998; Madsen, Shine, Loman, & Håkansson, 1992; Tregenza & Wedell, 1998). Many hypotheses have been proposed to explain how females gain benefits from multiple mating, which include both direct and indirect, genetic benefits (Hosken & Stockley, 2003; Jennions & Petrie, 2000; Simmons, 2005). For example, polyandry could provide females with genetic benefits by increasing offspring genetic diversity, as this can have positive effects on offspring performance and survival (Yasui, 1998). Therefore, multiple mating may depend upon the genetic similarity of potential mates and whether polyandry will increase the diversity of their litters. Increasing evidence also indicates that females' mate choice can be dependent on their own quality or condition, but almost nothing is known about whether polyandry is a facultative behaviour that depends on these factors.

Our goals were to investigate these hypotheses in an experiment with wild-derived house mice, *Mus musculus musculus*, in which we allowed females to select their mates and we measured the rates of multiple paternity.

In house mice, *Mus musculus domesticus*, genetic paternity analyses reveal that multiple paternity is common in enclosure populations (Lindholm, Musolf, Weidt, & König, 2013; Montero, Teschke, & Tautz, 2013; Potts, Manning, & Wakeland, 1991; Stockley et al., 2013). In feral populations, the rate of multiple-sired litters is 25% on average but it is unclear why there is so much variation among populations (6–43%, Dean, Ardlie, & Nachman, 2006; Firman and Simmons, 2008a). One study found that the rate of multiple-sired litters increases with population density (Dean et al., 2006; but see Firman and Simmons, 2008a), which suggests that polyandry is a facultative behaviour depending upon the number of available males or the risk of infanticide. Females actively engage in multiple mating (Rolland, MacDonald, de Fraipont, & Berdoy, 2003) and when females can choose to mate with either one or two males, 46% of their litters have multiple sires (Thonhauser, Raveh, Hettyey, Beissmann, & Penn, 2013a). Females are not consistent in producing multiple-sired litters when the same female is tested twice with different males, suggesting that females change their behaviour depending upon

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their own age, condition or perhaps differences in the available mates.

Most studies on multiple mating have focused on the good genes and compatible genes hypotheses, whereas the genetic diversity hypothesis has received relatively little attention (but see [Cohas, Yoccoz, & Allainé, 2007](#); [McLeod & Marshall, 2009](#); [Schmoll, Schurr, Winkel, Epplen, & Lubjuhn, 2007](#)). Increased offspring genetic diversity (among offspring within litters) may increase litter survival if it reduces the risk of infectious diseases spreading between siblings. Studies on other species (social insects and birds) provide observational evidence that females gain fitness benefits by producing genetically diverse litters ([Dunn, Lifjeld, & Whittingham, 2009](#); [Liersch & Schmid-Hempel, 1998](#); [Seeley & Tarpay, 2007](#)). A study in bumblebees, *Bombus terrestris*, for example, showed that high-diversity colonies had fewer parasites and increased reproductive success compared with low-diversity colonies ([Baer & Schmid-Hempel, 1999](#)). In tree swallows, *Tachycineta bicolor*, the immune responses of nestlings from multiple-sired clutches were stronger compared with single-sired clutches ([Dunn et al., 2009](#)). Comparative studies on birds revealed that the degree of extrapair paternity increases with the species' genetic diversity ([Gohli et al., 2013](#); [Petrie, Doums, & Møller, 1998](#)). We recently found higher levels of genetic diversity within multiple- versus single-sired litters in wild house mice, *M. m. musculus* ([Thonhauser, Thoß, Musolf, Klaus, & Penn, 2013](#)); however, to our knowledge, it has never been experimentally tested whether females engage in multiple mating and increase the rate of multiple-sired litters when they have the opportunity to increase the genetic diversity of their offspring. In fact, no study on polyandry to our knowledge has ever manipulated the genetic differences of potential mates.

Similarly, multiple mating has been suggested to function as a mechanism to increase offspring diversity at the genes of the major histocompatibility complex (MHC; [Bollmer, Dunn, Freeman-Gallant, & Whittingham, 2012](#); [Evans, Dionne, Miller, & Bernatchez, 2012](#)). For example, in the Seychelles warbler, *Acrocephalus sechellensis*, females were more likely to seek extrapair copulations when their social mate had low individual MHC diversity ([Richardson, Komdeur, Burke, & von Schantz, 2005](#)). Similarly, a study with house mice suggested that females seek extrapair matings with males that are more disparate at the MHC than their social mate ([Potts et al., 1991](#)). Therefore, we additionally tested whether the frequency of multiple paternity is higher when females have the opportunity to increase the MHC diversity of their offspring. MHC genes are good candidates to assess the genetic benefits of mate choice, as they are highly polymorphic, they control immune resistance to infectious diseases and they influence disassortative mating preferences in mice ([Penn & Potts, 1999](#); [Penn, 2002](#)). As MHC genes control resistance to pathogens and parasites ([Apanius, Penn, Slev, Ruff, & Potts, 1997](#)), increasing offspring MHC diversity is potentially advantageous for the survival of litters, as it might allow a broader range of pathogens to be detected and combated. It has also been suggested that promiscuity drives increased MHC diversity ([MacManes & Lacey, 2012](#)). However, it has never been experimentally tested whether increased MHC diversity of potential mates elevates rates of multiple paternity.

Multiple mating may also depend upon the females' own condition, such as their age, body mass or genetic quality (e.g. inbreeding status). Increasing evidence indicates that female mate sampling and mate preferences are dependent on the females' condition ([Burley & Foster, 2006](#); [Cotton, Small, & Pomiankowski, 2006](#); [Hunt, Brooks, & Jennions, 2005](#)), including their infection ([Buchholz, 2004](#)) and inbreeding status ([Mazzi, Künzler, Largiadèr, & Bakker, 2004](#); [Michalczyk et al., 2011](#)). For example, house mice females prefer the odour of outbred versus inbred males and this

preference is more pronounced in inbred versus outbred females ([Ilmonen, Stundner, Thoß, & Penn, 2009](#)). Moreover, a study in the red flour beetle, *Tribolium castaneum*, showed that females with an inbreeding history had higher rates of polyandry than outbred controls and that polyandry effectively doubled previously inbred females' reproductive success ([Michalczyk et al., 2011](#)). Therefore, our goal was to test whether females' inbreeding status affects the rate of multiple paternity, as this hypothesis has never been tested in a vertebrate species to our knowledge.

We conducted an experiment with wild-derived house mice (F2 from wild-caught *M. m. musculus*), in which we allowed females to choose to mate between two males. All males were unrelated to the females, but the males were experimentally selected to be either genetically similar (brothers with identical MHC haplotype) or dissimilar (unrelated with different MHC haplotype) to each other. We chose to manipulate MHC sharing as MHC is the only locus to our knowledge that is highly polymorphic, influences individual odour and mate choice and simultaneously can confer potential fitness benefits to offspring (i.e. MHC controls immune resistance to pathogens and parasites). We expected that the rate of multiple paternity (using genetic paternity analyses) would be higher when potential mates are genetically dissimilar as females would have the opportunity to increase the genetic diversity among offspring as expected from the genetic diversity hypothesis. To test whether female inbreeding status affects the likelihood of producing multiple-sired litters, the females were experimentally inbred (parents were full siblings) or outbred (parents from different families). We had no prediction for how inbreeding might affect multiple paternity because poor condition may increase ([Michalczyk et al., 2011](#)) or decrease ([Huchard et al., 2012](#)) multiple mating.

METHODS

Experimental Animals

All experimental animals were second-generation descendants of wild-trapped house mice, *M. m. musculus*, in Vienna (48°12'38"N; 16°16'54"E). Progenitor mice were trapped at 14 different locations within a 500 m radius and crossed between trapping sites. Before we assigned the breeding pairs, we genotyped mice to exclude individuals carrying *t* alleles, since these alleles cause meiotic drive and may influence females' mating preferences ([Lenington, 1991](#)). F1 mice were arranged in two breeding lines to generate both inbred and outbred mice. Inbred mice resulted from one generation of brother–sister matings and outbred mice resulted from matings of nonsiblings. One generation of full-sib mating has been shown to cause significant inbreeding depression ([Meagher, Penn, & Potts, 2000](#)) and it also influences female odour preferences for males ([Ilmonen et al., 2009](#)). Experimental mice were weaned at the age of 21 ± 1 days and then housed individually in standard mouse cages (type II cages, 26.5 × 20.5 cm and 14 cm high) containing woodchip bedding (ABEDD), wood shavings and a nestbox. Food (Altromin rodent diet 1324) and water were provided ad libitum. At weaning all animals received an ear punch which was necessary for individual identification and tissues were stored at -20°C for genetic analyses. A standard 12:12 h light cycle was maintained and the temperature was $22 \pm 2^\circ\text{C}$. All animals were sexually naïve and between 10 and 22 weeks of age when the experiment started.

Mate Choice Assay

Each female could choose to mate with one or two males and these males were either siblings (genetically similar) or unrelated (genetically dissimilar) to each other. Males were located in two

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