COSTS AND BENEFITS OF COPULATORY SILK WRAPPING IN THE NURSERY WEB SPIDER, *PISAURINA MIRA* WALCKENAER, 1837 (ARANEAE, PISAURIDAE)

by

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Males and females share the same goal in sexual reproduction - increased offspring production and viability - yet specialized traits can evolve in one or both of the sexes that serve to increase individual reproductive fitness, sometimes at a cost to a mating partner. Exploring the costs and benefits of such traits in both sexes can provide insights into the role that male-female conflict play in the evolution of mating systems. Under this framework we have explored the evolution of the unique mating behavior observed in the cannibalistic nursery-web spider, *Pisaurina mira*, where males restrain females by wrapping them with silk prior to and during copulation. First, we tested the function of copulatory silk wrapping by pairing females with males that were experimentally manipulated to either be capable or not capable of silk wrapping. We found that males capable of wrapping females were (a) more likely to obtain two verses one opportunity to transfer sperm (termed insertions) and were (b) less likely to be cannibalized after or during copulation. Following from our initial study, we explored male benefits of increased insertion numbers, which revealed that increased insertion number corresponds to increased sperm transfer and higher fertilization success.

Specifically, males transfer roughly two times the amount of sperm when achieving two insertions compared to only one, and this increase in sperm transfer results in males having approximately 25% more offspring. Two additional studies exploring the costs and benefits of males avoiding sexual cannibalism revealed that copulatory silk wrapping results in (a) females losing out on fitness benefits of sexual cannibalism while (b) allowing males to mate multiply. Specifically, we found that consumption of a male mating partner leads to females producing heavier and longer-lived offspring, however, silk wrapping keeps females from obtaining these benefits. Further, regardless of this shared fitness benefit, we also found that cannibalism avoidance by males allows them to mate multiply and achieve higher offspring production. Overall, our results highlight how male and female reproductive strategies can differ, and can ultimately lead to adaptations that clearly benefit one sex while inflicting costs on the opposite sex.

Dedicated to my husband, Austin Davin Brooks and my baby girl, Olive Mae Brooks –

"I know there was something before you, I just can't remember what it was."

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OVERVIEW

Males and females generally share the same goal in sexual reproduction – increased production and viability of offspring – yet factors such as differential investment in gamete production (eggs vs. sperm) (Bateman, 1948), realized operational sex ratio (Emlen & Oring, 1977) and differential investment in parental care (Trivers, 1972) (among others) can result in males and females attempting to achieve optimal fitness in different ways. For example, male fitness is predicted to be dependent on maximizing the number of eggs fertilized (Andersson, 1994; Bateman, 1948; Parker, 1984); thus, adaptations that allow males to secure matings and increase fertilization success should be under positive selection. Indeed, males often have exaggerated weapons, ornaments or courtship displays for gaining access to females. In contrast to males, females are expected to maximize their fitness by increasing quality (rather than quantity) of offspring and they can achieve this by investing resources into developing offspring and by being choosy in selecting mating partners (Andersson, 1994; Bateman, 1948; Trivers, 1972).

The reproductive strategies that evolve within each sex to maximize fitness may be in conflict with one another – specialized traits that evolve in one or both of the sexes to increase individual reproductive fitness may sometimes be costly to the other sex. Differences in optimal reproductive strategies have been proposed to explain the evolution of costly mating behaviors such as barbed or spiny male genitalia (e.g. Hotzy & Arnqvist, 2009), forceful copulations (Arnqvist & Rowe, 2013; Clutton-Brock & Parker, 1995), traumatic insemination (Stutt & Siva-Jothy, 2001), and sexual cannibalism (Elgar & Crespi, 1992a). Uncovering the function of a trait that appears potentially costly for

one of the sexes within the system provides unparalleled opportunities to understand how divergent reproductive strategies can influence male-female mating dynamics and the evolution of mating systems.

In an attempt to gain insight into the role that male-female mating dynamics plays in the evolution mating systems, this dissertation focuses on uncovering the function of unusual behavior of copulatory silk wrapping in the nursery web spider, *Pisaurina mira*. In this species, all males wrap females' legs with silk prior to and during copulation (Bruce & Carico, 1988; Fig. 1); a behavior that appears potentially costly for females. Further, mating in *P. mira* follows a typical sequence of behaviors (Fig. 2) that reveal the potential for differing mating strategies for each sex. Most virgin females are receptive to mating and allow males to mount and silk wrap them prior to

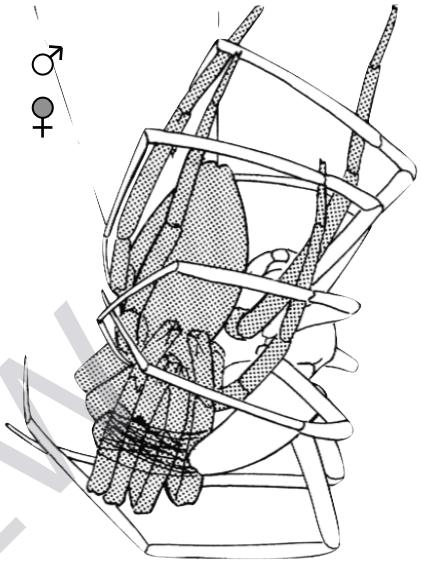

Figure 1 Male *Pisaurina mira* wrapping female's legs with silk prior to copulation. Adapted from Bruce & Carico (1988).

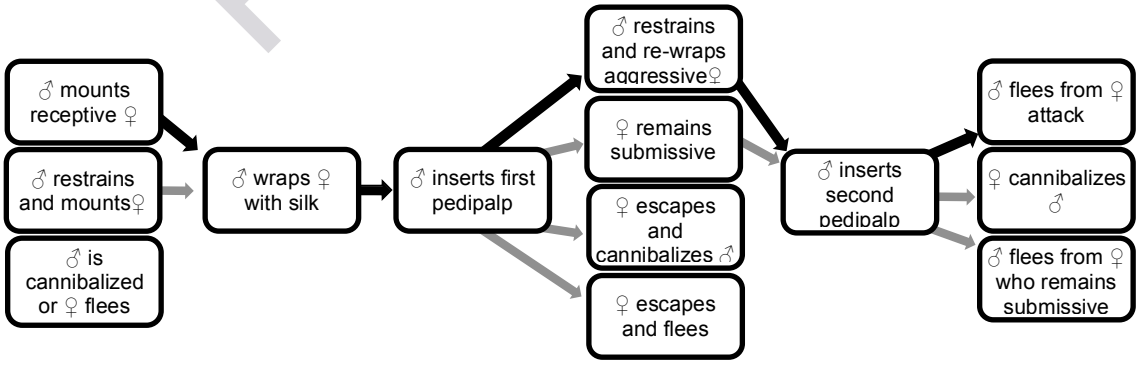

Figure 2. Overview of typical actions and reactions of male and female *P. mira* observed in un-manipulated mating trials carried out in the laboratory. The mating sequence begins when a male locates and approaches a mature female. The **black** arrows indicate the most common mating sequence observed.

transferring sperm. In some cases, males forcibly mount seemingly unreceptive females and once restrained, males then silk wrap the female. After males insert one of their two pedipalps (the male sperm storage organ) to transfer sperm (hereafter called an insertion), females often become aggressive. Males will typically restrain and re-wrap females and achieve one more insertion for a total of two insertions (and longer copulation durations), at which point they quickly flee from aggressive females.

In my first chapter, published in *Biology Letters*, I tested the current function of copulatory silk wrapping by pairing virgin females of random size with virgin males that were experimentally manipulated to either be capable or not capable of silk wrapping. Specifically, I placed dental silicone on either the male's spinnerets (no wrap) or on the dorsal side of the male's abdomen (wrap). While the silk wrapping had no effect on the likelihood of copulation or on sexual cannibalism prior to copulation, I found that males capable of wrapping females were less likely to be cannibalized after or during copulation and were more likely to obtain two versus one opportunity to transfer sperm (termed insertion) (Anderson & Hebets, 2016). When the silk wrapping was not present, females usually attacked and cannibalized males immediately after the first insertion (see Fig. 2). Because females typically show aggression after the first insertion, regardless of whether the wrapping is present or not, we presume that the silk acts as a physical restraint allowing males the opportunity to safely obtain a second insertion. Overall, results from this study suggest that silk wrapping is a sexually selected trait that benefits male reproductive success. Results from this first study led me to explore the potential costs and benefits of increased insertion number and sexual cannibalism avoidance for both males and females within the remaining chapters of my dissertation.

In addition to facilitating copulation, many male-specific mating strategies or morphological traits may function to increase copulation duration. Male "grasping traits" (Sakaluk et al., 1995) larger nuptial gifts (Svensson, Petersson, & Frisk, 1990), and barbed or spiny male genitalia (Edvardsson & Canal, 2006; Hotzy & Arnqvist, 2009) have all been documented to extend copulations. Given that copulatory silk wrapping increases the time males spend copulating through increased insertion number, I tested the hypothesis that increased insertion number corresponds to increased sperm transferred and higher fertilization success. Results from this experiment are reported in my second chapter, published in *Animal Behaviour*. In brief, by manipulating male insertion number, I found that males transfer roughly twice the amount of sperm when achieving two insertions compared to only one, and this increase in sperm transfer results in males having approximately 25% more offspring (Anderson & Hebets, 2017).

Copulatory silk wrapping reduces rates of post-copulatory sexual cannibalism. Sexual cannibalism may be a beneficial female strategy resulting in an immediate meal, or, if occurring before mating, may act as a form of mate rejection (Eberhard, 1996; Prenter et al., 2006). Further, sexual cannibalism during sperm transfer may act as a mechanism for females to control the duration of copulation and thus male fertilization success, especially if cannibalism terminates sperm transfer (Elgar et al., 2000). While cannibalism may benefit females in several ways, cannibalism can lead to male fitness costs such as the lost potential to secure future matings or reduced sperm transfer (Elgar & Crespi, 1992; Elgar & Schneider, 2004). Sexual cannibalism can also be an adaptive male strategy (Andrade, 1996; Schwartz, 2013). For example, in the fishing spider, *Dolomedes tenebrosus*, consumption of the male by females significantly increases