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Experimental evidence for the genetic benefits of female mate choice in the monandrous wolf spider *Pardosa astrigera*

Qijia Wu [a], Lelei Wen [a], Jian Chen [a], Daiqin Li [b], Xiaoguo Jiao [a], *

[a] *Centre for Behavioral Ecology & Evolution, Hubei Collaborative Innovation Center for Green Transformation of Bio-Resources, School of Life Sciences, Hubei University, Wuhan, China*
[b] *Department of Biological Sciences, National University of Singapore, Singapore*

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Material and/or genetic benefits are hypothesized to be the main drivers of female mate choice. Research on female mate choice has mainly focused on polyandrous species and has seldom considered monandrous species. Given the absence of postcopulatory mate choice in monandrous females, we predicted that precopulatory mate choice is important for monandrous species. Using the wolf spider *Pardosa astrigera* as a model monandrous species, we compared mating, reproductive output and offspring fitness between females with preferred mates (mates that were accepted on the first exposure) and females with nonpreferred mates (mates that were rejected on the first exposure but were induced to mate on the second exposure). Our results showed that the mating duration, latency to egg laying and to egg hatching, fecundity and egg hatching rate did not differ significantly between females with preferred versus nonpreferred mates. In contrast, female and male development time was significantly shorter and female carapace width was significantly greater for offspring of females with preferred versus nonpreferred mates. In addition, survival from egg hatching to maturity was twice as high for offspring of females with preferred mates. These results indicate that female mate choice by the monandrous *P. astrigera* provides genetic rather than material benefits.

Explanations for the development of mate choice concentrate on the benefits accrued by females or males that discriminate between potential reproductive partners. Mate choice can provide direct (material) benefits, indirect (genetic) benefits and inclusive fitness benefits (Puurtinen, Ketola, & Kotiaho, 2009). Direct benefits to females may result from male-donated nutrients (Fedorka & Mousseau, 2002; Gillot, 2002, 2003; Parker, Ball, Stockley, & Gage, 1997; South & Lewis, 2011), sufficient viable sperm (Gromko, Newport, & Kortier, 1984; Ridley, 1988), semen defensive compounds (González, Rossini, Eisner, & Eisner, 1999) and nests (in birds; Ruxton & Humphries, 2001). For example, the secretions released from the accessory reproductive glands of some male insects can stimulate mated females to lay eggs and may even accelerate the growth of eggs (Gillott, 2002, 2003) to improve fecundity. Genetic benefits, that is, heritable differences in fitness (‘good’ genes) or in genetic compatibility between mates (compatible genes; Tregenza & Wede, 2000; Puurtinen et al., 2009) could significantly improve offspring performance, such as hatching success, offspring survival and offspring size (Ivy & Sakaluk, 2005; Jennions & Petrie, 2000; Jennions, Drayton, Brooks, & Hunt, 2007). Inclusive fitness benefits of mate choice refer to the increased genetic representation that can be gained by increasing the reproductive success of relatives via mate choice (Puurtinen et al., 2009; Thünken, Bakker, Baldauf, & Kullmann, 2007). Although some meta-analyses have found that the direct benefits of mate choice are larger than the indirect benefits (Jennions, Møller, & Petrie, 2001; Møller & Alatalo, 1999; Møller & Jennions, 2001), females may still gain indirect (genetic) benefits through mate choice (Andersson, 1994; Jennions & Petrie, 2000).

In the animal kingdom, monandrous species are rarer than polyandrous species. Research on the mechanisms explaining female monandry (in which the female has only one mate) is far behind research on the mechanisms explaining female polyandry (in which the female has multiple mates; Arnqvist & Andrés, 2006; Hosken, Stockley, Tregenza, & Wedell, 2009; Jiao, Guo et al., 2011; King & Bressac, 2010). Most recent research on female mate choice has focused on polyandrous females, and little is known about monandrous females (Muller, Arenas, Thiéry, & Moreau, 2016; Verspoor, Cuss, & Price, 2015). In polyandrous species,

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* Correspondence: X. Jiao, School of Life Sciences, Hubei University, Youyi Street 368, Wuchang, Wuhan 430062, Hubei, China.
E-mail address: jiaoxg@hubu.edu.cn (X. Jiao).

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females may show weak mate preference and may depend more on postcopulatory mate discrimination (Verspoor et al., 2015). In some cases, the high-quality males among rivals may rely on sperm competition to fertilize the eggs of polyandrous females (Fisher, Double, Blomberg et al., 2006). Alternatively, polyandrous females may rely on female cryptic choice to bias fertilization towards the competitive sperm from the high-quality males (Eberhard, 1996; Fedina & Lewis, 2007; Rosengrave, Montgomerie, & Gemmell, 2016). Even though a polyandrous female may first mate with an inferior male, she could rely on postcopulatory mate choice to improve fitness. For example, the sperm from the first male could be displaced by subsequent mating, and, in some cases, females can choose the preferred father of their offspring regardless of mating order (Fedina & Lewis, 2007).

In monandrous species, however, the female may be unwilling to mate with any but the highest quality male (Kvarnemo & Simmons, 2013; Muller et al., 2016; Verspoor et al., 2015). Monandrous females may exhibit strong precopulatory mate choice due to the absence of postcopulatory mate choice or sperm competition (Hosken et al., 2009; Kvarnemo & Simmons, 2013; Verspoor et al., 2015). Some research indicates that mate choice of monandrous females does provide direct benefits. In the monandrous fruit fly *Drosophila subobscura*, for example, females prefer older males to increase offspring production (Verspoor et al., 2015). In the European grapevine moth, *Lobesia botrana*, the monandrous females discriminate against males with mating experience and prefer virgin males to maximize their direct benefits (Muller et al., 2016). However, there are no reports of indirect (genetic) benefits of female mate choice in monandrous arthropods.

The wolf spider *Pardosa astrigera* is widely distributed in East Asia (World Spider Catalog 2017). In the *P. astrigera* mating system, females are monandrous and males are polygynous throughout their lives (Jiao, Chen et al., 2011). We previously reported that female monandry is female rather than male driven, and that the direct benefits to females were not substantially affected when females were induced to mate multiple times with the same male or with different males (Jiao, Guo et al., 2011). In nature, males are protandrous. The male:female sex ratio of *P. astrigera* ranges from 1.0:1.0 to 1.0:1.5 (Jiao, Chen et al., 2011). In addition, our previous results indicated that half of the males studied were able to copulate successively with five virgin females in a 24 h period (Jiao, Chen et al., 2011). It seems likely that the early maturing and more competitive males may copulate with many more females than late maturing, less competitive males. Jiao, Chen et al. (2011) suspected that female mate choice and strong male–male competition occur in this species. In monandrous species, strong competition between males may incur fitness costs. In the monandrous *D. subobscura*, for example, males housed with rivals had a significantly reduced ability to obtain a mate and a significantly reduced longevity (Lizé, Price, Heys, Lewis, & Hurst, 2014).

In the present study, we used *P. astrigera* as a model to compare the differences in mating, reproductive output and offspring fitness between females with preferred and nonpreferred mates. To compare these two groups of females, we used an experimental design in which each female was exposed to only one male at a time. As there is no postcopulatory mate choice in monandrous species, it seems likely that precopulatory mate choice is more important for them than for polyandrous species (Verspoor et al., 2015). We therefore predicted that precopulatory mate choice may increase the fitness of *P. astrigera* females, that is, we predicted that the fitness (reproductive output, offspring development, survival and body size) of *P. astrigera* females with preferred mates would be greater than that of females with nonpreferred mates.

METHODS

Spider Collecting and Rearing

In March 2012, we collected subadult *P. astrigera* from Ma'anshan Forest Park, Wuhan (30°52′N, 114°31′E), Hubei Province, PR China. Spiders were kept individually in cylindrical glass tubes (2 cm in diameter, 10 cm high) with a layer of sponge (1.5 cm thick) moistened with water on the bottom. The tubes were plugged with cotton. We kept the spiders in a chamber at 25 °C and with 70–90% relative humidity and a 14:10 h light: dark cycle. Spiders were supplied with water ad libitum and were fed every 3 days with a mixed diet of *Drosophila melanogaster* and mosquitoes (Chironomidae). Individuals were monitored daily, and moulting of subadults was recorded and used to indicate the exact date on which an individual reached adulthood. We randomly selected mature males aged 5–10 days postmaturation and arbitrarily assigned each to pair with one female aged 3 days postmaturation (Xiao et al., 2015). All tested spiders were virgin and were used only once.

Experimental Methods

Mating trials were carried out in an arena consisting of a glass petri dish and a cylindrical glass container that was open at both ends (10.5 cm in diameter, 12.0 cm high). Before each trial, a female was placed in the petri dish (12 cm in diameter) with a piece of filter paper (Double ring brand, Hangzhou, Zhejiang, China, 12 cm in diameter) covering the bottom and with a lid on the top. The female was allowed to move freely on the filter paper surface for 12 h, which enabled her to deposit pheromone-associated silk on it. We then removed the petri dish lid and set the cylindrical glass container on the silk-covered filter paper. A male was randomly selected and gently introduced into the arena; male courtship behaviours were videotaped (HDRCX580E Sony video camera) for 5 min after his introduction. Videos were analysed later using The Observer (version 4.1, Noldus Information Technology, Wageningen, The Netherlands), a software package for the detailed analysis of behavioural data. Male courtship intensity was defined as the bouts (number) of male body shakes/min (Xiao et al., 2015).

Prior to mating, females are static while males display foreleg raising and body shaking, which are typical male courtship behaviours. If the females are not ready to mate, they are aggressive towards the males (Wu, Jiao, Chen, Peng, & Liu, 2008). If the pair mated within 5 min, the female was considered to have selected a preferred mate. If the pair did not mate within 5 min, the female was gently removed and returned to her original glass tube. After 6 h, the female was anaesthetized with CO_2 for 1.5 min and immediately introduced into the arena and paired with the previous male again (Jiao, Guo et al., 2011). If the male successfully mated with the anaesthetized female within 5 min, the female was considered to have selected a nonpreferred mate. If the female did not mate with the male during the second exposure, no data were recorded, and the pair was returned to their natural habitat. To ensure that the anaesthesia did not bias the results, we also anaesthetized the females that had selected preferred mates; as before, the females were treated with CO_2 for 1.5 min 6 h after they mated. We recorded the mating duration of females mated with the preferred or nonpreferred mates. After each mating, the petri dish was swabbed with alcohol and allowed to dry, and the filter paper was replaced.

After mating trials, the mated males were anaesthetized with CO_2, and their carapace width was measured to the nearest 0.01 mm with the aid of a binocular microscope. There were no significant differences in male size (male carapace width) between the preferred and the nonpreferred males ($t_{38} = -1.443, P = 0.157$).