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## Mating and cannibalism dynamics of the fishing spider *Dolomedes scriptus* Hentz, 1845 (Araneae: Pisauridae)

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**Abstract.** Sexual cannibalism is common in many species of arachnids. Studies investigating *Dolomedes tenebrosus* Hentz, 1844, have even discovered the occurrence of obligatory male self-sacrifice during copulation. In this system, females subsequently cannibalize males, and this cannibalism leads to higher fitness for both partners. Unfortunately, our understanding of the evolution of such an extreme mating system is challenged by the absence of information for close relatives. To that end, this study explores the courtship behavior, mating system and cannibalism dynamics of the spider *Dolomedes scriptus* Hentz, 1845. To determine whether female and male *D. scriptus* mate multiply, we recorded interactions of repeatedly exposed focal females and focal males to new mating partners for three days. We also quantified attacks and cannibalism events that occurred both before and after every copulation. We found male *D. scriptus* court females by waving their forelegs during their approach and tapping the females prior to mounting. In our remating trials, none of the female *D. scriptus* accepted additional males after their first mating over the three-day period. In contrast, male *D. scriptus* were polygynous, often mating with multiple females. Across the trials, sexual size dimorphism was a predictor of whether mating occurred, with similarly sized pairs being more likely to mate. Additionally, previously mated females were less likely to cannibalize males—an unusual pattern for spiders. Like other species of *Dolomedes* Latreille, 1804, our results suggest a strong role of female aggression in *D. scriptus* mating system dynamics.

**Keywords:** polygamy, experience, mating system, sexual conflict, sexual size dimorphism

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A number of factors – e.g., operational sex ratios, ecological and phylogenetic factors, and differential investment in parental care (Emlen & Oring 1977)—influence how animals come together to reproduce, including whether they are likely to mate with one or more member(s) of the opposite sex (mating system). The operational sex ratio, or the average available ratio of fertilizable females to sexually active males at a given time, will influence mating systems dynamics as the number of available mates can vary within (over time) or between species. Additionally, the spatial distribution of mates, and the spatial and temporal distribution of resources will determine the potential for obtaining and defending those mates and resources. Further, the amount of parental care required by one or both parents to successfully raise offspring will affect the parent's energy allocation to either raise young or find additional mates. The mating system adopted by a particular animal group, in terms of the number of mating partners members of each sex typically acquire, depends on a combination of these factors and can lead to apparent conflict within and between the sexes for control over fertilization (Eberhard 1996; Birkhead & Møller 1998; Andersson & Simmons 2006).

In species where males can monopolize conspecific females or resources and there is little fitness benefit to helping raise offspring, a polygynous mating system is often seen (Emlen & Oring 1977; Rubenstein & Alcock 2019). Polygynous mating systems, in which males mate with multiple females, are common relative to cases of monogyny, where a male will mate with a single female over his lifetime. Monogyny is predicted if males can increase their fitness by investing more energy in the offspring of a single mate, given potentially low mate availability or resources (Emlen & Oring 1977; Rubenstein & Alcock 2019). In spider species where monogyny is

typical, mating is often coincident with unusual male behavior such as self-sacrifice.

Terminal investment strategies in spider species, such as sacrificing oneself as a meal to a mate, are hypothesized to arise from situations where males are unlikely to mate more than once due predominantly to a male-biased operational sex ratio (Fromhage et al. 2005; Schneider & Fromhage 2010). Male sacrifice refers to instances where males die or facilitate their own cannibalism by their female mating partner. For example, male *Argiope aurantia* Lucas, 1833, an orb-weaving spider, die spontaneously upon their second pedipalp insertion (Foellmer & Fairbairn 2003), as do male *Dolomedes tenebrosus* Hentz, 1844 upon their first insertion (Schwartz et al. 2013). Other examples include male behavior that allows easier cannibalism of the male by the female. For instance, male redback spiders, *Latrodectus hasseltii* Thorell, 1870, facilitate their own cannibalism by somersaulting into the mouthparts of females while *in copula* (Andrade 1996). Further, male *Argiope bruennichi* (Scopoli, 1772) modulate copulation length to either escape being eaten or to allow the female to consume them (Welke & Schneider 2010). Benefits of sexual cannibalism such as more offspring, increased paternity, offspring with increased survivorship, increased chances of offspring hatching, and shorter time to egg sac production, have been reported for a few different animals [*L. hasseltii*: Andrade 2003; *Dolomedes triton* (Walckenaer, 1837): Johnson 2001; the praying mantis *Tenodera sinensis* Saussure, 1871: Brown & Barry 2016; *D. tenebrosus*: Schwartz et al. 2016; *Pisaurina mira* (Walckenaer, 1837): Anderson & Hebets 2018], and are generally evoked to explain the evolution of such extreme behavior.

Coincident with the high male-biased sex ratio that is often associated with extreme mating systems is increased competition amongst males to find and locate the less common

females. Such competition for early access to mates is, in turn, often associated with species displaying smaller males and larger females, or sexual size dimorphism. Sexual size dimorphism (SSD) can be selected for, for example, in systems where early maturation of males results in higher chances of survival and finding a mate. Males thus forego future growth to instead search for females. In invertebrates, including spiders, such early male maturation is sometimes associated with male ‘dwarfism’ (Vollrath & Parker 1992; Andersson 1994; Vollrath 1998), or extraordinarily small males in comparison with females. Selection for increased fecundity, however, can also lead to exaggerated SSD. Larger females in a variety of invertebrate species, for example, have been shown to have higher fecundity than smaller females (Coddington et al. 1997; Higgins 2002). Exaggerated cases of SSD may be the result of the combined effects of selection on males for early maturation and selection on females for increased fecundity (Coddington et al. 1997; Hormiga et al. 2000). As well, exaggerated SSD is evolutionarily associated with extreme male-biased sex ratios and terminal investment strategies. Kuntner & Coddington (2020) refer to the correlation between extreme sexual phenotypes and extreme SSD as the eSSD mating syndrome.

Extreme sexual size dimorphism (eSSD) – where females of a species are at least twice the size of males – is found in a variety of spider species (reviewed in Kuntner & Coddington 2020). Across spiders, female biased eSSD is hypothesized to arise from diverse selection pressures and evolutionary pathways, with no single hypothesis sufficient to explain eSSD across spiders (Kuntner & Coddington 2020). For example, despite the common association between eSSD, male-biased sex ratios, and terminal investment strategies (i.e., the eSSD mating syndrome), there are species that exhibit eSSD that do not exhibit either of these other traits [e.g., *Misumena vatia* (Clerck, 1757); Holdsworth & Morse 2000]. Extreme female-biased SSD (eSSD) is also proposed to be an evolutionary dead-end as there is lack of species diversity in known eSSD clades (Kuntner & Coddington 2020). Given the likelihood that multiple pathways may lead to eSSD, it is necessary to understand selective pressures acting on size as well as reproductive behavior in individual species observed to exhibit eSSD, and their close relatives. The fishing spider *Dolomedes tenebrosus* (Family Pisauridae) is important in this context as it exhibits female-biased eSSD while most sister species do not.

The recent discovery of male monogyny in *D. tenebrosus* provides an excellent example of an eSSD mating syndrome: (i) early male maturation leading to a male-biased sex ratio, (ii) extreme female-biased SSD, and (iii) a terminal investment strategy involving spontaneous male death and subsequent cannibalism (Schwartz et al. 2013, 2016). In *D. tenebrosus*, males may also be cannibalized prior to mating, as females can be quite aggressive (Schwartz et al. 2014). Males that approach females wave their legs and tap her legs once within reach (Sierwald & Coddington 1988). When successful in acquiring a mating, seemingly coincident with the first pedipalp insertion, males curl up and hang unresponsively from the female’s genital opening. Shortly thereafter, the male dies – in 100% of observed matings – and the female consumes him (Schwartz et al. 2013). The consumption of the male by the female – as compared to the consumption of nothing or a size-matched

cricket – leads to an increased clutch size, offspring size, and offspring survivability in *D. tenebrosus* (Schwartz et al. 2016). Thus, *D. tenebrosus* females are aggressive, are much larger than the males, and the consumption of their mate (and ultimately his sacrifice) increases their collective fitness. The system fits well with existing hypotheses of extreme mating system evolution but does not allow us to disentangle the causes and consequences of these various correlated traits – e.g., SSD, mating system (i.e., the number of female and male mating partners), and operational sex ratio. Understanding this requires a comparative approach with knowledge of the mating systems, natural history, degree of SSD, and general natural histories of closely related species.

**Study System.**—Fishing spiders of the genus *Dolomedes* Latreille, 1804 are nocturnal sit-and-wait predators found on or near bodies of water and streams (Carico 1973). Of the nine described Nearctic species of the genus *Dolomedes* (Carico 1973), the mating behavior of only a few has been observed and reported. Across the few *Dolomedes* species studied to date, we see variation in male courtship behavior, risk of cannibalism, and the role of SSD in mediating female-male interactions. Below we provide a brief description of what is currently known about the mating system of two other *Dolomedes* species.

In *D. fimbriatus*, approaching males display leg waving and produce vibratory signals with their abdomen. Once physical contact is possible, they tap the female’s legs and abdomen (Arnqvist 1992). Female *D. fimbriatus* display high levels of aggression (but see Fisher & Price 2019), but relatively low cannibalism rates regardless of mating status. SSD predicts female aggressiveness in female-male pairings, with females being more likely to attack relatively smaller males (Arnqvist 1992; Kralj-Fisher et al. 2016). In terms of mating system dynamics, female *D. fimbriatus* do mate multiply (polyandrous). Males have been suggested to mate multiply as well (Kralj-Fisher et al. 2016) and tend to use only one of their two pedipalps (Arnqvist 1992), though these points remain to be tested empirically.

In *D. triton*, males approach the female similarly to *D. fimbriatus* and females may respond by creating vibrations with their legs or pedipalps on the water’s surface (Roland & Rovner 1983). Mating trials showed that virgin females attacked males 20–30% of the time before copulation and over 50% of the time after the first pedipalp insertion (Johnson 2001, 2005; Johnson & Sih 2005). These females successfully killed the male approximately 50% of the time (Johnson & Sih 2005) (but see Wojcicki 1992). Interestingly, *D. triton* females are less likely to attack males after a second insertion, when they do accept it (Johnson 2001). It appears the females have peak aggressiveness after accepting one insertion (Wojcicki 1992; Johnson 2001) then become much less aggressive after accepting a second (Johnson 2001). Other experiments have shown that male *D. triton* are polygynous during their reproductive lifetime but only use one pedipalp per female and do not attempt a second insertion with the same female (Wojcicki 1992).

Given the extreme behavior observed within the genus *Dolomedes*—e.g., extreme female aggressiveness including frequent female cannibalism of males before, during, and after copulation, and male self-sacrifice—this genus provides



an excellent system within which to study the evolution of mating systems and female-male mating dynamics. Here, we add comparative power to this system by exploring the previously undescribed mating interactions of *D. scriptus*. Previous descriptions and observations indicated that *D. scriptus* – congeneric to and sympatric with *D. tenebrosus* – are neither extremely sexually size dimorphic nor do they exhibit terminal investment (Carico 1973), making this species ideal for a first step to a comparative study.

*Dolomedes scriptus* are nocturnal fishing spiders that are part of the neuston – the organisms inhabiting the surface of bodies of water – of swift moving creeks and streams. In the area of our study, Lincoln (Nebraska USA), they are found in the same general habitat as *D. tenebrosus* but are more likely to be on the water's surface. We use repeated mating trials to describe and examine (i) the courtship of *D. scriptus*, (ii) the frequency of remating by females and males, (iii) the odds of female attacks and cannibalism, and (iv) the role of SSD in these interactions.

## METHODS

**Spider collection and maintenance.**—Female and male *D. scriptus* were collected from Salt Creek in Wilderness Park, Lincoln, Nebraska, USA from late April to early June 2017, as the weather permitted, between sundown and midnight. We collected most individuals as immatures, though some were mature at the time of capture. All spiders were housed in 87.3 × 87.3 × 112.7 mm plastic containers (763C, AMAC Plastics, Petaluma, CA, USA) and were kept on a 12:12 hour light:dark cycle. Females received two ~12 mm crickets (Ghann's cricket farm, GA, USA) three times per week. Males received two ~12 mm crickets twice per week, and all had access to water *ad libitum*. Most individuals consumed all the crickets they received at each feeding (Schoenberg pers. obs.). If crickets were still in the cage the following feeding, the feeding was modified so the spider had only two crickets at a time, e.g., if one cricket remained on a feeding day only one more cricket was introduced. All individuals were monitored for molts daily to determine the date of the final maturation molt. The final developmental stage was determined by the presence of proper epigynum or pedipalp morphologies (Carico 1973).

**Size dimorphism.**—Given that extreme SSD is often related to extreme reproductive behavior (Wilder & Rypstra 2008a; Wilder et al. 2009), we quantified the degree to which *D. scriptus* was sexually dimorphic. We recorded the cephalothorax widths (CW, a common measure of body size in spiders; Greenstone et al. 1985; Eberhard et al. 1998) for all females and males (Fig. 1). To obtain accurate measurements, we placed live individual spiders (or preserved spiders if they had previously died) into a petri-dish that rested on top of a graduated grid (mm). We photographed the spider using a Leica MZ16 microscope with a Diagnostic Instruments Inc. Spot Flex 15.2 64Mp digital camera. We subsequently used the program ImageJ (1.48v) to measure the widest cross section of the cephalothorax. We used the average of three measurements as our value for spider size. We used an Ohaus Adventurer Pro AV64 scale to weigh all the spiders prior to every trial as well. Focal individuals were thus weighed three times and the average of these measurements used in the analysis. The degree of sexual size dimorphism was determined



Figure 1.—Male *D. scriptus* with black bar showing location of cephalothorax measurement.

using both CW and mass. In addition to quantifying SSD in this species, we examined whether SSD in *D. scriptus* influenced copulation success and/or the likelihood of cannibalism (see Statistical analyses, below).

**Mating system.**—We conducted mating trials in the laboratory to observe and describe courtship behavior in *D. scriptus* as well as to determine whether female and/or male *D. scriptus* would re-mate, i.e., to determine their mating system.

To determine the presence/absence of female and male re-mating, we ran a total of 42 virgin females and 40 virgin males through a series of three mating trials. All mating trials were conducted 24 hours apart for three consecutive days. Ultimately, each focal female and male was paired with three different potential mating partners, all of whom were virgins. Thus, for female trials, we used a total of 168 spiders – 42 focal females and 126 partner males (42\*3). For male trials, we used a total of 40 virgin males and 120 partner females (40\*3).

Mating trials were conducted in 20.14 cm ht. x 19.05 cm diam covered plastic containers (250C, Pioneer Plastics, North Dixon, KY) with filter paper lining the arena floor. A plastic cylinder (85 mm ht. x 40 mm dia.) covered with fiberglass screen at the center of the arena and two strips of fiberglass screen mounted on opposed sides extended the full height of the arena and allowed the spiders to climb as needed. The arenas were cleaned with a 70% ethanol solution between trials and new filter paper was used for each trial. All mating trials were conducted from 15 June to 08 August 2017 and were initiated between 0920 and 1522h. Individuals were paired haphazardly and put through trials at least 15 days after their

final maturation molt. Females were 17 days to 54 days old and males were 27 days to 52 days old across all trials.

Females (regardless of whether they were focal females or potential mating partners) were given between 15 and 25 hours to deposit pheromone-laden silk in the arena prior to the start of all mating trials. This silk facilitated the initiation of courtship from males when they were eventually introduced. Females were also given two ~12 mm crickets as they were introduced to the arena to control for hunger and reduce the likelihood of hunger-motivated pre-copulatory sexual cannibalism. Any crickets remaining in the arena prior to the start of the trial were removed before starting the trial, with careful attention to avoid disturbing any silk the female may have deposited.

Males were introduced at the point furthest away from the female and the pair was observed for a minimum of 30 minutes after the silk-laying period. The trial was ended if the male did not court the female within 30 minutes. All other trials were left to continue until 5 minutes past copulation. The trial could also end if the male courted through to the end of the initial 30-minute period then walked away from the female for 5 minutes without copulating. If the male returned to the female within 5 minutes of walking away the trial continued, and the pair was left until copulation occurred. Trials were ended 5 minutes after the pair separated on their own to avoid post-copulation cannibalism due to proximity within the arena. We assumed that in nature, the male would have successfully moved away from the female within 5 minutes.

**Statistical analyses.**—To determine whether there is SSD in *D. scriptus*, we used Welch's t-tests to compare female and male *D. scriptus* size using CW and mass. We used the average values of our size measurements (3 per individual) in our analyses. The t-tests were conducted in JMP 14 (SAS Institute Inc).

To determine whether females and/or males mated with multiple partners, we calculated the number of females and males that mated one, two, or three times. Mating was determined by observing the proper mating positioning between the female-male pair (Carico 1973) and the expansion and deflation of the haematodochal sac of the male pedipalp.

To determine the extent to which SSD influenced mating success, we used generalized linear mixed models (GLMM) to explore predictor variables of mating success across all mating trials for both focal females and focal males. The mating success outcome was modeled as binomial (family = binomial in the `glmer()` function). The models' fixed effects included each focal individual's age, mass, the mating pair mass difference, and trial order. We included identification number as a random effect because focal individuals were used more than once. We then tested the significance of each fixed effect with the `Anova()` function in R version 4.0.3.

To determine how SSD influenced the number of mating successes that males were able to acquire, we used a logistic regression with the difference in mass as our independent variable and the occurrence of mating (y/n) as our dependent variable. This regression was performed in JMP 14 (SAS Institute Inc).

Ordinal logistic regressions were used to calculate how often females cannibalized males using only the female-focused trials. First, we used female mating status and average age

from the three-day trial period. Similarly, we ran a second statistical test with the addition of the females' average mass over the three-day trial period. Further logistic regression analyses exploring (i) female aggression, (ii) pre-copulatory cannibalism, and (iii) post copulatory cannibalism were also performed. These three tests used only first encounters across both female and male-focused trials in order to avoid pseudoreplication and confounding effects of prior experience. Female age and SSD of the mating pair were used as predictors for all three tests as well. We performed these analyses in JMP 14 (SAS Institute Inc).

We used two logistic regression models to determine whether SSD predicted (i) pre-copulatory cannibalism or (ii) post-copulatory cannibalism. The `Anova()` function was used to test the significance of the predictor for each model. This analysis was conducted in R version 4.0.3.

An ordinal logistic regression was used to test the effect of SSD on whether or not males completed one or two insertions with the same female. We used difference in mass as the independent variable and number of insertions as the dependent. Only first trials from both female and male-focused trials were used in the analysis. This was conducted in JMP 14 (SAS Institute Inc).

## RESULTS

**Sexual size dimorphism (SSD).**—Female *D. scriptus* had larger cephalothorax widths (CW) on average than males ( $t = 19.02$ ,  $df = 307$ ,  $P < 0.05$ ; Fig. 2). Across all females ( $n = 162$ ), the average CW was  $6.54 \text{ mm} \pm \text{SD } 0.78$ . Females ranged in CW from 4.44 mm to 8.85 mm. Average male CW ( $n = 166$ ) was  $5.05 \text{ mm} \pm \text{SD } 0.62$  with the males ranging from 3.81 mm to 7.52 mm. Using all mating pairs ( $n = 246$ ), the average female CW to male CW ratio was 1.30. Females also had more mass than males on average ( $t = 23.98$ ,  $df = 251$ ,  $P < 0.05$ ). The average mass of the females used in the trials ( $n = 162$ ) was  $0.55 \text{ g} \pm \text{SD } 0.15$  with a mass range from 0.20 g to 1.0 g. Male ( $n = 166$ ) mass averaged  $0.23 \text{ g} \pm \text{SD } 0.08$  and ranged from 0.09 g to 0.73 g.

Virgin females ( $n = 162$ ) were between 17 days and 54 days old (post-maturation) at the time of trials. Virgin males ( $n = 166$ ) were between 27 days to 52 days old (post-maturation) during trials. The largest difference in age between any pair during the trials was 22 days.

**Courtship behavior.**—*Dolomedes scriptus* males searched for the female upon detecting female silk draglines. While approaching, the male would tap the substrate with his first pair of legs, flexing the leg at the tarsal-metatarsal and metatarsal-tibial joints and keeping the rest of the leg stiff. No abdomen movements were observed during the male approach.

The female, most of the time, would be positioned vertically on the fiberglass screen facing downwards at the male's introduction. Once within reach of the female, the male would begin tapping the female's legs starting near the tarsi and moving toward the body. The male waved and tapped mostly with leg pair I but occasionally used leg pair II. Approach direction to the female was mostly from the side or posterior but could also be from the front. On occasion, the female responded to the male using the same leg waving behavior. She would then position herself on the screen before the male

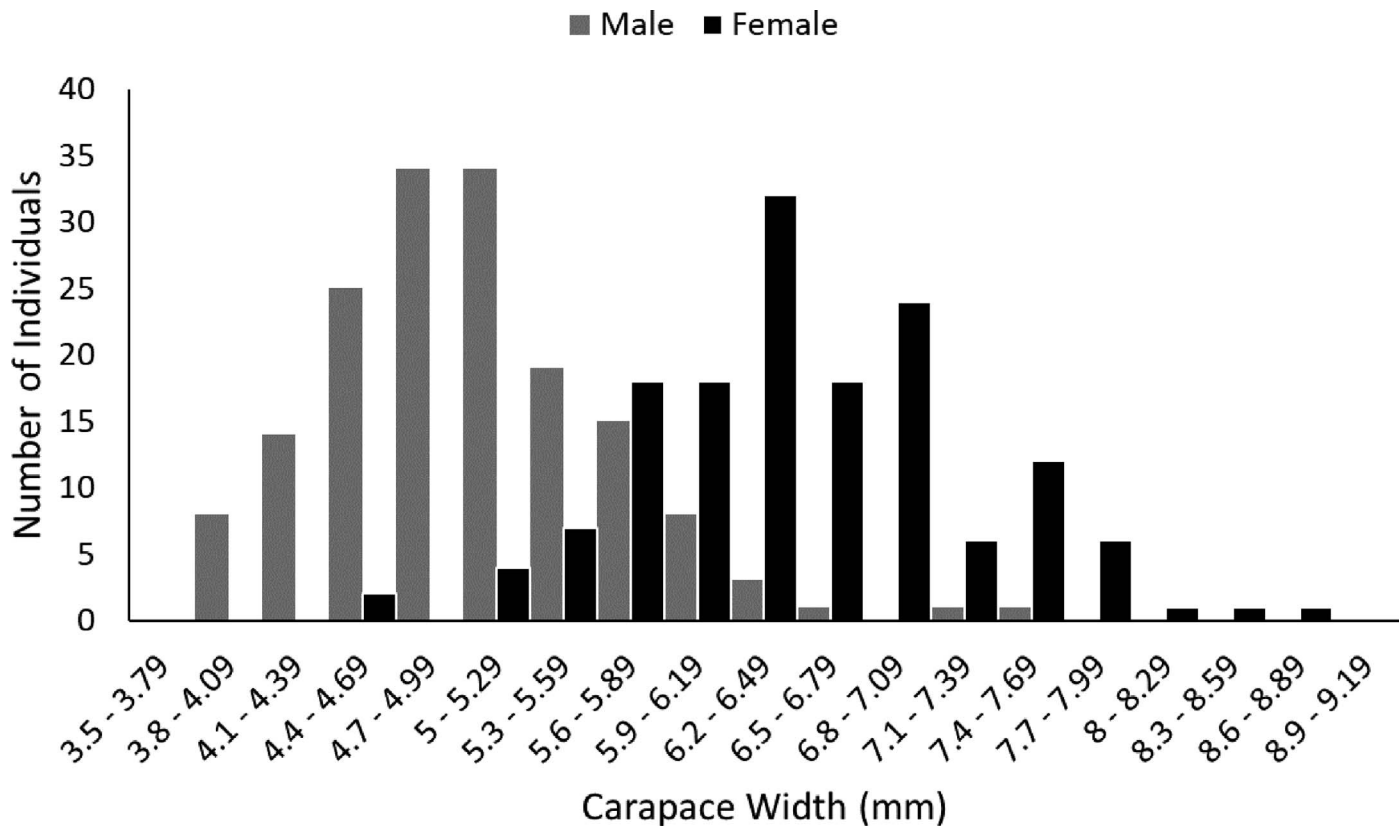


Figure 2.—Histogram of female ( $n = 162$ , black) and male ( $n = 166$ , grey) cephalothorax width (averages of three measurements per spider).

approached her, palpated her legs, and mounted. Female leg-waving did not appear to be necessary to the courtship but did occur somewhat frequently.

Once mounted, the male positioned himself on top of the female, facing the opposite direction of the female with his cephalothorax above her abdomen. He would then begin palpating the female's abdomen with his pedipalps and reaching around the female's abdomen between the females' legs III and IV, searching for her epigynum. This pedipalpal "searching" could happen multiple times before the male engaged with the female's epigynum and inserted his pedipalp. Just before male pedipalp insertion, the female would lift her legs up so that the femora of all four leg pairs were nearly perpendicular to the wall surface with a bend at the patellae, resulting in a 45 to 90 degree angle between each femur and patella. The remaining distal leg segments were held straight. The male would reach between the females' legs, as described in pedipalpal searching, then wrap his legs underneath the females' legs and pull them up further, holding them so her legs would be bundled together and perpendicular to the arena wall. He then reached to insert his embolus, using either his left palp for her left genital opening or his right for her right. Insertion duration averaged 11.23 seconds ( $n = 99$ ,  $SD = 18.65$ ), and could be as short as 2.25 seconds or as long as 135 seconds. During the male's insertion and presumed sperm transfer, the female remained motionless. Within a few seconds after the male completed the sperm transfer, the pair would separate extremely quickly. It was unclear as to whether

the male jumped away from the female or if the female reacted in a way that threw the male off.

**Mating system.**—*Females:* Sixty-nine percent of the focal females copulated ( $n = 29$  copulated), with the majority copulating on the first day (72%) and zero females copulating with more than one male (Fig. 3A).

Of the 29 males that copulated with our focal females, 22 (76%) acquired only one pedipalp insertion. The remaining seven (24%) were able to obtain two pedipalp insertions with the same female (Fig. 4). Each of these seven males used each pedipalp (left and right) once. Five of those males dismounted and remounted the female prior to their second insertion, while the remaining two were able to remain on the female to obtain the two insertions.

*Males:* Eighty-three percent of males copulated, with 38% to 58% of pairs copulating on each of the three days (Fig. 3B). Fifty-three percent of males copulated multiply ( $n = 33$  males copulated with multiple females) over a three-day trial period.

Twenty-seven of the 33 males that copulated (82%) acquired only one pedipalp insertion; the remaining six (18%) were able to obtain two pedipalp insertions with a single female (Fig. 4). Of these six males that obtained two insertions, one individual used the same pedipalp twice, but the remaining five males used each palp once. Additionally, five of those males dismounted and remounted while only one was able to remain on the female for both insertions.

Of the 87 copulations we observed, 74 males (85%) were able to acquire only one insertion and 13 (15%) were able to



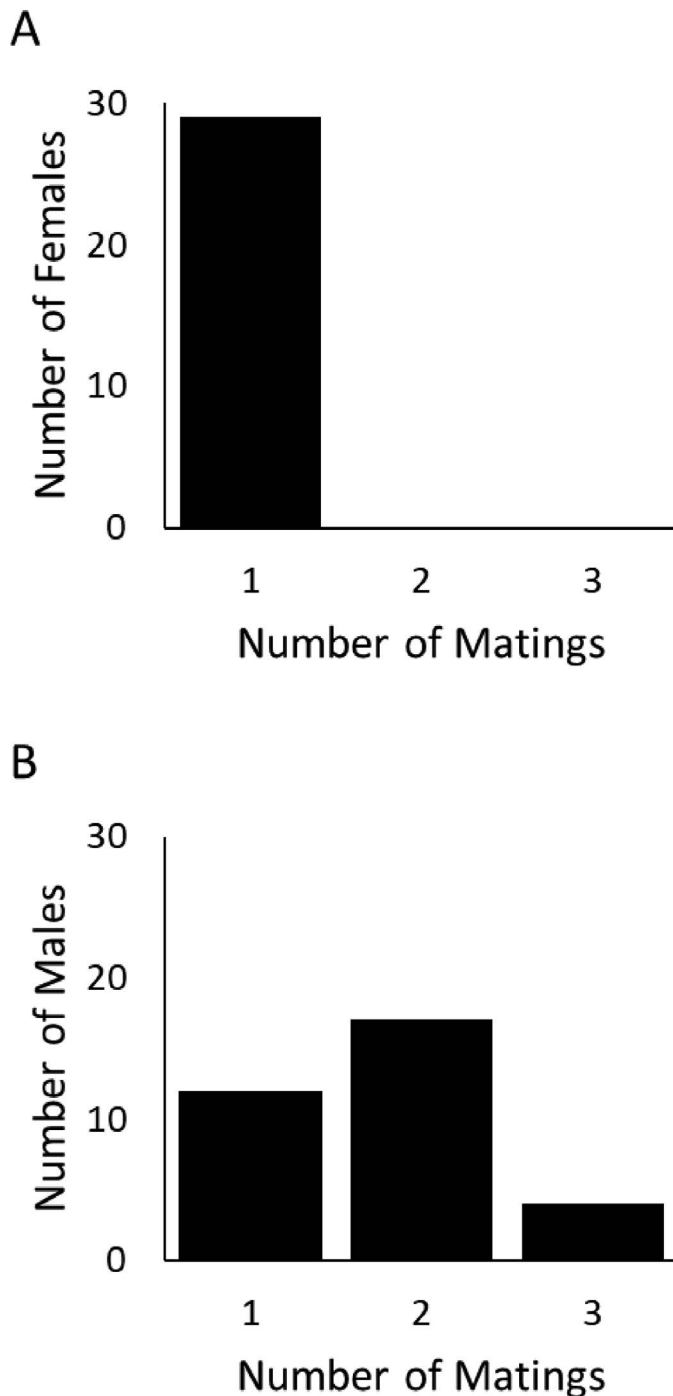


Figure 3.—Results of mating trials, including only trials in which at least one mating took place. (A) Focal females ( $n=42$ ) were offered a different potential mate on three consecutive days; no female mated more than once. (B) Focal males ( $n=40$ ) were offered a different potential mate on three consecutive days; most males mated with more than one female.

acquire two insertions. In the male-focused trials, all males that were able to get two insertions with the same female were also able to copulate with multiple females ( $n=6$ ). Of those that acquired two insertions across all trials ( $n=13$ ), only three males were able to remain on the female throughout the duration of the mating.

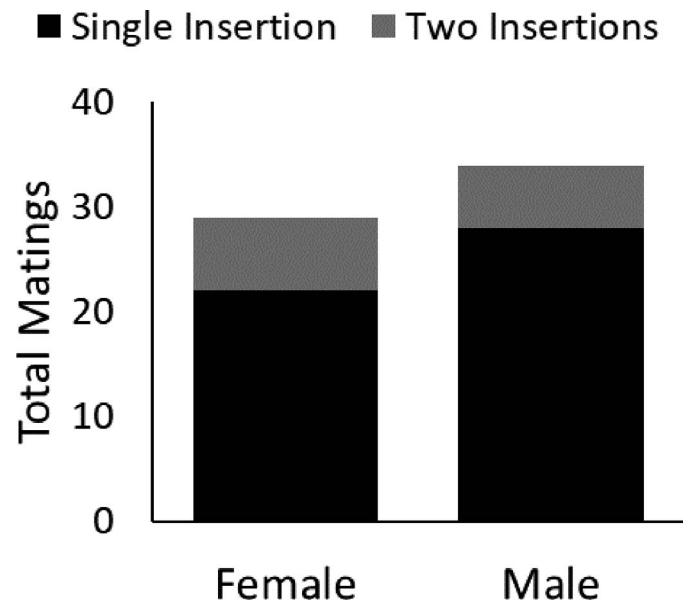


Figure 4.—Stacked graph showing number of insertions a single male made with any female irrespective of how many females the male mated with. Most male *D. scriptus* inserted a maximum of one time with any female while few inserted twice. Single (black) versus two (grey) insertions per focal sex. Female focus trials: single insertion ( $n=22$ ), two insertions ( $n=7$ ). Male focus trials: single insertions ( $n=28$ ), two insertions ( $n=6$ ).

**SSD and copulation success.—Females:** A generalized linear mixed model that explored the likelihood of copulation across all female-focused mating trials ( $n=126$ ) shows the difference in mass between the female and male pair predicted copulation success ( $\chi^2=7.363$ ,  $df=1$ ,  $P=0.007$ ) (Fig. 5A). Female age ( $\chi^2=0.025$ ,  $df=1$ ,  $P=0.875$ ), female mass ( $\chi^2=2.484$ ,  $df=1$ ,  $P=0.115$ ), and animal identification number as a random effect were also included in the model, but did not significantly influence the likelihood of copulation. Lastly, trial order was considered in the model and was statistically significant ( $\chi^2=17.506$ ,  $df=1$ ,  $P<0.001$ ). We do not expect this effect of trial order to be biologically significant, since it is a reflection of our finding that females only mated one time and most (72%) mated in the first trial (see Fig. 3A). Further experimentation exploring whether female *D. scriptus* are monogamous or polygamous will need to be conducted on a longer time scale to properly evaluate factors leading to copulation success.

**Males:** A generalized linear mixed model that explored the likelihood of copulation across all male-focused mating trials ( $n=120$ ) shows mass difference between the female and male of a pair predicts copulation success ( $\chi^2=9.39$ ,  $df=1$ ,  $P=0.002$ ) (Fig. 5B). Non-significant fixed effects included male age ( $\chi^2=0.01$ ,  $df=1$ ,  $P=0.917$ ), male mass ( $\chi^2=0.0569$ ,  $df=1$ ,  $P=0.450$ ), whether or not they had previously copulated ( $\chi^2=0.021$ ,  $df=1$ ,  $P=0.884$ ), and trial order ( $\chi^2=0.0004$ ,  $df=1$ ,  $P=0.985$ ). Animal identification number was used as a random effect.

Given that SSD, in terms of difference in mass between females and males, predicted mating success in both focal female and focal male mating trials, we combined trials to further test this effect. A logistic fit using the combined focal female and male datasets finds a significant influence of SSD

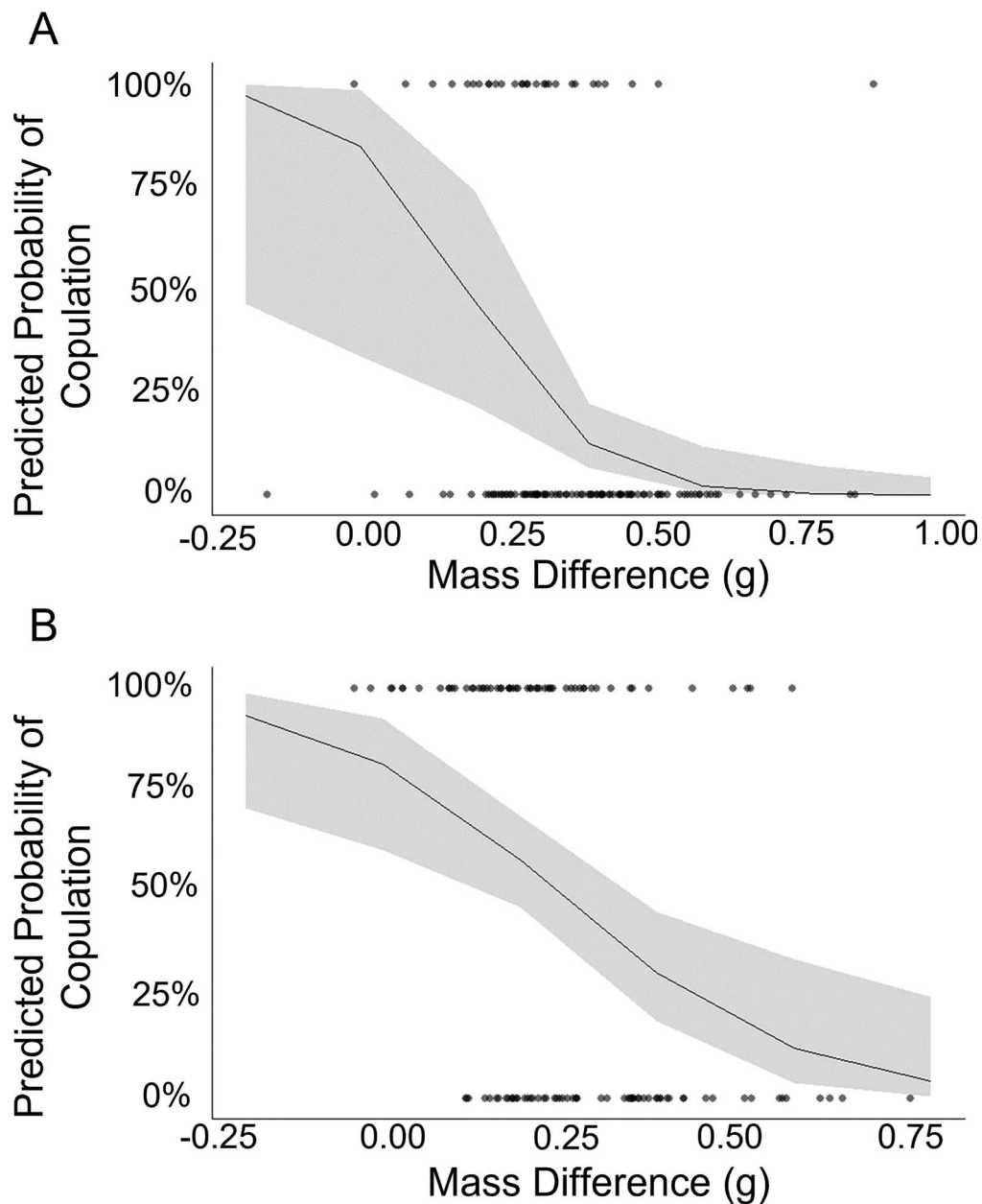


Figure 5.—Probability of copulation plots by difference in mass (g) using the data from (A) female- focused mating trials and (B) male-focused trials. The dots at top and bottom of each graph are the absolute differences in mass between the males and females of the pairs. The top dots are the pairs that mated, the bottom are the pairs that did not mate. Copulation is more likely when the individuals of the mating pair are more similarly sized.

on mating success, with an increased likelihood of mating for pairs that are similarly sized ( $\chi^2 = 38.77$ ,  $df = 1$ ,  $P < 0.001$ ,  $n = 246$ ).

An ordinal logistic regression testing whether SSD helps predict the number of insertions a male obtained across all first trials from both female- and male-focused trials ( $n = 82$ ) shows strong significance ( $\chi^2 = 20.91$ ,  $df = 1$ ,  $P < 0.001$ ), i.e., males in larger male to female ratio pairs are more likely to insert twice.

**Female aggression and sexual cannibalism.**—In the female trials (focal female  $n = 42$ , trial  $n = 126$ ) 79% percent ( $n = 100/126$ ) of the trials had a female attacking the male at least once.

Of the female trials in which the female attacked the male, 38% ( $n = 38/100$ ) ended in cannibalism. All 42 females used in the female mating trials attacked a male at least once. Twenty-five of 42 females (60%) cannibalized at least one male prior to copulation during the trials. The number of males a female cannibalized was dependent upon her mating status and not her age (Likelihood ratio Test:  $n = 42$ ,  $df = 1$ , mating status;  $\chi^2 = 6.66$ ,  $P = 0.009$ , female age;  $\chi^2 = 2.39$ ,  $P = 0.122$ ). A similar analysis also including female mass reduces the effect of mating status (Likelihood ratio test:  $n = 42$ ,  $df = 1$ , mating status;  $\chi^2 = 2.78$ ,  $P = 0.095$ , female age;  $\chi^2 = 6.69$ ,  $P = 0.010$ , female mass;  $\chi^2 = 5.79$ ,  $P = 0.016$ ) though this is probably due



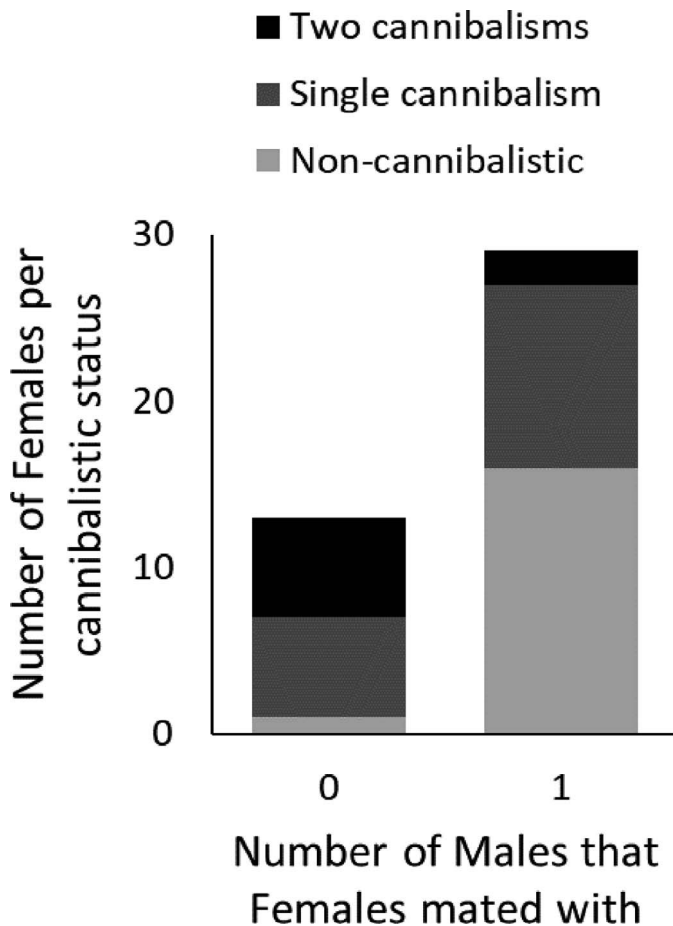


Figure 6.—Stacked graph of pre-copulatory cannibalistic and non-cannibalistic females by mating status, female-focused trials only. Virgin female *D. scriptus* are more likely to cannibalize males than non-virgin females. Black indicates two cannibalisms, dark grey indicates single cannibalisms, light grey indicates non-cannibalistic females. Virgin ( $n = 13$ ), non-virgin ( $n = 29$ ).

to the higher chances of similarly sized pairs mating (see Mating system and SSD and copulation success). Females that were unmated were more likely to cannibalize males than those that mated with one male (Fig. 6). Nine of 29 (31%) females cannibalized their male post-copulation.

Across all the male-focused trials, (focal male  $n = 40$ , trial  $n = 120$ ) 58% ( $n = 70/120$ ) of females attacked the male at least once. Of all the final trials in the male-focused trial sets where a female attacked ( $n = 20/40$ ), 20% ( $n = 4/20$ ) of the female attacks ended in cannibalism.

When we analyze the first day trials of both female and male trial sets together ( $n = 82$ ), female attacks were not predicted by the age of the female nor the SSD (logistic regression, female age:  $\chi^2 = 0.392$ ,  $df = 1$ ,  $P = 0.531$ ; SSD:  $\chi^2 = 1.035$ ,  $df = 1$ ,  $P = 0.309$ ). However, in analyzing pre-copulatory cannibalism, logistic regressions involving female age and SSD show SSD does predict the occurrence of cannibalism (female age:  $\chi^2 = 0.51$ ,  $df = 1$ ,  $P = 0.480$ ; SSD:  $\chi^2 = 27.56$ ,  $df = 1$ ,  $P < 0.0001$ ). Yet, when predicting post copulatory cannibalism with female age and SSD in a logistic regression, neither predict post-copulatory cannibalism (female age:  $\chi^2 = 3.04$ ,  $df = 1$ ,  $P = 0.081$ ; SSD:  $\chi^2 = 1.63$ ,  $df = 1$ ,  $P = 0.20$ ). To further

clarify these findings logistic regressions show SSD does predict the occurrence of cannibalism. Specifically, SSD predicts pre-copulatory cannibalism (Day 1 only  $\chi^2 = 27.07$ ,  $df = 1$ ,  $P < 0.001$ ,  $n = 82$ ) but does not predict post-copulatory cannibalism (Day 1 only  $\chi^2 = 1.26$ ,  $df = 1$ ,  $P = 0.263$ ,  $n = 82$ ) with larger females being more likely to cannibalize smaller males prior to copulation.

## DISCUSSION

*Dolomedes scriptus* spiders show female-biased sexual size dimorphism (SSD) – where females are larger than males and can be quite aggressive towards males. However, the SSD observed in *D. scriptus* is not “extreme”, i.e., males are not half the size of females or smaller (Hormiga et al. 2000; Kuntner & Coddington 2020). Similarly, our observed mating system was not “extreme”, in that we did not observe any terminal investment strategies employed by males. We did, however, see high levels of female aggression, with 60% of mating trials resulting in cannibalism prior to mating and with cannibalizing females more likely to attack smaller males (in pre-copulatory cannibalisms only). The courtship behavior of male *D. scriptus* appears generally similar to other known *Dolomedes* species (e.g., male leg waving and tapping of female) and this is consistent with the brief description provided by Carico (1973).

With respect to the mating system of *D. scriptus*, our results show that females only mate with a single male over a three-day period. In contrast, 53% of focal males mated with a second female over the same time, suggesting male polygyny. In addition to mating with a single male over our observation period, most females also received sperm from only one of the two male pedipalps. Only a small percentage of males—24% in female-focused trials and 18% in male-focused trials—were able to achieve two pedipalp insertions with a single female. Finally, though cannibalism was more likely to occur prior to mating (60% of all cannibalisms), post-copulatory sexual cannibalism was not uncommon (31% of matings). Interestingly, previously mated females were less likely to engage in pre-copulatory cannibalism on successive mating trials despite their unwillingness to engage in a second mating.

Female-biased SSD is not uncommon in spiders (Elgar 1992; Vollrath & Parker 1992). In many spider species, males are smaller than females but still of relatively similar size (Prenter et al. 1998), while in other species the sexes are significantly different in size. Within the genus *Dolomedes*, two species exhibit “extreme” SSD (Scharff & Coddington 1997; Hormiga et al. 2000). *Dolomedes tenebrosus* females weigh fourteen times more than males and have a cephalothorax width 2.5 times that of males (Schwartz et al. 2013). The cephalothorax length of *D. okefinokensis* is similarly 2.8 times that of males (Carico 1973). Nothing is currently known about the mating system of *D. okefinokensis*, but male *D. tenebrosus* are known to engage in a terminal investment strategy whereby males obligately die following their first pedipalp insertion and sperm transfer (Schwartz et al. 2013, 2014, 2016). In *D. tenebrosus*, females will mate multiply (polyandry) while males appear physiologically restricted to a single, terminal mating. Male terminal investment strategies are hypothesized to be favored when there is a male-biased sex ratio (Fromhage et al. 2005). In *D. tenebrosus*, there is an

evolutionary and functional link observed between female-biased eSSD and mating system form, specifically as it relates to male monogyny (Fromhage et al. 2005; Miller 2007; Schneider & Fromhage 2010). The female biased SSD in *D. scriptus* (this study) is not as extreme as that observed in *D. tenebrosus* or *D. okefinokensis*.

*Dolomedes scriptus* is moderately dimorphic with females 1.3 times larger than males by cephalothorax width (this study). This result is similar to the ratio reported by Carico (1973) – females are 1.17 times larger by cephalothorax length. Coincident with lower relative size dimorphism in *D. scriptus*, there does not appear to be a large sex-bias in the field (Schoenberg, pers. obs.). Furthermore, our mating system data demonstrate a system in which females are likely to mate once and males are likely to mate multiply. Thus, *D. scriptus* does not show extreme SSD and males do not engage in a terminal investment strategy. Nonetheless, the high level of female aggression in *D. scriptus* and the likely inability of most males to acquire two pedipalp insertions suggests that female aggression is likely influencing the evolution of mating systems in this genus.

Despite holding sperm in both pedipalps (Schoenberg, unpublished data), the majority of male *D. scriptus* were not able to use both sperm transfer organs during matings. An extremely rapid separation of the sexes following the first insertion was the most common outcome of matings. Immediately following this separation, females appeared highly aggressive towards males and in 31% of instances, females ultimately cannibalized the male. Such cannibalism associated with mating is not uncommon across spiders. In some species, such as the Australian redback spider (*Latrodectus hasseltii*), males actually facilitate their own cannibalism by somersaulting themselves towards the female's mouthparts (Andrade 1996, 2003). In other systems, however, we see the evolution of behavior that appears to function in avoiding cannibalism. In some spiders, this involves bringing food offerings that occupy the female (nuptial gifts: Toft & Albo 2016) while in others it involves seeming attempts to restrain females. For example, in the nursery web spider *Pisaurina mira*, males wrap females with silk during mating (Anderson & Hebets 2016). Scientists artificially ablated the male's ability to wrap the female and found that without wrapping, males were less likely to acquire two pedipalp insertions and more likely to be cannibalized by the female (Anderson & Hebets 2016, 2017). Thus, female aggression during mating is known to be a strong selective force on reproductive behavior and mating system dynamics in spiders. As mentioned previously, in *D. scriptus*, it appears as though female aggression is what limits a male's sperm transfer capacity.

The finding that females typically received sperm from a single male's single pedipalp raises questions about (i) the potential for sperm limitation in females and (ii) the role and/or importance of female mate choice. In terms of sperm limitation, it is unknown whether a single transfer of sperm in *D. scriptus* is sufficient to fertilize all of a female's eggs. In other spider systems, the number of sperm from a single pedipalp varies in whether it is enough to fertilize all eggs produced by the female. *Latrodectus hasseltii* males are able to fertilize all the eggs produced by a female in her lifetime with

one insertion (Andrade & Banta 2002) while females in other species require multiple matings to fill their spermathecae. In species that require multiple insertions, it may be because males only transfer a portion of their ejaculate during an insertion/copulation, the female terminates the copulation before the male can transfer all of his sperm, or the female spermatheca is so large that the male cannot fill it [*Trichonephila clavipes* (Linnaeus, 1767): Christenson 1989; *Micrathena gracilis* (Walckenaer, 1805): Bukowski & Christenson 1997; Ramos et al. 2005; *Trichonephila senegalensis* (Walckenaer, 1841): Schneider & Michalik 2011]. Future work on *D. scriptus* is now required to examine the costs and benefits of single versus double pedipalp insertions to females and males.

Regarding female choice, if females only mate with a single male throughout their lifetime, selection on mate choice may be high. It is possible that the high likelihood of pre-copulatory sexual cannibalism in *D. scriptus* reflects the means by which female *D. scriptus* exert mate choice. Indeed, females tended to cannibalize smaller males, consistent with cannibalism functioning in indirect mate choice (Prenter et al. 2006). Cannibalism as a form of mate choice has been proposed previously (Elgar & Nash 1988; Prenter et al. 2006; Kralj-Fišer et al. 2012). Evidence in other spider systems support this hypothesis with mixed results due to the difficulty of discerning the influences of morphological and behavioral characteristics on the possibility of cannibalizing a mate or being cannibalized (Persons & Uetz 2005; Prenter et al. 2006; Gavín-Centol et al. 2017). The fact that previously mated females are less likely to cannibalize subsequent suitors, however, is additionally consistent with the role of cannibalism as mate choice. For example, since these previously mated females are no longer assessing males as potential mates, they may be less likely to exert choice through cannibalism. Regardless, cannibalism is unlikely to be due to adaptive foraging (Newman & Elgar 1991), since mated females have higher nutrition needs due to their developing eggs (Wilder & Rypstra 2008b), yet they were less likely to cannibalize males.

Although none of the female *D. scriptus* accepted a second male across our three-day period, it remains possible that our time window was not wide enough. In *D. fimbriatus*, ~7% of females were observed to accept a second mating over a time window spanning 1 day to more than one week, with a median of 2 days (Kralj-Fišer et al. 2016). In *D. tenebrosus*, 50% of females will re-mate after 3 days (Schwartz et al. 2014). In order to confirm female monogamy, future studies should explore a longer time window for potential re-matings.

In summary, this study elucidates many details of the *D. scriptus* mating system while raising many new questions for future study. Our data reveal a mating system in which females likely acquire one mating and males acquire many, though they are often limited to a single pedipalp insertion per female. Furthermore, our data reveal that female aggression plays a large role in the mating system dynamics of *D. scriptus*. We suggest that female aggression is likely to be a major selective force in the genus more broadly, and a comparative approach to understanding the relationship between female aggression and mating system dynamics across *Dolomedes* may ultimately provide an understanding of the evolutionary pathways to terminal investment strategies.

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