



Research

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Animal behaviour

Benefits of size dimorphism and copulatory silk wrapping in the sexually cannibalistic nursery web spider, *Pisaurina mira*

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In sexually cannibalistic animals, male fitness is influenced not only by successful mate acquisition and egg fertilization, but also by avoiding being eaten. In the cannibalistic nursery web spider, *Pisaurina mira*, the legs of mature males are longer in relation to their body size than those of females, and males use these legs to aid in wrapping a female's legs with silk prior to and during copulation. We hypothesized that elongated male legs and silk wrapping provide benefits to males, in part through a reduced likelihood of sexual cannibalism. To test this, we paired females of random size with males from one of two treatment groups—those capable of silk wrapping versus those incapable of silk wrapping. We found that males with relatively longer legs and larger body size were more likely to mate and were less likely to be cannibalized prior to copulation. Regardless of relative size, males capable of silk wrapping were less likely to be cannibalized during or following copulation and had more opportunities for sperm transfer (i.e. pedipalpal insertions). Our results suggest that male size and copulatory silk wrapping are sexually selected traits benefiting male reproductive success.

1. Introduction

For most males, reproductive success is dependent on the ability to acquire mates and successfully fertilize a female's eggs [1,2]. Research across diverse animal taxa has documented elaborate courtship displays and seemingly coercive strategies that exist to secure matings (reviewed in [1–3]). In systems with the potential for high levels of sperm competition, males can increase fertilization success by preventing females from successfully remating through mate guarding or the production of sperm plugs and seminal toxins, among others (reviewed in [4]). For a small number of taxa in which females are sexually cannibalistic, however, males have an additional challenge—surviving a reproductive encounter. While cannibalism prior to sperm transfer results in zero male fitness, cannibalism after the transfer of sperm can be beneficial to a male [5,6]. Nonetheless, even post-copulatory sexual cannibalism carries a potentially high cost (e.g. reduced sperm transfer and loss of future reproductive opportunities) and can strongly influence the evolution of male mating strategies and associated morphologies [7,8].

Given the costs of sexual cannibalism, we expect positive selection for male traits/behaviours that reduce the likelihood of being eaten. Indeed, across cannibalistic spider taxa (Class Arachnida, Order Araneae), sexual cannibalism is commonly associated with extreme morphologies and striking mating systems (reviewed in [9,10]). For example, sexual size dimorphism (SSD) is often associated with sexual cannibalism [11,12]. It has been suggested that longer male legs have been selected to avoid pre-copulatory cannibalism in a number of orb-weaving



Figure 1. Male *Pisaurina mira* wrapping female with silk prior to copulation. (Online version in colour.)

spiders [13]. Additionally, larger male fishing spiders (*Dolomedes fimbriatus*) are more successful in avoiding cannibalistic attempts by females [14]. Many species with SSD, however, are not cannibalistic and the cause/effect relationship between SSD and sexual cannibalism is not well understood. Unusual behaviours such as death feigning [15], opportunistically mating with feeding females [16,17] and rendering females unconscious with sedative pheromones [18] are also presumably associated with avoiding sexual cannibalism. This study focuses on another particularly unusual mating behaviour—the wrapping of females in silk by males in the sexually dimorphic nursery web spider *Pisaurina mira* (Walchenaer).

Pisaurina mira spiders exhibit a sexually dimorphic body shape with males presenting seemingly elongate front legs (forelegs), and an unusual mating strategy wherein a male will wrap a female's legs with silk prior to and during sperm transfer [19] (figure 1). This unusual behaviour has been postulated to reduce female mobility and the likelihood of sexual cannibalism [19], but this hypothesis has not been directly tested. A function in decreasing pre-copulatory cannibalism seems unlikely as receptive females appear to passively allow males to initially wrap them with silk. Following the first act of sperm transfer (i.e. the first insertion of the male's pedipalp), however, females begin to engage in movements that look like an attempt to free themselves from the silk wrapping (electronic supplementary material, video S1).

We hypothesized that size dimorphism influences the ability of *P. mira* males to initially engage a female in copulation while silk wrapping enables them to acquire additional sperm transfer events (hereafter termed insertions) without being cannibalized. We test these hypotheses by randomly pairing phenotypically manipulated males (silk wrapping versus no silk wrapping) with females of variable size and assessing proxies of fitness.

2. Material and methods

We collected immature male and female *Pisaurina mira* (Lancaster County, NE, USA) in Spring 2014. Spiders were maintained in the

laboratory under controlled conditions. To assess the effect of size dimorphism and copulatory silk wrapping, we ran mating trials in which males were assigned to either a (i) wrap ($n = 15$) or (ii) no wrap ($n = 16$) treatment and paired with females of random size. We phenotypically manipulated males in each treatment by applying dental silicone (Take 1[®] Advanced[™] Kerr, Orange, CA, USA) to either (i) the dorsal side of a male's abdomen (wrap treatment) or (ii) a male's spinnerets (no wrap treatment). During mating trials, we live-scored copulation success, pre- and post-copulatory cannibalism, and the number of insertions that a male obtained. We obtained body size measurements (i.e. carapace width (CW) and leg length) from preserved specimens following mating trials. For additional methodological details, see the electronic supplementary material.

If size dimorphism in *P. mira* benefits males in terms of reproductive success, we predicted seeing males with higher male:female leg length or larger body size: (1a) achieve higher mating success and (1b) experience fewer pre-copulatory cannibalism events. We had no *a priori* predictions for the relationship between size dimorphism and post-copulation cannibalism or insertion number, as we expected these to be influenced more by the silk wrapping. Specifically, we predicted that silk wrapping males would (2a) experience fewer cannibalism events during or after sperm transfer and (2b) experience two versus only one pedipalpal insertions. We predicted no relationship between silk wrapping and mating success or pre-copulatory cannibalism, as these both occur prior to silk wrapping. We used separate binomial linear regressions to test the effects of size and Fisher's exact tests to examine the effects of silk wrapping on reproductive behaviour. For details on statistical analyses, see the electronic supplementary material.

3. Results

(a) Size dimorphism and proxies of fitness

Male *P. mira* have relatively longer legs and a larger leg length to body ratio than females, but females have a larger CW (i.e. larger body size) than males (electronic supplementary material, table S1). As predicted, male:female leg length predicted copulation success ($\chi^2_{1,29} = 12.96$, $p < 0.0001$; figure 2a) and pre-copulatory cannibalism ($\chi^2_{1,29} = 7.76$, $p = 0.005$; figure 2b); results are identical for male:female CW (see the electronic supplementary material). Males were more likely to copulate and less likely to be cannibalized when their legs were longer than those of their mating partner and male:female CW was larger. For all males (i.e. those in the wrap and those in the no wrap treatment), we found no effect of male:female leg length or body size (see the electronic supplementary material) on a male's likelihood of being cannibalized post-copulation (wrap: $\chi^2_{1,10} = 0.246$, $p = 0.620$; no wrap: $\chi^2_{1,8} = 0.412$, $p = 0.521$) or on the number of insertions obtained (wrap: $\chi^2_{1,10} = 0.300$, $p = 0.584$; no wrap: $\chi^2_{1,8} = 0.826$, $p = 0.363$). For simplicity, we performed both tests with the two male treatments combined and present these combined results in our figure (post-copulatory cannibalism: $\chi^2_{1,19} = 0.0002$, $p = 0.988$, figure 2c; insertion number: $\chi^2_{1,17} = 0.275$, $p = 0.600$, figure 2d).

(b) Silk wrapping and proxies of fitness

Copulation success and rates of pre-copulatory cannibalism did not differ between males that could and could not wrap females (Fisher's exact test, $p = 0.458$; figure 2e and $p = 0.394$; figure 2f, respectively). In line with our predictions, copulatory silk wrapping affected rates of post-copulatory

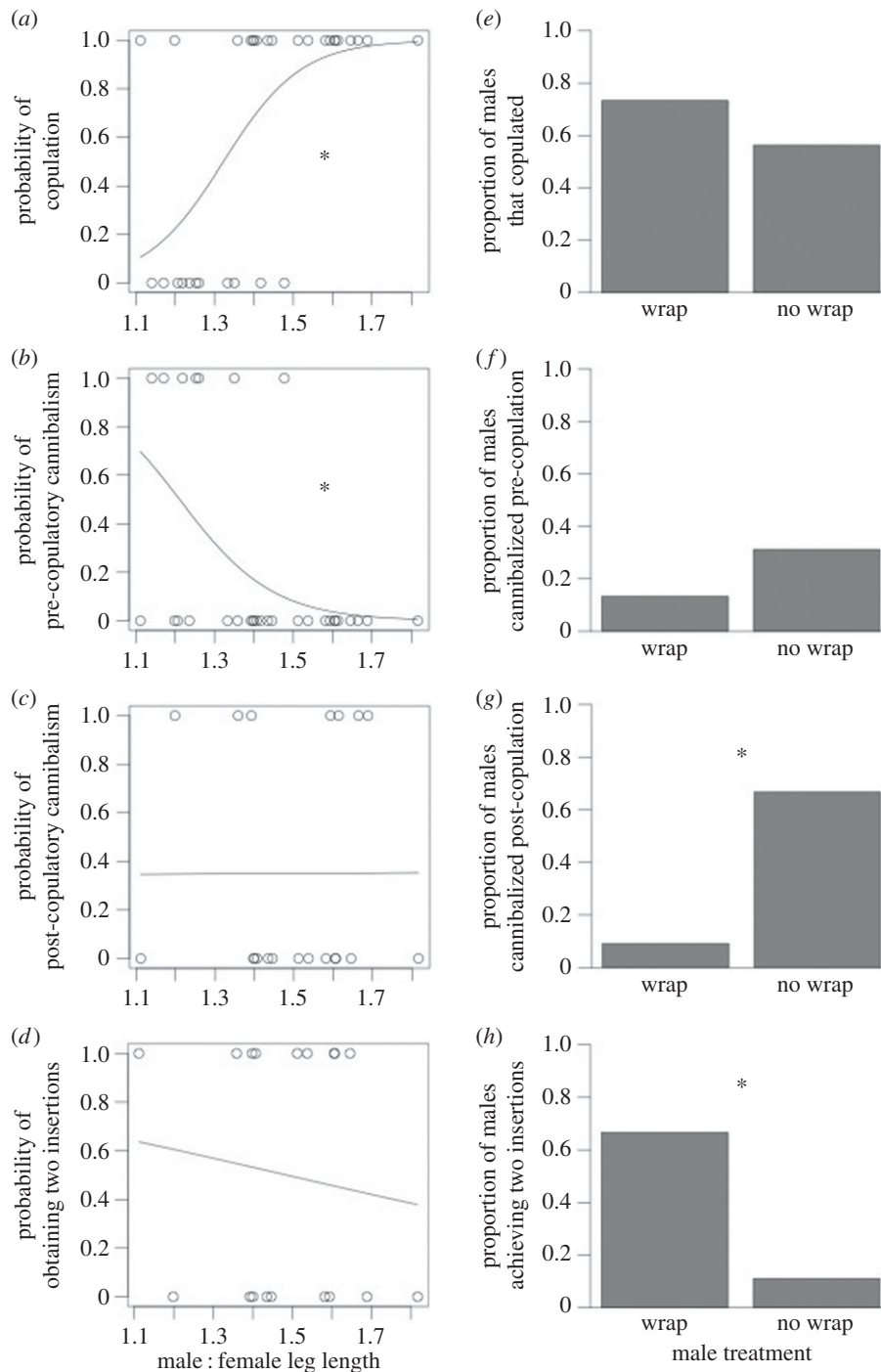


Figure 2. The probability of males (a) copulating, (b) being cannibalized pre-copulation, (c) being cannibalized post-copulation and (d) obtaining two insertions as a function of male : female leg length ($n = 31$). The proportion of males that (e) copulated, (f) were cannibalized pre-copulation, (g) were cannibalized post-copulation and (h) achieved two insertions during copulation when allowed to wrap ($n = 15$) and not wrap ($n = 16$) females. The two males that obtained 1.5 insertions were excluded from the analyses presented in d and h. The asterisk signifies significance based on a p -value < 0.05 .

cannibalism and the number of insertions a male obtained. Males that could not wrap females were more likely to be cannibalized after insemination compared with males that could wrap females (Fisher's exact test, $p = 0.017$; figure 2g). Males in our wrap treatment were also more likely to achieve two insertions (versus one) compared with males in our no wrap treatment (Fisher's exact test, $p = 0.049$; figure 2h).

4. Discussion

Size dimorphism and male silk wrapping in the nursery web spider *P. mira* are important for male mating success and

survival. Mature males possess longer forelegs, relative to body size, than their female counterparts and this dimorphism is important for male reproductive success as males with relatively longer legs were: (i) more likely to achieve a successful mating and (ii) less likely to be cannibalized prior to copulation. Using phenotypic manipulations to remove a male's ability to wrap his mate, we also demonstrate that silk wrapping: (i) reduces the likelihood of cannibalism during or after sperm transfer and (ii) increases the number of insertions a male can achieve during mating.

Though males with relatively longer legs obtained mating advantages, male leg length and CW are strongly correlated (see the electronic supplementary material and figure S1),

making it difficult to confirm a direct benefit of longer legs *per se*. Our results do suggest, however, a reproductive benefit of males being larger (or closer in size) relative to their mating partner, a pattern found across a number of distinct taxa, including red-sided garter snakes [20], *Drosophila* [21,22] and the tobacco moth [23]. In addition to increased mating success, longer male legs (and larger males) also reduced the risk of pre-copulatory sexual cannibalism, a pattern consistent with other cannibalistic species ([11,12,24] but see [25]). With pre-copulatory cannibalism resulting in a complete loss of fitness for males, it is not surprising to observe larger body size and/or grasping traits that reduce the risk of cannibalism. In *P. mira*, males' relatively longer legs appear to aid in their ability to manipulate, wrap and restrain females. As has been previously suggested across multiple cannibalistic orb-weaving spiders [13], we propose that longer leg length is a sexually selected trait in male *P. mira*.

Sexual cannibalism can lead to obvious male fitness costs (e.g. lost potential to secure future matings or reduction of sperm transferred) [7,8], yet sexual cannibalism can also be an adaptive male strategy [5,6]. In the dark fishing spider (*Dolomedes tenebrosus*), male consumption by females significantly increases offspring number, weight and survival [6]. It is currently unknown if *P. mira* males receive any fitness benefits from being cannibalized. Given that silk wrapping reduces the likelihood of post-copulatory sexual cannibalism, however, we hypothesize that male silk wrapping evolved to enable males to obtain increased benefits from multiply mating.

In addition to reducing rates of sexual cannibalism, we found that silk wrapping increases the number of insertions that a male can obtain. We suspect that a male's ability to achieve more insertions corresponds to increased sperm transfer, which in turn corresponds (to some degree) to fertilization success. In the cannibalistic orb-weaving spider, *Argiope aurantia*, males experienced 25% higher fertilization success when achieving two versus one insertion [26]. Additionally, the transfer of more sperm might out-dilute or displace rival sperm, thereby increasing the proportion

of the female's eggs fertilized by a given male [2,4]. In preliminary trials, we find evidence that female *P. mira* mate multiply (primarily through forced copulations), suggesting a potential benefit of increased sperm transfer.

Though females may also benefit from mating with larger males, the striking behaviour of copulatory silk wrapping may reflect an evolutionary history of conflicting reproductive strategies between males and females. Within mating trials, females attempt to be freed from the silk wrapping, which suggests they may incur a cost by being wrapped (e.g. missed post-mating cannibalism). Yet, virgin females often passively allow the wrapping to take place. Costs versus benefits of wrapping for virgin versus mated females and males may differ substantially as sperm competition could play an important role in this system. This study provides strong evidence that size dimorphism and copulatory silk wrapping have been sexually selected through fitness benefits to males, but the putative fitness cost(s) of these traits for females remain unknown.

Ethics. The work conducted complies with the ethical regulations in the USA.

Data accessibility. Datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. A.G.A. discovered the system, carried out all experiments and statistical analyses and wrote and revised the manuscript. E.A.H. participated in the experimental design, the interpretation of data, and the writing and revising of the manuscript. All authors agree to be held accountable for the content provided within the manuscript and give final approval for its publication.

Competing interests. We have no competing interests.

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