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# Obligate male death and sexual cannibalism in dark fishing spiders

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Male dark fishing spiders (*Dolomedes tenebrosus* Araneae, Pisauridae) always die during their first and only copulation, making all males monogynous. Such obligate male death can be adaptive if it facilitates sexual cannibalism, and if sexual cannibalism results in male reproductive benefits, such as an advantage in sperm competition through reduced female remating. We first conducted an experiment to determine the extent to which *D. tenebrosus* (1) males are cannibalized by females and (2) females engage in remating, both of which are prerequisites for several adaptive hypotheses of male self-sacrifice. We then conducted an experiment to test the hypothesis that the cannibalism of the male by the female reduces the likelihood of female remating. We found that obligate male death appears to facilitate sexual cannibalism in *D. tenebrosus*; females always cannibalize males postcopulation. We also found that half of all females copulated with multiple males. Finally, we found no support for the hypothesis that cannibalizing a male reduces the likelihood of female remating. We were additionally able to document that even though males may appear to act as whole-body mating plugs immediately after death, by hanging from the female's genital opening, this rarely functions in preventing subsequent copulations (i.e. mate plugging). In summary, obligate male death and associated cannibalism in the dark fishing spider *D. tenebrosus* does not appear to function to reduce sperm competition through reduced female remating.


Understanding how reproductive strategies vary within and between species (i.e. mating system variation) is essential to understanding sexual selection and its potential role in evolutionary change (Andersson, 1994). Mating systems are usually classified in terms of the number of mates per male or per female (Shuster & Wade, 2003), and researchers consider the mating system at either the individual or population level (Thornhill & Alcock, 1983). In many animals, individuals within a population may show different mating systems, with some proportion of males and/or females acquiring more than one mating partner and others acquiring only one (e.g. polygynous males, polyandrous females and monogamous males/females) (Thornhill & Alcock, 1983). In a relatively small number of species, all or most males within a population acquire only a single lifetime mating. Such a mating system has been referred to as male monogamy or monogyny (Fromhage, Elgar, & Schneider, 2005).

Mating systems with monogynous males are relatively rare in terms of the number of species displaying such a mating system; yet monogyny is phylogenetically widespread and has evolved a number of times independently, especially among arthropods (Miller, 2007; Schneider & Fromhage, 2010). For example, in honeybees, males have evolved genitalia that explode into the female, causing the male to die after a single mating (Michener, 1974). In some molluscs, crustaceans and fishes, males do not die when they mate, but they remain permanently attached to the female, rendering them unable to acquire additional matings (reviewed in Schneider & Fromhage, 2010). In yet other animals, females impose monogamy on males. In the queenless ant *Dinoponera quadriceps*, the female severs the end of the copulating male's abdomen, killing the male and leaving his genitalia linked to hers (Monnin & Peeters, 1998); and in burying beetles, females interfere when males attempt to attract additional females (Eggert & Sakaluk, 1995). In monogynous spiders, males are often rendered unable to mate with more than one female because of the occurrence of sexual cannibalism and/or genital damage during or following mating (reviewed in Schneider & Fromhage, 2010).

Some of the most notorious examples of monogyny come from spiders, and it is from researchers working with these animals that the most recent theoretical and conceptual advances have been made. The most well-studied, predominantly monogynous spider species is the Australian redback, *Latrodectus hasselti*, in which males actively sacrifice themselves during copulation by somersaulting their bodies onto the fangs of their mating partner in an

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apparent attempt to induce sexual cannibalism. Initial studies suggested that males receive two benefits from such self-sacrifice behaviour: (1) increased paternity and (2) reduced female remating (Andrade, 1996). Research on such cannibalistic mating systems has inspired the development of multiple hypotheses regarding adaptive self-sacrifice associated with cannibalism (Andrade, 1996, 1998, 2003; Snow & Andrade, 2004). For example, cannibalized males can increase the proportion of eggs they fertilize under sperm competition through either transferring more sperm or reducing female receptivity (mating effort: Andrade, 1996, 1998; Elgar, 1992; Low, 1978; Simmons & Parker, 1989). They can also donate somatic nutrients (i.e. their bodies) to a female through their cannibalism, and these nutrients may be subsequently transferred to their own offspring, thereby increasing offspring quantity or quality (paternal effort: Buskirk, Frohlich, & Ross, 1984; Elgar, 1992; Low, 1978; Parker, 1979; Simmons & Parker, 1989; Thornhill, 1976). Importantly, these hypotheses are not mutually exclusive and all require the presence of cannibalism (cannibalism increases either male success in sperm competition and/or offspring quantity or quality). The sperm competition hypothesis, however, requires the potential for female multiple mating; if females rarely mate with multiple mates, self-sacrifice cannot increase male success in sperm competition.

Theoretical and empirical explorations of the evolution of monogyny indicate that its presence is often correlated with male-biased effective sex ratios (Fromhage et al., 2005) and female-biased sexual size dimorphisms (Fromhage et al., 2005; Miller, 2007; Schneider & Fromhage, 2010). Mathematical modelling, for example, has demonstrated that if there is a male-biased effective sex ratio (the ratio of males to females among the individuals in a population that mate at least once), monogyny can evolve over polygyny (Fromhage et al., 2005). Similarly, female-biased size dimorphism, as is often associated with patterns of early male maturation, is frequently seen to correlate, across taxa, with male monogyny (Miller, 2007; Schneider & Fromhage, 2010). Consistent with this earlier theoretical and empirical work, a new form of obligate male death was recently documented in a spider with a male-biased effective sex ratio and extreme female-biased size dimorphism, the dark fishing spider *Dolomedes tenebrosus* (Schwartz, Wagner, & Hebets, 2013). The present study explores potential hypotheses for how monogyny might be adaptive in this exceptional animal system.

*Dolomedes tenebrosus* is unique among its Nearctic congeners as it shows extreme female-biased sexual size dimorphism (Hormiga, Scharff, & Coddington, 2000; Scharff & Coddington, 1997; Schwartz et al., 2013) and a naturally occurring male-biased sex ratio (Schwartz et al., 2013). Males of this species show obligate death as all males immediately curl up and their hearts eventually stop beating following palpal expansion and sperm transfer (Schwartz et al., 2013). This study explores one aspect of the putative adaptive nature of such obligate male death. Specifically, we set out to achieve three major goals: (1) determine the occurrence and frequency of sexual cannibalism associated with obligate male death, (2) determine the occurrence and frequency of female multiple mating and (3) test whether sexual cannibalism of males by females decreases female receptivity. If females mate multiply, and if they cannibalize males, the cannibalized males may gain an advantage in sperm competition by reducing the likelihood of female remating.

## GENERAL METHODS

*Dolomedes tenebrosus* males inflate their first haematodochal bulb when copulating with a female and immediately curl up and become unresponsive as their body hangs from the female's genital opening (Schwartz et al., 2013), making them an easy target for consumption by the female. It has not yet been established, however, whether or not females indeed make a meal out of their unresponsive mates. In addition, in the field, mature male *D. tenetrosus* can encounter multiple females on a given night (Schwartz et al., 2013), yet prior work has not established the occurrence and/or prevalence of female multiple mating. Two major goals of this study were to determine the occurrence and frequency of both sexual cannibalism associated with obligate male death and female multiple mating.

Immature male and female *D. tenebrosus* were collected at night using a light-emitting diode (LED) headlamp during the spring (April–May) of 2008 (experiment 1) and 2009 (experiment 2) in Lancaster County near Lincoln, Nebraska (U.S.A.). Field-caught individuals were transported back to the laboratory and housed individually in 87.3 × 87.3 × 112.7 mm plastic containers (763C, AMAC Plastics, Petaluma, CA, U.S.A.). Containers were housed in a climate-controlled room (24–27 °C) and placed on a light:dark cycle that was adjusted twice a month to match the outside summer environment (April–August, 13:11–15:9 h light:dark). Female spiders were fed two 2-week-old (~6 mm) crickets, *Acheta domesticus*, three times per week, and male spiders were fed two 1-week-old (~3 mm) crickets, *A. domesticus*, once per week (Bassett's Cricket Ranch, Visalia, CA). In addition, all spiders were provided water ad libitum. Males and females matured in the laboratory and were thus known to be virgins when used in experiments. All spiders were weighed (Ohaus Explorer balance 0.0001 g) twice, first when transported to the laboratory and once again prior to their assigned experimental trial.

## EXPERIMENT 1: FREQUENCY OF SEXUAL CANNIBALISM AND FEMALE MULTIPLE MATING

### *Methods*

This experiment aimed to determine both (1) the frequency of sexual cannibalism (precopulatory and postcopulatory) in this system and (2) the frequency of female remating. To determine the occurrence and frequency of cannibalism in the laboratory, we allowed male–female pairs to interact naturally, with no researcher intervention, and recorded cannibalism events. To explore the potential for female remating, following their initial pairing, all females were given the opportunity to mate with two additional males, 72 h apart (i.e. at 72 and 144 h after their initial mating). We chose this time interval because we were interested in documenting female mating behaviour over 1 week. Because we did not remove males from female epigyna following mating, thus allowing them to be eaten, and we subsequently attempted to remate females with up to two additional males, we were also able to determine whether the female's likelihood of remating at 72 h intervals was influenced by (1) male cannibalism and/or (2) prior copulations (and/or seminal materials transferred).

During mating interactions, females were placed individually in a 252.4 × 90.5 mm (diameter × depth) plastic arena (250C, Pioneer Plastics, North Dixon, KY, U.S.A.) for a minimum of 24 h prior to the introduction of the male. The arena floor was covered with a disk of filter paper (Double Rings, 102 Qualitative, 24 cm) and at the centre of the arena was a 47.6 × 84.1 mm plastic vial (40 DRAM, Thornton Plastics, Salt Lake City, UT, U.S.A.) covered in fibreglass mesh on which the female could climb and position herself. Generally, mating in *D. tenebrosus* occurs on a vertical surface, and in the field, pairs are usually seen copulating on vertical surfaces (i.e. overhanging roots, trees, etc.) in riparian areas. We videotaped (Sony DCR-HC96 MiniDV Handycam) staged mating trials during the summer of 2008 ($N = 114$). All individuals used were field-caught