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Spontaneous male death and monogyny in the dark fishing spider

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Abstract

Monogyny (male monogamy) is found in a diverse assemblage of taxa, and recent theoretical work reveals that a male-biased sex ratio can favour the evolution of this relatively rare mating system. We integrate this theoretical framework with field observations and laboratory experiments involving the sexually size dimorphic fishing spider, *Dolomedes tenebrosus*, to test the prediction that this species exhibits monogyny. Field surveys revealed a male-biased sex ratio, likely resulting from different life-history strategies (early male maturation). Results from mating trials supported our prediction of monogyny as we discovered that males mate with a single female. Unexpectedly, however, we observed that mating results in obligate male death and genital mutilation. Additional field observations of released individuals suggest that males are not limited by their ability to encounter additional females. Controlled laboratory assays demonstrated that males discriminate among virgin and non-virgin female silk cues, consistent with predictions of first-male sperm precedence. In summary, we report a novel case of male self-sacrifice in a species that exhibits female-biased sexual size dimorphism, male-biased sex ratio, genital mutilation and a suggestion of first-male sperm precedence; all of which are consistent with theoretical predictions of the evolution of monogyny.

Keywords: mating system, monogyny, self-sacrifice, sexual size dimorphism, sex ratio, sperm precedence

1. Introduction

Males of many animal taxa mate with multiple females, a phenomenon generally explained by the notion that male reproductive success is limited by the number of eggs they fertilize. Males can thus increase their reproductive success by indiscriminately mating with many females [1]. By contrast, females are thought to be limited by their ability to convert resources into eggs and, ultimately, into viable offspring. Females are thus predicted (and often observed) to mate less frequently than males and to be choosy about their mating partners [1–3]. While such patterns may be common in some animal groups such as mammals, males in other groups such as birds and fishes mate less frequently than expected; instead of mating with multiple females, these males enhance their reproductive success by caring for offspring, thereby trading offspring quantity for quality [4]. Surprisingly, males in some groups neither mate with multiple females nor in-

vest in paternal care, but instead invest in fertilizing the eggs of a single female [5]. This phenomenon, known as monogyny (male monogamy), is taxonomically widespread and has been shown to have numerous independent origins [5,6]. Its existence has provided a challenge to evolutionary biologists, as it is not initially apparent what benefits males might gain by foregoing additional matings.

Recent theory provides clear and straightforward predictions of the circumstances under which monogyny can evolve—monogyny is favoured over polygyny when there is a male-biased effective sex ratio [7], defined as the ratio between adult males and females that mate at least once. Furthermore, such male-biased sex ratios are suggested to arise in concert with female-biased sexual size dimorphism [5–7], as males in such systems often reach sexual maturation earlier and are more likely to survive to maturity [2,8,9]. Such life-history patterns have led scientists to predict an evolu-

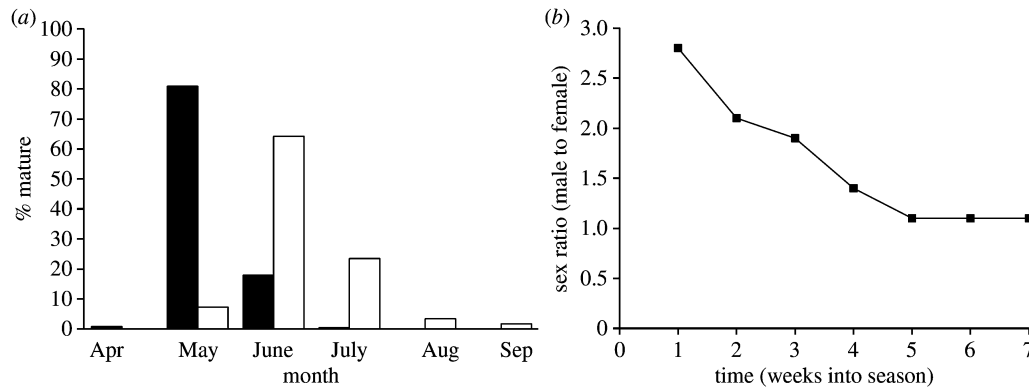


Figure 1. Male-biased sex ratio in *Dolomedes tenebrosus*. (a) Proportion of individuals collected (2006–2009) that reached maturity throughout the season (81% of males mature in May versus 7% of females). Closed bars represent males, and open bars represent females. (b) Ratio of males to females collected throughout the breeding season.

tionary correlation between female-biased sexual size dimorphisms, male-biased sex ratios and monogyny [5]. In addition, monogyny is often coincident with the evolution of extreme mating behavior (reviewed in [5]).

This study set out to test for monogyny in the dark fishing spider *Dolomedes tenebrosus* Hentz, 1843 (Araneae, Pisauridae), one of nine Nearctic species in the genus [10]. While females and males of most *Dolomedes* species are similarly sized, *D. tenebrosus* exhibits extreme female-biased sexual size dimorphism [11,12]: females weigh 14 times more than males and have cephalothoraxes that are 2.5 times as wide (see the Supplementary Figure S1). Like many spiders, *D. tenebrosus* live for 1–2 years, but the sexes appear to have different life-history strategies. Of hundreds of juveniles collected in the field and reared in the laboratory over a 4-year period, males always matured the same season, whereas females took an additional year to mature (S. K. Schwartz 2007–2010, personal observation). Additionally, within a season, males mature earlier than females (Figure 1a). These life-history differences are predictive of a male-biased sex ratio, a hypothesized prerequisite for the evolution of monogyny. This study aimed to examine the sex ratio in the field and to conduct laboratory assays to determine the mating system of *D. tenebrosus*.

2. Material and methods

We collected immature male and female *D. tenebrosus* over a 4-year period in Lancaster County near Lincoln, Nebraska and recorded the sex ratio and individual maturation times. Over 2 years, we ran mating trials in the laboratory to investigate mating system dynamics. Following our observation of obligate male death (see Results), we measured the postcopulation heartbeat of males. We also dissected the pedipalps (sperm transfer organs) of virgin males to determine whether *D. tenebrosus* males carry sperm in both their pedipalps. In the field, we monitored the mate search behavior of released males to determine the accessibility of multiple females. Finally, as monogyny is predicted to evolve in systems with first-male sperm precedence [5], we ran behavioral trials in the laboratory to test predictions of first-male sperm precedence by investigating whether males discriminate among virgin and non-virgin silk cues. For the details of our methods and data, see the electronic supplementary material.



Figure 2. Postcopulation the male hangs from the female's genital opening by the single pedipalp (circled) that he inserted during copulation.

3. Results and discussion

Field collections revealed that male *D. tenebrosus* outnumber females almost 3 : 1 at the beginning of the breeding season (Figure 1b), thus confirming a male-biased sex ratio. The mating behavior observed in the laboratory ($n = 24$) and once in the field was similar to that described previously [13] except that in every mating, instantaneous with the act of sperm transfer and with no apparent involvement by the female, the male's legs curled underneath its body and it hung motionless from the female's genital opening, appearing dead (Figure 2; electronic supplementary material, video S1). All males in this position were unresponsive to touch and never recovered from this immobile state. Observations of a subset of males ($n = 15$) confirmed that heartbeats stop within a few hours (164 ± 9 min; Supplementary Figure S2). Our results reveal a novel case of monogyny involving obligate male death.

Sperm transfer in spiders involves the inflation of the haematodochal bulb in the male pedipalp. Upon maturation, males ejaculate onto a sperm-web and subsequently pick up the sperm and carry them in their pedipalps [14]. The haematodochal bulb expands hydraulically due to an increase in haemolymph pressure and in most spiders, after sperm transfer, the bulb subsequently contracts. In *D. tenebrosus*,

the haematodochal bulb remains expanded (see Supplementary Figure S3) and presumably non-functional. This type of genital disfiguration is known to occur in only one other distantly related self-sacrificing species, *Tidarren sisypoides* [15]. Curiously, unlike *T. sisypoides* (which removes one pedipalp), *D. tenebrosus* males retain their second, unused pedipalp. We dissected both pedipalps of virgin males to determine the presence/absence of sperm. All males examined ($n = 5$) had sperm in both pedipalps, and although sperm numbers were not quantified, they appeared to be similar between the two. Thus, *D. tenebrosus* males may die “prematurely,” prior to realizing their full reproductive potential (*sensu* [16]).

Similar to the observed single palpal discharge of *D. tenebrosus*, males of another *Dolomedes* species discharge one pedipalp and immediately dismount their mate. In *Dolomedes triton*, few females accept a second insertion from the initial suitor and over half of the females observed attacked a male after accepting a single insertion [17]. Successful attacks by *D. triton* females are known to provide a reproductive advantage to both partners as females that successfully cannibalize their mate increase the likelihood that their egg sac will hatch [17]. Sexual cannibalism associated with self-sacrifice behavior in the Australian redback spider, *Latrodectus hasselti*, has similarly been considered adaptive [18]. Male *L. hasselti* who are successful at feeding themselves to females during mating receive two advantages over males who are not successful: (i) cannibalized males increase their paternity and (ii) females who cannibalize are less receptive to additional matings [18,19]. The occurrence of sexual cannibalism in *D. tenebrosus* was not examined in this study, and potential advantages from self-sacrifice to *D. tenebrosus* males have not yet been identified.

The pedipalps of *D. tenebrosus* are obligately disfigured during copulation, representing a form of genital mutilation. In a broad phylogenetic study of self-sacrifice behavior and genital mutilation across araneoid (web-building) spiders, self-sacrifice was hypothesized to have evolved at least five or six times in lineages with genital mutilation [6]. Given the obligate nature of premature self-sacrifice behavior and genital mutilation in *D. tenebrosus*, our data cannot address the evolutionary timeline regarding the origin of these traits. Nonetheless, Miller [6] suggested that when both genital mutilation and male-biased sex ratios are present, the stage is set for the evolution of adaptive male self-sacrifice behavior. Following from this, we hypothesize that early male maturation resulting in female-biased sexual size dimorphism in *D. tenebrosus* may have given rise to male-biased sex ratios, which set the stage for the evolution of monogyny in this species. We further suggest that the mechanism(s) underlying the genital mutilation and self-sacrifice are connected and that they evolved in concert.

High male mortality (80–92%) during mate searching has been suggested as an important factor influencing the evolution of monogyny in *L. hasselti* [18,20]. When the chance of encountering a second female is exceedingly small, males are expected to invest all of their resources in the first female they encounter [21]. Despite its likely role in the evolution of monogyny in the redback spider, theoretical explorations into the evolution of monogyny do not find high search

costs to be a necessary component [7]. Nonetheless, in order to determine whether high search costs may be a driving force in *D. tenebrosus*, we conducted field observation of released males. An astonishing 50 per cent found a female within 1 h of release (50 ± 9 min). In one extraordinary situation, a single male encountered five different females over a 94-min period, yet did not mate with any of them, suggesting a degree of choosiness in males. Finally, we observed no instances of predation and ultimately found no evidence of a high cost to mate searching in *D. tenebrosus*—supporting the theoretical findings that high search costs are not a necessary component of monogyny [7].

Given a male-biased sex ratio, it has been suggested that monogyny is likely to evolve in taxa with first-male sperm precedence [5]. While sperm precedence patterns are not known for many animal taxa, particular traits and behavior are often coincident with first-male sperm precedence, for example, early male maturation and precopulatory mate guarding [22]. Additionally, males in such systems are expected to exhibit a strong preference for virgin versus non-virgin females, as males will have an increased paternity share with the former [22]. While sperm precedence patterns in *D. tenebrosus* are not known, males in the related *D. triton* guard females prior to mating and both *D. triton* and *D. tenebrosus* exhibit early male maturation ([17] and this study)—observations that are consistent with first-male sperm precedence. In *D. tenebrosus*, we tested the prediction that males discriminate among females. In support of our prediction, when exposed to virgin and non-virgin silk, males spent significantly more time exploring an arena if it had silk from a virgin female (repeated measures ANOVA: $F_{1,14} = 51.42$, $p < 0.001$). All available data are consistent with the hypothesis that *D. tenebrosus* have first-male sperm precedence—a hypothesis that remains to be tested directly.

In summary, we document a novel case of monogyny involving an unusual form of male self-sacrifice—obligate male death. While monogyny and associated self-sacrifice behavior have been reported in a few other species (see the Supplementary Table S1), male *D. tenebrosus* die after a single act of sperm transfer with no apparent involvement from females. Additionally, while some classic unconventional mating systems are found in spiders, all prior examples come from araneoid spiders, where self-sacrifice is hypothesized to have evolved multiple times [6]. We provide the first full description of an extraordinary form of self-sacrifice behavior in a non-araneoid spider, providing an independent evolutionary test of hypotheses relating to the evolution of monogyny. In *D. tenebrosus*, this study provides multiple avenues of data consistent with prior studies that suggest evolutionary correlations between female-biased sexual size dimorphism, male-biased sex ratio, genital mutilation and first-male sperm precedence.

Acknowledgments — We thank the Lincoln Parks & Recreation Department for access and the University of Nebraska-Lincoln for financial support.

References

1. Bateman A. 1948 Intra-sexual selection in *Drosophila*. *Heredity* 2, 349–368. (doi:10.1038/hdy.1948.21)
2. Andersson M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
3. Trivers RL. 1972 *Parental investment and sexual selection*. In *Sexual selection and the descent of man 1871–1971* (ed. B Campbell), pp. 136–179. Chicago, IL: Aldine.
4. Clutton-Brock TH. 1991 *The evolution of parental care*. Princeton, NJ: Princeton University Press.
5. Schneider JM, Fromhage L. 2010 *Monogynous mating strategies in spiders*. In *Animal behaviour: evolution and mechanisms* (ed. PM Kappeler), pp. 441–464. Heidelberg, Germany: Springer.
6. Miller JA. 2007 Repeated evolution of male sacrifice behavior in spiders correlated with genital mutilation. *Evolution* 61, 1301–1315. (doi:10.1111/j.1558-5646.2007.00115.x)
7. Fromhage L, Elgar MA, Schneider JM. 2005 Faithful without care: the evolution of monogyny. *Evolution* 59, 1400–1405. (doi:10.1111/j.0014-3820.2005.tb01790.x)
8. Ghiselin MT. 1974 *The economy of nature and the evolution of sex*. Berkeley, CA: University of California Press.
9. Segev O, Ziv M, Lubin Y. 2003 The male mating system in a desert widow spider. *J. Arachnol.* 31, 379–393. (doi:10.1636/S01-101)
10. Carico JE. 1973 The Nearctic species of the genus *Dolomedes* (Araneae: Pisauridae). *Bull. Mus. Comp. Zool.* 144, 435–488.
11. Scharff N, Coddington JA. 1997 A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zool. J. Linn. Soc.* 120, 355–434. (doi:10.1111/j.1096-3642.1997.tb01281.x)
12. Hormiga G, Scharff N, Coddington JA. 2000 The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). *Syst. Biol.* 49, 435–462. (doi:10.1080/10635159950127330)
13. Sierwald P, Coddington JA. 1988 Functional aspects of the male palpal organ in *Dolomedes tenebrosus*, with notes on the mating behavior (Araneae, Pisauridae). *J. Arachnol.* 16, 262–265.
14. Foelix RF. 1996 *Biology of spiders*, 2nd edn. Oxford, NY: Oxford University Press.
15. Knoflach B, Benjamin SP. 2003 Mating without sexual cannibalism in *Tidarren sisyphoides* (Araneae, Theridiidae). *J. Arachnol.* 31, 445–448. (doi:10.1636/S02-56)
16. Stoltz JA, Elias DO, Andrade MCB. 2009 Male courtship effort determines female response to competing rivals in redback spiders. *Anim. Behav.* 77, 79–85. (doi:10.1016/j.anbehav.2008.09.012)
17. Johnson JC. 2001 Sexual cannibalism in fishing spiders (*Dolomedes triton*): an evaluation of two explanations for female aggression towards potential mates. *Anim. Behav.* 61, 905–914. (doi:10.1006/anbe.2000.1679)
18. Andrade MCB. 1996 Sexual selection for male sacrifice in the Australian redback spider. *Science* 271, 70–72. (doi:10.1126/science.271.5245.70)
19. Snow LSE, Andrade MCB. 2004 Pattern of sperm transfer in redback spiders: implications for sperm competition and male sacrifice. *Behav. Ecol.* 15, 785–792. (doi:10.1093/beheco/arh080)
20. Andrade MCB. 2003 Risky mate search and male self-sacrifice in redback spiders. *Behav. Ecol.* 14, 531–538. (doi:10.1093/beheco/arg015)
21. Buskirk RE, Frohlich C, Ross KG. 1984 The natural selection of sexual cannibalism. *Am. Nat.* 123, 612–625. (doi:10.1086/284227)
22. Elias DO, Andrade MCB, Kasumovic MM. 2011 Dynamic population structure and the evolution of spider mating systems. *Adv. Insect Physiol.* 41, 65–114. (doi:10.1016/B978-0-12-415919-8.00002-1)

Supplementary materials follow: Methods, Figures S1 & S2, Table S1, & References.

Data files in xls spreadsheet attached to html cover page.

Supplementary video online at: http://www.youtube.com/watch?v=8jAM9Uz3uN0&feature=player_embedded

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Methods

(a) Animal collections

Immature male and female spiders were collected during the spring (April-May) of 2006-2010 in Lancaster County near Lincoln, Nebraska (U.S.A.). Male and female *Dolomedes tenebrosus* were collected at night using a light-emitting diode (LED) headlamp. Night collection takes advantage of the eyeshine seen in *D. tenebrosus* (and other fishing spiders), which assists us to locate and capture the spiders in the field. Field caught individuals were transported back to the laboratory and housed individually in 87.3 mm x 87.3 mm x 112.7 mm plastic containers (763C, AMAC Plastics, Petaluma, CA). Containers were housed in a climate-controlled room (24-27° C) and placed on a light:dark cycle that matched the outside summer environment (April-August, 13:11-15:9 light:dark). Female spiders were fed two 2-week-old (1/4”) crickets, *Acheta domesticus*, three times a week and male spiders were fed two 1-week-old (1/8”) crickets, *A. domesticus*, once a week (Bassett's Cricket Ranch, Visalia, CA). In addition, all spiders were provided water *ad libitum*. 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.

(b) Mating trials

Staged mating trials were videotaped (Sony DCR-HC96 MiniDV Handycam) during the summer of 2006 ($n = 4$) and 2007 ($n = 20$). All individuals used were field caught virgins, which moulted to maturity in the laboratory (spiders are not sexually mature prior to their final moult). Mature male and female spiders were used only once during the mating trials. Males were assigned to females at random and females were

placed individually in a 252.4 mm x 90.5 mm (diameter x depth) plastic arena (250C, Pioneer Plastics, North Dixon, KY) for a minimum of 24 hours prior to the introduction of the male. The arena floor was covered with a disc of filter paper (Double Rings, 102 Qualitative, 24 cm) and at the center of the arena was a 47.6 mm x 84.1 mm plastic vial (40 DRAM, Thornton Plastics, Salt Lake City, UT) covered in fiberglass mesh on which the female could climb and position herself. On average, mating trials lasted 1.5 hours from the introduction of the male to the insertion of his first pedipalp. Video S1 (see the electronic supplementary material) shows one of the first mating trials from 2006.

(c) Heartbeat measurements

To determine when males died following mating, we measured the time from palpal insertion to the termination of the heartbeat postcopulation during the summer of 2007 ($n = 8$), 2009 ($n = 4$), and 2010 ($n = 3$). Only male spiders that were fully intact (i.e. males that had not been punctured by the female and/or damaged when removed from the mating arena) were used for heartbeat measurements. In order to measure the heartbeat, males were removed from the arena following the insertion of their first pedipalp and their heartbeat was monitored by counting the pulse rate of the abdomen (opisthosoma) every 15 minutes via stereo microscope (Leica M216, Buffalo Grove, IL) postcopulation until it terminated.

(d) Palpal dissections

In the summer of 2009 we removed and dissected the pedipalps of mature virgin male spiders ($n = 5$) to determine if *D. tenebrosus* males charge both of their pedipalps with sperm. Following a simplified method similar to Bukowski and Christenson [1], we removed the pedipalps of each male under a stereo microscope (Leica M216, Buffalo Grove, IL). The pedipalps were then crushed with metal forceps and placed on a microscope slide with a drop of water. Finally each pedipalp was viewed using a light microscope (Leica DM4000 B, Buffalo Grove, IL) and the presence or absence of sperm cells was recorded.

(e) Field monitoring

In the summer of 2010 we collected males from the field and held them in the laboratory until their maturity moult, at which time they were released in the field and their mate search behaviour was monitored. Following their maturity moult, male spiders were marked with a paint pen (DecoColor, Uchida of America, Torrance, CA) and returned to the field (to their original collection location) for observations. Over a series of nights, June-July 2010, male spiders ($n = 18$) were released at their initial collection points and monitored. By following individual male spiders throughout the night, we were able to quantify the probability of a *D. tenebrosus* male locating and contacting a *D. tenebrosus* female in the field.

(f) Silk trials

In the summer of 2009 we videotaped (Sony DCR-HC96 MiniDV Handycam) the behaviour of male spiders ($n = 15$) when presented with the silk from a virgin and a non-virgin female spider. Mature virgin and non-virgin female spiders were used only once during the silk trials and mature male spiders were used twice (repeated measures design). Female spiders were placed in an individual 252.4 mm x 90.5 mm (diameter x depth) plastic arena (250C, Pioneer Plastics, North Dixon, KY) which had the floor covered with a disc of filter paper (Double Rings, 102 Qualitative, 24 cm). Female spiders (virgin and non-virgin) then spent a minimum of 24 hours in the arena laying down silk. With the female spiders removed, male spiders were individually introduced into a silken arena. The order of the presentation (virgin vs. non-virgin silk) was randomized and males were presented with virgin or non-virgin silk a minimum of 24 hours apart. During the silk trials, we recorded male activity (i.e. time spent moving) and male courtship signals (visual and seismic) for a period of 15 minutes.

Figures and Table

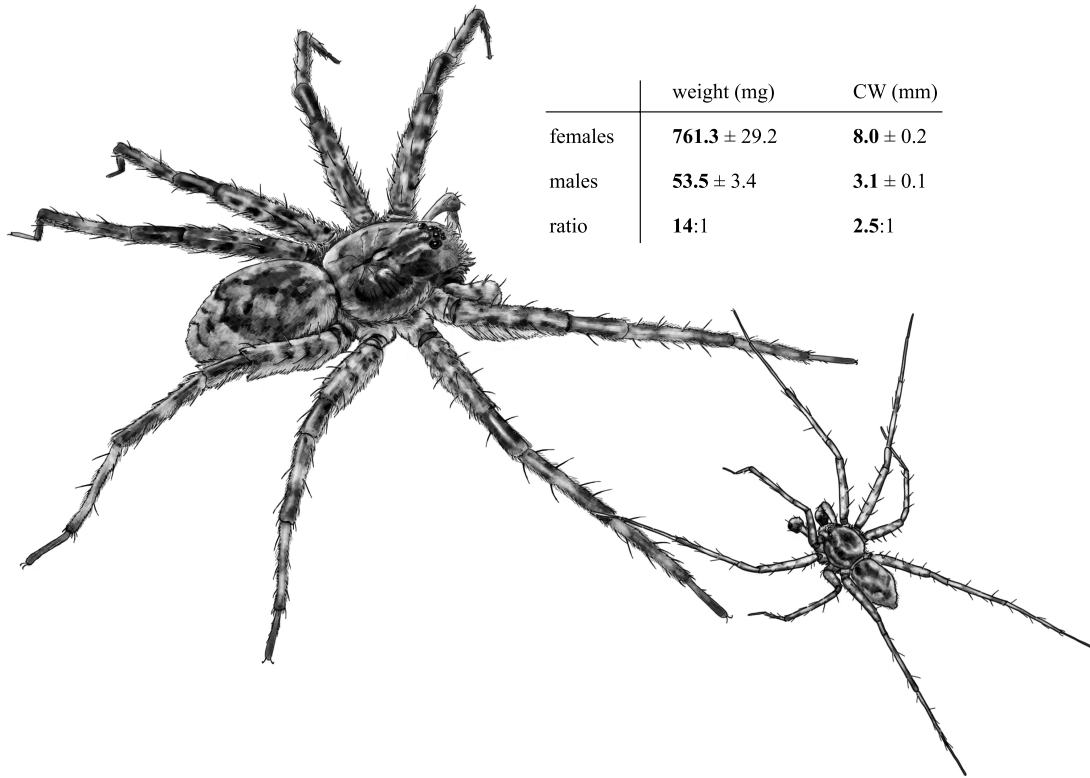


Figure S1. Female-biased sexual size dimorphism in the dark fishing spider, *Dolomedes tenebrosus*. Females ($n = 25$) weigh more than males and have wider cephalothoraxes (prosoma), measured in carapace width (CW), than males ($n = 25$). Data are mean \pm s.e. Image by Karina I. Helm.

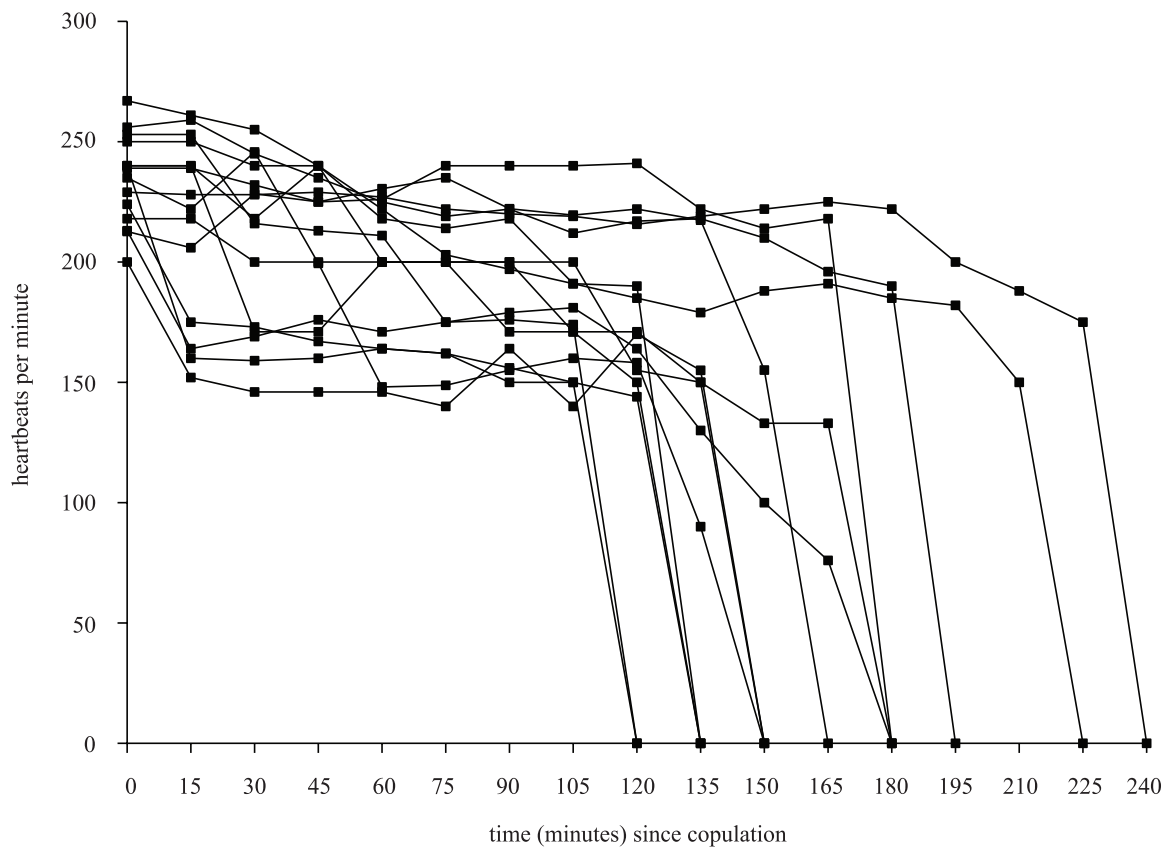


Figure S2. Changes in the heartbeat of males ($n = 15$) postcopulation. Following palpal insertion and expansion of the haematodochal bulb (i.e. copulation), the mean time to heartbeat cessation was 164 ± 9 minutes. Copulation in *Dolomedes tenebrosus* results in 100% male mortality.



Figure S3. The haematodochal bulb of the male postcopulation. In *Dolomedes tenebrosus* males the haematodochal bulb (*circled*) remains in the expanded state following copulation. Photograph by Steven K. Schwartz.

Table S1. The three published araneoid examples of self-sacrifice behaviour in the form of spontaneous death associated with copulation.

species	spontaneous death characteristics	reference
<i>Argiope aemula</i>	Male death is associated with the insertion of their second pedipalp.	Sasaki & Iwahashi [2]
<i>Argiope aurantia</i>	Male death is triggered by the insertion and inflation of the distal bulb of their second pedipalp.	Foellmer & Fairbairn [3]
<i>Tidarren sisypoides</i>	Male death is associated with the insertion of their first and only pedipalp (due to palp-amputation).	Knoflach & Benjamin [4]

References

1. Bukowski TC, Christenson TE. 1997 Determinants of sperm release and storage in a spiny orbweaving spider. *Anim. Behav.* **53**, 381–395.
2. Sasaki T, Iwahashi O. 1995 Sexual cannibalism in an orb-weaving spider *Argiope aemula*. *Anim. Behav.* **49**, 1119-1121.
3. Foellmer MW, Fairbairn DJ. 2003 Spontaneous male death during copulation in an orb-weaving spider. *Proc. R. Soc. Lond. B.* **270**, S183-S185.
4. Knoflach B, Benjamin SP. 2003 Mating without sexual cannibalism in *Tidarren sisypoides* (Araneae, Theridiidae). *J. Arachnol.* **31**, 445-448.