

LETTER

Male house mice evolving with post-copulatory sexual selection sire embryos with increased viability

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Abstract

Although mating is costly, multiple mating by females is a taxonomically widespread phenomenon. Theory has suggested that polyandry may allow females to gain genetic benefits for their offspring, and thus offset the costs associated with this mating strategy. For example, the good sperm hypothesis posits that females benefit from mating multiply when genetically superior males have increased success in sperm competition and produce high quality offspring. We applied the powerful approach of experimental evolution to explore the potential for polyandry to drive evolutionary increases in female fitness in house mice, *Mus domesticus*. We maintained polygamously mated and monogamously mated selection lines of house mice for 14 generations, before determining whether selection history could account for divergence in embryo viability. We found that males from lineages evolving with post-copulatory sexual selection sire offspring with increased viability, suggesting that polyandry results in the production of higher quality offspring and thus provides long-term fitness benefits to females.

Keywords

Genetic benefits, good sperm hypothesis, mammals, offspring fitness, polyandry.

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INTRODUCTION

Reproduction is costly. Copulation alone requires a large amount of energy and can lead to an increased risk of predation or disease (Daly 1978). Despite these costs, males and females of many species mate multiply (Birkhead & Møller 1998; Simmons 2001a). However, the reproductive interests of males and females do not always coincide. For example, under polygamous regimes the optimum mating frequency is usually higher for males than it is for females (Bateman 1948). Male fitness is maximised when paternity success exceeds the cost associated with soliciting multiple mates. Conversely, female fitness is typically constrained either by ova production, and/or by the number of offspring that can be nurtured. Traditionally, a single fertile mating was thought to be sufficient to maximise female fitness, so that accounting for the evolution of polyandry has been a complex problem in evolutionary biology.

Polyandry generates positive associations between mating frequency and female reproductive success when females gain material benefits prior to, during or following copulation (Arnqvist & Nilsson 2000). However, polyandry has also been shown to increase female fitness in the absence of material benefits (Jennions & Petrie 2000; Tregenza & Wedell 2000; Simmons 2005). Consequently, genetic benefit hypotheses have been developed to account for the origin of this behaviour (Keller & Reeve 1995; Yasui 1997; Zeh & Zeh 1997). The good sperm hypothesis predicts that females mate multiply to incite sperm competition, allowing males of high genetic quality with increased competitive fertilisation success to sire the offspring (Yasui 1997). Among mammals, polyandrous species have increased rates of embryo viability compared with monogamous species, offering correlative support for the notion that post-copulatory sexual selection can promote female fitness (Stockley 2003). Surprisingly, empirical evidence linking sperm competitiveness to offspring viability is limited (Hosken *et al.* 2003; Fisher *et al.* 2006; García-González & Simmons 2007), and only a single study has shown that male success

in sperm competition was not related to offspring viability or performance (Simmons 2001b).

We used the powerful approach of laboratory evolution to explore the potential for polyandry to drive evolutionary increases in female fitness. We generated selection lines of house mice evolving with (polygamous) and without (monogamous) post-copulatory sexual selection. In accordance with sperm competition theory (Parker 1990) males evolving under polygamy increased their sperm production, and produced ejaculates of higher quality, with greater proportions of motile sperm and faster swimming sperm, compared to males from the monogamous lines (Firman & Simmons 2010; Firman *et al.* 2011). Competitive matings revealed that males from the polygamous lines had greater fertilisation success when competing against males from the monogamous lines, and that increased ejaculate quality translated to improved sperm competitiveness in house mice (Firman & Simmons 2011). Here, after 14 generations of selection, we used our evolving mouse lineages to test the good sperm hypothesis for the evolution of polyandry. In doing so, we provide the first trans-generational, empirical demonstration that post-copulatory sexual selection drives increased embryo viability in a vertebrate.

MATERIALS AND METHODS

Experimental evolution and reciprocal crosses

Wild-derived house mice were sourced from the Animal Resources Centre (Murdoch, WA, Australia), and used to establish monogamous (4) and polygamous (4) selection lines (Firman & Simmons 2010). Detailed information on the selective mating regime is provided elsewhere (Firman & Simmons 2010). Briefly, males and females in the monogamous lines were mated with a single partner, whilst animals in the polygamous lines were mated with three partners in quick succession. In the monogamous lines, 18 females and 18 males contributed to each generation. In the polygamous lines, the same

three males mated with the same three females, so that 18 females but potentially < 18 males contributed to each generation. Males were selected at random so that there was no pre-copulatory sexual selection. This mating design ensured that the effective population sizes of the monogamous lines were potentially greater than the polygamous lines at each generation. Thus, the monogamous lines would be expected to have lower inbreeding coefficients than the polygamous lines (Wigby & Chapman 2004), and any observed fitness benefits associated with post-copulatory sexual selection would be conservative. Although these evolving mouse populations may be considered to be small relative to natural populations, molecular based estimators have shown neither effective population size nor genetic diversity differs between treatments experiencing different sexual selection intensities in studies of experimental evolution (Snook *et al.* 2009). Following 15 generations of selection, litter sizes were recorded and analysed from the four replicate monogamous lines and four replicate polygamous lines.

To assess whether male and/or female selection history influenced embryo viability, we used animals from generation 14 and conducted reciprocal crosses between the replicate selection lines. Male–female pair combinations were generated via a full-factorial design (4 monogamous line males \times 4 polygamous line females, 4 monogamous line females \times 4 polygamous line males, 4 monogamous line males \times 4 monogamous line females, 4 polygamous line males \times 4 polygamous line females), to produce embryos that had (1) a polygamous mother and a monogamous sire, (2) a monogamous mother and a polygamous sire, (3) pure polygamous parentage and (4) pure monogamous parentage. The full-factorial design allowed us to examine the main effects of male and female selection history, and their interaction. Sixteen females were used from each of the eight selection lines, so that embryo viability was scored for a total of 128 females.

Experimental matings

Matings were conducted under red lighting during the dark phase of a 14 : 10 dark : light cycle. Males and females (10 weeks old) were paired at the onset of a dark phase, and checked every 2 h for the presence of a mating plug. Once a plug was observed the female was separated from the male, and given nesting paper. Of the 128 females, 15 were not pregnant at 14 days gestation (monogamous male \times polygamous female = 4; polygamous male \times monogamous female = 5; monogamous \times monogamous = 3; polygamous \times polygamous = 3). These crosses were repeated with different animals.

Embryo viability

At 14 days gestation, the females were sacrificed via lethal injection and dissected. Total embryo number was recorded, and each embryo was scored as appearing either normal in size and shape (viable) or as a large haematoma that was discernable in shape and being resorbed (non-viable).

RESULTS

Previously, we reported a significant divergence in average litter size, whereby litter size increased steadily in the polygamous lines but remained constant in the monogamous lines across the first 10

generations of selection (Firman & Simmons 2010). Here, we performed a nested ANOVA to test whether this divergence was still evident at generation 15. Indeed, the analysis revealed that the average size of litters within the polygamous lines (6.65 ± 0.24) was larger than the average size of litters within the monogamous lines (4.94 ± 0.27) (Table 1). Consequently, we were interested in assessing whether male and/or female selection history influenced the total number of implanted embryos (i.e. both viable and non-viable embryos combined). A nested ANOVA showed that there was no effect of male or female selection history on the total number of implanted embryos (Table 2). We calculated partial effect size estimations (Pearson's r) and their 95% confidence intervals (CIs) to gauge the magnitude of the observed effect of male selection history [$r = 0.695$ ($-0.121, 0.950$)] and female selection history [$r = 0.032$ ($-0.739, 0.766$)] on the total number of implanted embryos (Nakagawa & Cuthill 2007). The 95% CIs suggest caution in rejecting the hypothesis that male selection history had no effect on the total number of implanted embryos (Fig. 1).

We assessed whether female and/or male selection history influenced embryo viability among the selection lines. Generalised linear mixed models (GLMMs) combine the properties of two statistical frameworks, linear mixed models (which incorporate random effects) and generalised linear models [which handle nonnormal data by using link functions and exponential family (e.g. binomial) distributions] (Bolker *et al.* 2008). Therefore, offspring viability was modelled with a GLMM fit by the Laplace approximation using the 'lme4' library from the R-statistical analysis package (Pinheiro & Bates 2000; R Development Core Team 2011). Fixed effects in the GLMM were male selection history, female selection

Table 1 Analysis of litter sizes following 15 generations of selection

	SS	d.f.	MS	<i>F</i>	<i>P</i>
Selection history	86.89	1	86.89	6.70	0.041
Line[selection history]	77.86	6	12.98	3.23	0.005
Female weight	32.89	1	32.89	8.18	0.005
Error	542.61	135			

ANOVA of average litter sizes within selection lines of house mice maintained with (polygamous) and without (monogamous) post-copulatory sexual selection. To account for non-independence of data within replicate selection lines, replicate line was nested within selection history and treated as a random factor. SS, sums of squares; MS, mean squares.

Table 2 Analysis of the total number of implanted embryos

	SS	d.f.	MS	<i>F</i>	<i>P</i>
Female selection history	5.09	1	5.09	1.47	0.270
Female line[selection history]	20.74	6	3.46	1.45	0.202
Male selection history	14.28	1	14.28	5.61	0.056
Male line[selection history]	15.28	6	2.55	1.07	0.385
Female weight	37.15	1	37.15	15.60	< 0.001
Error	266.74	112			

ANOVA of the total number of embryos produced from reciprocal crosses between selection lines of house mice evolving with (polygamous) and without (monogamous) post-copulatory sexual selection. To account for non-independence of data within replicate selection lines, replicate line was nested within selection history and treated as a random factor.

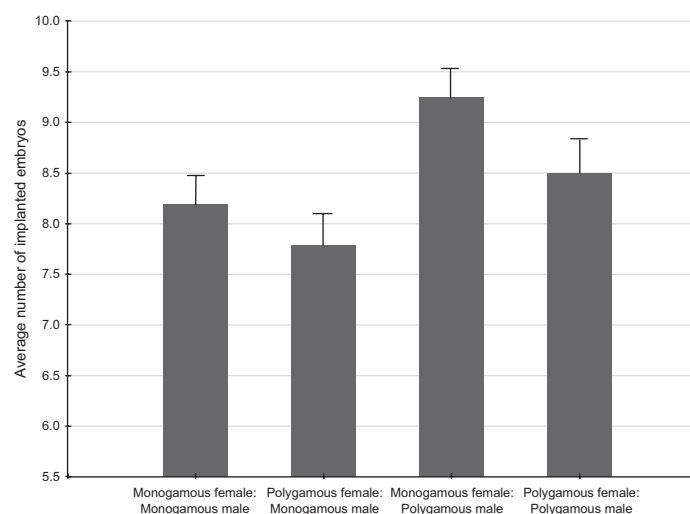


Figure 1 The average (+ SE) number of implanted embryos produced from crosses between females and males with either a monogamous or polygamous selection history.

Table 3 Analysis of offspring viability

Random effects	Variance	SD		
Male line	0.002	0.015		
Female line	< 0.001	< 0.001		
Female ID	2.353	1.534		
Fixed effects	Estimate	SE	t_5	P
(Intercept)	1.588	0.295	5.383	0.003
Male selection history	1.129	0.364	3.106	0.027
Female selection history	0.002	0.347	0.006	0.995

A GLMM fit by the Laplace approximation using 'lme4' library from the *R*-statistical analysis package testing the viability of embryos produced from reciprocal crosses between selection lines of house mice evolving with (polygamous) and without (monogamous) post-copulatory sexual selection.

history and their interaction, whilst female identity, male replicate selection line and female replicate selection line were modelled as random effects (Table 3). The interaction effect was nonsignificant, and thus removed from the model [estimate = -0.852 , SE = 0.698 , $t_4 = -1.220$, $P = 0.222$]. There was a significant effect of male selection history on the viability of embryos, but the effect of female selection history was not significant (Table 1, Fig. 2).

DISCUSSION

Evolutionary theory proposes that females must benefit from polyandry to offset the costs associated with soliciting multiple partners (Jennions & Petrie 2000; Tregenza & Wedell 2000; Simmons 2005). Following 15 generations of selection, we found that female house mice evolving under polyandry produced larger litters compared with females evolving under monogamy. A comparative analysis across mammals revealed that species in which females mate multiply experience lower rates of reproductive failure (i.e. greater proportions of ova are fertilised and develop into embryos) compared with species in which females mate monogamously (Stockley 2003). We performed

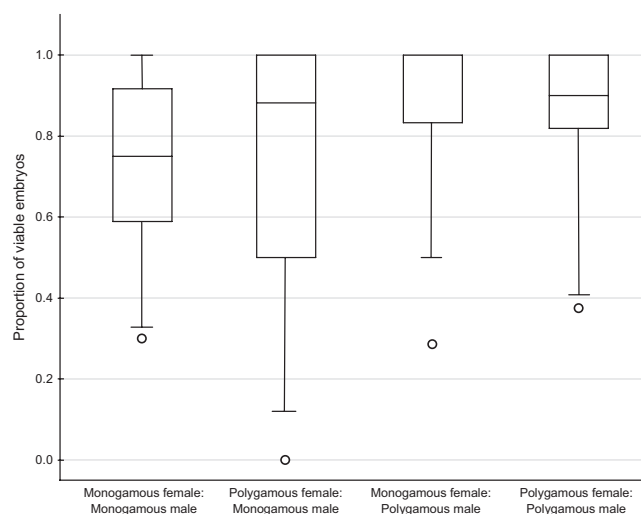


Figure 2 The proportion of viable embryos produced from crosses between females and males with either a monogamous or polygamous selection history. The center line of each box represents the median value. Where there is no center line, the median value equals 1. The box (90%) and whiskers (95%) describe the variation. Outliers are represented by circles.

reciprocal crosses between our monogamous and polygamous mouse lineages to test the hypothesis that polyandry can reduce variation in embryonic mortality, and assess whether differences in embryo survival accounted for the observed phenotypic divergence in litter size among our selection lines. Our analysis revealed that female selection history did not explain variation in embryo viability. However, males from the polygamous lines sired embryos of greater viability compared with males from the monogamous lines. Consequently, we can conclude that increased embryo survival was an indirect effect of post-copulatory sexual selection on males in the polygamous lines, which has resulted in a greater number of live young at birth, and thus generated divergence in litter size between the evolving mouse lineages. We have provided one of the first empirical demonstrations in a mammal that polyandry can generate evolutionary increases in female fitness across successive generations.

It has been theorised that females may acquire good genes for their offspring by mating multiply and enabling genetically superior males that have increased sperm competitiveness to fertilise their ova (Yasui 1997). Studies of two insect species have shown that males that are successful in sperm competition also produce high quality offspring (Hosken *et al.* 2003; Simmons & García-González 2008; Simmons 2011; Simmons & Holley 2011). However, to date the most convincing evidence in support of the good sperm hypothesis comes from an empirical investigation on the Australian marsupial, *Antechinus stuartii*, which reported a direct correlation between male sperm competitiveness and offspring survival (Fisher *et al.* 2006). Our previous experiments have shown males from the polygamous selection lines have both greater sperm quality (Firman & Simmons 2010; Firman *et al.* 2011) and sperm competitive ability (Firman & Simmons 2011) compared with males from the monogamous selection lines, and our reciprocal line cross experiment revealed that males from the polygamous lines produced offspring of greater viability compared with males from the monogamous lines. Consequently, we have provided conclusive experimental evidence in support of the good sperm hypothesis for the evolution of polyandry.

We have shown previously that the number of ova released in a single oestrous cycle does not differ between females from the polygamous and monogamous selection lines (Firman & Simmons 2010). Here, after controlling for female size, we found that female selection history did not account for variation in the number of implanted embryos. However, there was a trend of polygamous line males generating more implanted embryos than monogamous line males. We know that males from the polygamous lines produce increased numbers of better quality sperm compared with males from the monogamous lines (Firman & Simmons 2010; Firman *et al.* 2011). Consequently, increased male fertility in the polygamous lines may have resulted in an increase in the number of fertilised ova, and thus an increase in the number of implanted zygotes. Alternatively or additionally, polygamous line males may possess an intrinsic trait that influences zygote quality and/or the rate of successful zygote implantation. Unfortunately, due to the methodological limitations of working with an internally fertilising species, we were unable to score zygote viability. Regardless, the embryo viability data generated from our reciprocal line cross experiment have revealed that selection for good genes via post-copulatory sexual selection in the polygamous lines has resulted in improved embryo quality.

In the current study, we are unable to establish the genetic mechanism responsible for polygamous line males inducing increased implantation rates and increased embryo viability. However, a large number of studies on assisted reproduction in humans and domestic animals have shown that sperm DNA integrity is a significant predictor of embryo quality. Among these studies DNA damage in the male germ line has been shown to be associated with poor ejaculate quality (e.g. Tomlinson *et al.* 2001; Saleh *et al.* 2003), impaired pre-implantation development (e.g. Tesarik *et al.* 2004; Fatehi *et al.* 2006), increased abortion rates (e.g. Ahmadi & Ng 1999; Carrell *et al.* 2003) and decreased offspring quality (e.g. Aitken *et al.* 2003; Ruiz-López *et al.* 2010). Furthermore, male accessory sex gland secretions have been shown to be the major source of antioxidant enzymes in the ejaculate, and preserve the DNA integrity of sperm from oxidative stress experienced in the female reproductive tract (O *et al.* 2006). Removal of the male accessory sex glands in the golden hamster was shown to result in a greater degree of sperm DNA damage, which did not influence fertilisation rates but did influence embryonic cleavage and implantation rates (O *et al.* 1988, 2006). Consequently, because we have observed increased sperm quality and performance within the polygamous lines (Firman & Simmons 2010; Firman *et al.* 2011), we suggest that post-copulatory sexual selection may have also contributed to increased sperm DNA integrity, possibly through the upregulation of accessory sex gland secretions, which in turn has resulted in the production of more viable offspring. Decreased sperm DNA fragmentation in the polygamous lines would also explain a significant effect of male selection history, but not female selection history, on embryo viability. Further experimentation is required to assess whether there are differences in the levels of sperm DNA fragmentation among the selection lines.

It is difficult to conclude that the evolutionary effects on litter size that we have observed in our study of experimental evolution would be beneficial to females in natural populations. Among mammals theory predicts a negative correlation between the number and quality of offspring (Roff 1992). Small litters with large neonates and weanlings should increase the quality of offspring through faster growth and maturation, and/or better survival rates (Smith & Fretwell

1974). In our selection lines of house mice, despite a significant increase in litter size in the polygamous lines, we found little evidence of reduced weight of weanlings (Firman & Simmons 2010). Thus, at this stage in their evolution we suggest that females from our polygamous lines accrue benefits from multiple mating. However, further increases in litter size may prove detrimental to the lifetime fitness of polyandrous females; so that litter size might eventually reach some stable optima whereby potential costs associated with this mating strategy are balanced against the fitness benefits of larger litters.

In conclusion, a reciprocal line cross experiment utilising monogamous and polygamous lineages of house mice revealed that female selection history did not account for variation in embryo viability. However, males evolving with post-copulatory sexual selection were shown to sire offspring with greater viability compared with males evolving under monogamy. We provide unequivocal evidence that superior sperm competitors sire high quality offspring, and thus provide support for the good sperm hypothesis for the evolution of polyandry. Importantly, we show that an evolutionary history of polygamy leads to increased embryo viability, and thus demonstrate the long-term fitness benefits of multiple mating in mice.

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AUTHORSHIP

RCF reared the selection lines and performed the experimental procedures. Both authors developed the concept of the experiment, assisted in analysing the data and writing the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Embryo viability and mean embryo number (\pm SE) for each replicate selection line.

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