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Obligate male death and sexual cannibalism in dark fishing spiders

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Abstract

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.

Keywords: dark fishing spider, *Dolomedes tenebrosus*, mating effort, mating plug, monogyny, self-sacrifice, sexual cannibalism, sperm competition, spontaneous death

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 mollusks, 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 apparent attempt to induce sexual cannibalism. Initial studies suggested

that males receive two benefits from such self-sacrifice behavior: (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 hematochal 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. tenebrosus* 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 behavior 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 center 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 fiberglass 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 virgins, which molted to maturity in the laboratory (spiders are not sexually mature prior to their final molt). Males were assigned to females at random, and mature male spiders ($N = 114$) were used only once, while female spiders ($N = 38$) were used three times during the mating trials.

Statistical analysis

To compare the rates of cannibalism and copulation, we recorded the behavior of individual females ($N = 38$) across three mating opportunities. We used generalized linear mixed models (GLMM) that included “female” as a random effect to account for the repeated measures and “male” (first, second, or third) as a fixed effect, allowing us to look at how female behavior (cannibalism/copulation) changed with exposure to subsequent males. In addition, we used a Fisher’s exact test to determine whether the proportion of females that received different numbers of copulations (and thus that received different amounts of seminal materials) differed in their likelihood of remating. All analyses were conducted using the R statistical software (R Development Core Team, 2012) version 2.15.1. For the generalized linear mixed models, we used the R statistical software package ‘lme4’ (Bates, Maechler, & Bolker, 2012).

Results

Postcopulatory sexual cannibalism appears to be a fundamental aspect of mating behavior in *D. tenebrosus*, as all females (100%) cannibalized their mating partners following copulation (mean \pm SE: time until copulation: 78 ± 5 min, $N = 61$; copulation duration: 22 ± 3 min, $N = 61$). Mated females plucked the unresponsive male from their epigynum and proceeded to eat them (time spent eating: 98 ± 6 min, $N = 42$). Even though some females were seen to bite males during copulation (22 out of 61, 36%), every instance of postcopulatory sexual cannibalism was initiated after the male had curled up following palpal insertion.

Precopulatory sexual cannibalism was also observed. In lieu of mating, some females cannibalized their potential mating partners (first male: 26%; second male: 29%; third male: 68%). There was a significant increase in precopulatory sexual cannibalism of the third mating partner (GLMM: $Z = 3.553$, $P < 0.001$; Fig. 1).

Dolomedes tenebrosus females will readily remate, even after consuming their mating partner. When given three mating opportunities 72 h apart, half of the females mated multiply (i.e. mated

with more than a single male during the 1 week cycle). While 19 out of 38 (50%) copulated with only a single male, 15 out of 38 (39.5%) copulated with two males and 4 out of 38 (10.5%) copulated with three males. Females were equally likely to copulate with their first and second mating partners (first male: 68%; second male: 66%), but were significantly less likely to copulate with their third mating partner (third male: 26%, GLMM: $Z = 3.553$, $P < 0.001$; Fig. 1). Thus, half of the *D. tenebrosus* females mated multiply when they had the opportunity to do so, setting the stage for competition among males for the fertilization of a single female’s eggs (i.e. introducing the potential for sperm competition).

Given that all females cannibalized their mating partners before or after copulation, we were unable to examine how cannibalism itself might influence female remating in this experiment. However, the number of males successfully achieving copulation varied across individual females, enabling us to ask directly whether the number of copulations (and potentially the amount of seminal materials transferred) influences female remating behavior. We found no influence of the number of copulations on female remating. The proportion of females that remated did not differ between females that received different numbers of copulations (Fisher’s exact test: $P = 1.0$). For females that copulated once, 4 out of 13 (31%) remated. For females that copulated twice, 5 out of 19 (26%) remated. These results suggest that doubling the amount of seminal materials received does not affect the likelihood of female remating.

Experiment 2: Influence Of Sexual Cannibalism On Female Remating

Methods

Results from experiment 1 demonstrate the pervasiveness of sexual cannibalism as well as the potential for female remating in *D. tenebrosus*. It is thus possible that male self-sacrifice functions to delay female remating. Our second experiment directly tested the hypothesis that sexual cannibalism, putatively facilitated by obligate male death, provides males an advantage in sperm competition by reducing their partner’s likelihood of remating. Importantly, in contrast to experiment 1, this experiment examined a much shorter remating interval (30 min). This shorter interval more realistically mimics the potential for multiple mating during a single night (Schwartz et al., 2013). This shorter interval also allowed us to test whether the male’s hanging body and/or the female’s active consumption of the male reduces female remating.

In the summer of 2009, we randomly assigned 36 *D. tenebrosus* females to one of three postcopulation feeding treatments: (1) male treatment: females were allowed to cannibalize their mate ($N = 12$); (2) cricket treatment: females were prevented from cannibalizing their mate but were provided a cricket to eat ($N = 12$); (3) nothing treatment: females were prevented from cannibalizing their mate and were not provided anything to eat ($N = 12$). All individuals used were field-caught virgins, which molted to maturity in the laboratory. For all females, regardless of the treatment, the curled body of the male was removed by the researcher following his natural removal by the female. Specifically, upon a male’s hematochal expansion, his motionless body remained attached to the female until the female pulled him out to begin consuming him. It was at this point that we removed the male’s body. Following the male’s removal, females were then either provided with (1) the same male’s body, (2) a cricket that matched (± 3.0 mg) the mass of the male removed, or (3) nothing. The average \pm SE mass of males was 81.5 ± 4.4 mg ($N = 36$). Males and crickets were provided to females using large forceps (30.5

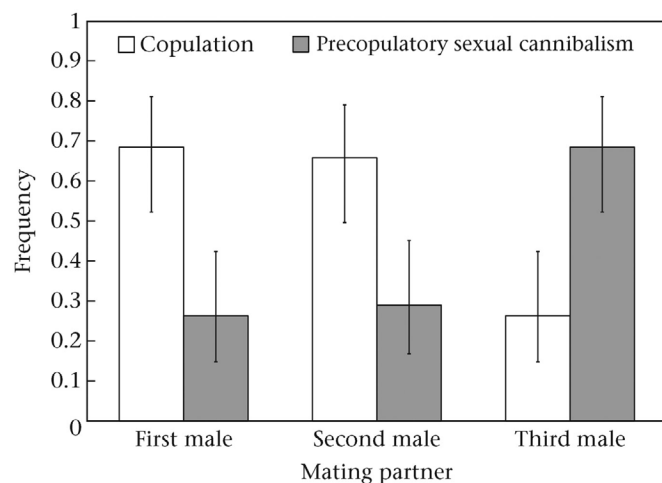


Figure 1. Frequency of copulation and precopulatory sexual cannibalism in *Dolomedes tenebrosus*. The mating behavior of 38 females was recorded over three mating opportunities at 0, 72, and 144 h. Error bars represent 95% confidence limits.

cm), and all females readily accepted their postcopulation food item when offered.

Exactly 30 min from the start of copulation by the first male, we introduced the second male into the arena and recorded the frequency of female remating. The second male was left in the arena with the female for up to 3 h. We chose a 30 min interval since females may encounter multiple males within a single night (Schwartz et al., 2013) and this time period enabled us to explore the potential for obligate male death to provide males an advantage in sperm competition through a whole-body mating plug (see Foellmer & Fairbairn, 2003; Knoflach & van Harten, 2001), a hypothesis independent of any adaptive significance of cannibalism (i.e. cannibalism is not necessary). Specifically, if a male was still hanging from the female (i.e. had not naturally been removed by the female) at 30 min postcopulation, his body could physically prevent the second male from mating. We videotaped (Sony DCRHC96 MiniDV Handycam) staged mating trials during the summer of 2009 ($N = 72$), but all data (time until copulation, copulation time, time until cannibalism, etc.) were recorded from direct observations during the mating trials.

Statistical analysis

To investigate whether female cannibalism of a male postcopulation affects that female's likelihood of remating, we recorded the behavior of individual females ($N = 36$) under three postcopulation feeding treatments (male, cricket, or nothing). We used a Fisher's exact test to determine whether the proportion of females that remated differed across the three treatments. All analyses were conducted using the R statistical software (R Development Core Team, 2012) version 2.15.1 and results are reported as means \pm SE.

Results

We found no difference in the likelihood of remating in females from our different treatment groups (male treatment: 8 out of 12 (67%) females remated; cricket treatment: 8 out of 12 (67%) females remated; nothing treatment: 9 out of 12 (75%) females remated; Fisher's exact test: $P = 1.0$; Fig. 2). These results suggest that the consumption of a male postcopulation does not affect the likelihood that a female will remate.

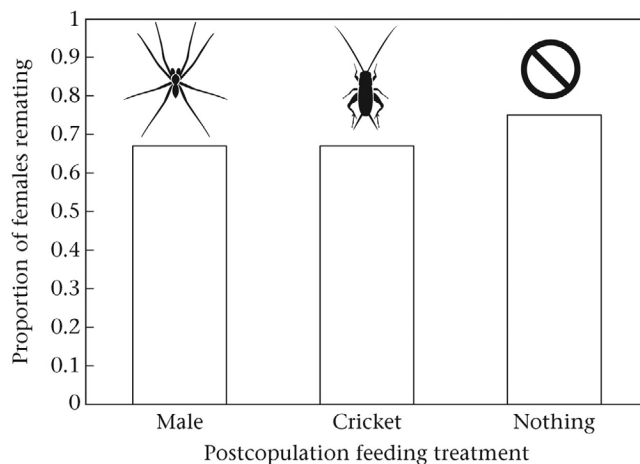


Figure 2. Proportion of *Dolomedes tenebrosus* females remating at 30 min following an initial mating. The remating rate of females was recorded under three postcopulation feeding treatments: (1) male treatment, 8 out of 12 (67%) remated; (2) cricket treatment, 8 out of 12 (67%) remated; and (3) nothing treatment, 9 out of 12 (75%) remated.

Our experimental design also enabled us to investigate whether the hanging body of a mated male can act as a whole-body mating plug and/or if feeding on the body of a male *D. tenebrosus* may itself reduce a female's likelihood of accepting another mate. Given that some females waited as long as 87 min in experiment 1 (22 ± 3 min, $N = 61$) until they removed the male's body from their epigynum, a dead male's body could physically prevent a rival male from copulating. However, in experiment 2, females waited only a maximum of 40 min (10 ± 1 min, $N = 36$) until they removed the first male. Thus, within the constraints of our experimental design, we found that only 1 out of 36 successfully copulating males (2.8%) delayed copulation of a subsequent male. Specifically, in the nothing treatment, when one female removed the male, the male's pedipalp tore off and remained securely attached to the female's epigynum postcopulation. The lodged pedipalp was successful in delaying copulation of the second male for 190 min (average time until copulation for all second males: 67 ± 8 min, $N = 24$) before the palpal plug was removed.

In the male treatment, all females were busy feeding on the first male when the second male started courting (time spent eating: 96 ± 9 min, $N = 12$). The act of sexual cannibalism does not appear to deter female remating, since five out of the eight females that remated were actively consuming the first male when they copulated with the second male.

Discussion

The present study indicates that in the dark fishing spider, *D. tenebrosus*, males that obligately die following copulation are subsequently consumed by their female mating partner, and that previously mated females are willing to remate, regardless of whether or not they have consumed a male. Our first experiment established that females cannibalize their mating partners 100% of the time following obligate male death, and that many of these females (50%) subsequently mate with additional males. In our second experiment, we provided mated females with a male, a cricket or nothing following an initial mating to test whether sexual cannibalism reduces the likelihood of female remating. We predicted that if the cannibalism of the male reduces female remating rates, then females that eat their mate should be less likely to remate than those that eat nothing. Furthermore, if the somatic material of a *D. tenebrosus* male is unique (e.g. provides specific nutrients or contains antiaphrodisiac compounds), then remating rates of females that consume their mate should be lower than those of females that consume a cricket postcopulation. We found no evidence of a reduced likelihood of remating following sexual cannibalism. Our results are in contrast to previous findings in the Australian redback spider, *L. hasselti* (Andrade, 1996). Postcopulatory sexual cannibalism in *D. tenebrosus* thus does not appear to reduce the likelihood of female remating.

The seemingly obligate sexual cannibalism in *D. tenebrosus* differs from sexual cannibalism in other spiders as it occurs on average more than 10 min after a male's initial hematochal bulb expansion, and thus presumably after sperm transfer. Since these self-sacrificing males are not actively cannibalized during copulation, sexual cannibalism itself cannot have a direct effect on the transfer of their sperm, specifically the rate of sperm transfer. This is not to say that self-sacrifice in *D. tenebrosus* does not facilitate increased sperm transfer, but sexual cannibalism per se does not appear to be involved. Dying *D. tenebrosus* males remained attached to the female for a mean \pm SE of 22 ± 3 min in experiment 1 and 10 ± 1 min in experiment 2, and although they remain motionless and unresponsive to probing stimuli (i.e. being prodded with forceps), their heart continues to beat (Schwartz et al., 2013). During

this time the male may be transferring sperm to the female, and the duration of attachment may be correlated with the amount of sperm transferred. Such a scenario is similar to the remote copulation hypothesis proposed for theridiids in the genera *Echinotheridion* and *Tidarren* (Knoflach, 2002; Knoflach & van Harten, 2001), which suggests that severed pedipalps may continue to transfer sperm. Similarly, *D. tenebrosus* pedipalps attached to dying males may continue to transfer sperm in this system. However, in a number of spider species, sperm transfer is relatively quick (i.e. a few minutes), and a lengthy copulation does not equal the transfer of more sperm (Schneider & Andrade, 2011). For example, in *L. hasselti*, the majority of sperm is transferred in the first 5 min. Thus, copulation duration may serve as a form of copulatory courtship, with females selectively storing/using sperm from males that copulate longer (Snow & Andrade, 2004). In the spiny orbweaver, *Micrathena gracilis*, sperm are transferred early in copulation and are not related to copulation duration. In addition, males may vary the amount of sperm they transfer depending on female mating history, by transferring most of their sperm (85–90%) when mating with a virgin female and by transferring very little or no sperm when mating with a nonvirgin female (Bukowski & Christenson, 1997). At this point, additional work is needed to determine whether and how copulation duration (i.e. time attached after spontaneous death) is correlated with sperm transfer in *D. tenebrosus*.

Our research with *D. tenebrosus* thus far provides no evidence that obligate male death in *D. tenebrosus* is adaptive because the male's body functions as a whole-body mating plug (Foellmer & Fairbairn, 2003; Knoflach, 2004; Knoflach & van Harten, 2001). The body of a *D. tenebrosus* male curls up and hangs from the female's genital opening following copulation, introducing the potential to act as a whole-body mating plug (see Miller, 2007). Over 5 years (2006–2010) and covering 225 copulations (Schwartz et al., 2013; present study), only once have we observed the potential for a male to act as a mating plug (present study, experiment 2). Importantly, we did not introduce a second male immediately following copulation, when the first male's body had the highest probability of being attached and acting as a whole-body mating plug. In only two cases during experiment 2 was the first male still attached to the female when the second male was introduced. Regardless, even after the removal of the male, there were no obvious palpal fragments remaining in the female's epigynum that would have inhibited subsequent mating (reviewed in Uhl, Nessler, & Schneider, 2010).

Our results provide no evidence for reduced female remating following copulation and sexual cannibalism either from seminal materials transferred by males or from materials contained in the bodies of males. However, the act of sexual cannibalism itself may occupy the female, thus reducing her receptivity to subsequent courting males if she is busy feeding. We explicitly chose a 30 min remating interval (experiment 2) to explore whether females are less likely to remate during the act of cannibalism (i.e. while consuming the male). We expected that some females would still be engaged in sexual cannibalism when the second male was introduced, and indeed, all females were feeding on the first male when the second male was introduced. Since there was no influence of cannibalism on female remating, remating by female *D. tenebrosus* is not hindered by the consumption of a previous mate.

In addition to documenting the pervasiveness of postcopulatory sexual cannibalism in *D. tenebrosus*, our first experiment also revealed that precopulatory sexual cannibalism is not uncommon. Precopulatory sexual cannibalism can be a risky behavior, especially for virgin females, since they may remain unmated because of their actions, assuming no additional suitors are encountered

(Arnqvist & Henriksson, 1997; Elgar, 1992). However, precopulatory sexual cannibalism may become more likely if males are perceived to be more abundant and if females use cannibalism as a mechanism of mate choice, selectively cannibalizing nonpreferred mates (Darwin, 1871; Elgar, 1992; Elgar & Nash, 1988; Elgar & Schneider, 2004; Hebets, 2003; Johnson, 2005; Prenter, MacNeil, & Elwood, 2006). Given the significant increase in the frequency of precopulatory sexual cannibalism after females had encountered two males (68% cannibalized the third male prior to copulation, experiment 1), *D. tenebrosus* females may be using precopulatory sexual cannibalism as a means of rejecting additional mates, whether or not the males are preferred.

In summary, in addition to establishing the prevalence of sexual cannibalism and female remating in the dark fishing spider, *D. tenebrosus*, we tested one hypothesis regarding adaptive obligate death: obligate male death facilitates sexual cannibalism and sexual cannibalism reduces female remating. While obligate male death does seem to facilitate sexual cannibalism in *D. tenebrosus*, we found no support for the hypothesis that sexual cannibalism reduces female remating; females continued to remate at a variety of timescales following the cannibalism of a male. While this study tested one potential hypothesis directly, additional adaptive hypotheses remain for the unusual behavior of obligate death and cannibalism in *D. tenebrosus*. For example, sexual cannibalism may allow self-sacrificing males to increase offspring quantity and/or quality. That is, a male may benefit from increasing a female's fecundity or offspring quality through the sacrifice of his body (i.e. from paternal investment; Simmons & Parker, 1989). Examining offspring quantity and quality from females that did and did not consume their mates could address this hypothesis. Nevertheless, the possibility remains that self-sacrifice in *D. tenebrosus* simply facilitates increased sperm transfer, with sexual cannibalism itself providing males no additional benefits. For example, sexual cannibalism might be an incidental consequence of spontaneous male death, which is triggered by the hydraulic expansion of the hematochoal bulb during copulation (*Argiope aurantia*; Foellmer & Fairbairn, 2003). More work is needed to fully explore these, and other, hypotheses. Regardless, *D. tenebrosus* offers an exciting new example of monogyny and provides an opportunity to explore the causes and consequences of an unusual mating system where male death and postcopulatory sexual cannibalism are obligatory.

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