Spontaneous male death and monogyny in the dark fishing spider

Steven K. Schwartz, William E. Wagner Jr and Eileen A. Hebets

School of Biological Sciences, University of Nebraska – Lincoln, Lincoln, NE 68588, USA

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.

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 invest 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 evolutionary 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 behaviour (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 electronic supplementary material, 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 perquisite 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 behaviour 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 behavioural 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.

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 behaviour 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; electronic supplementary material, 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 the electronic supplementary material).
material, figure S3) and presumably non-functional. This type of genital disfigurement is known to occur in only one other distantly related self-sacrificing species, Tidarren sisyphoides [15]. Curiously, unlike T. sisyphoides (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 behaviour 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 pedipals of D. tenebrosus are obligately disfigured during copulation, representing a form of genital mutilation. In a broad phylogenetic study of self-sacrifice behaviour 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 behaviour 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 behaviour. 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 behaviour 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_{1,34} = 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 behaviour have been reported in a few other species (see the electronic supplementary material, 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 behaviour 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.

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References

5. Schneider JM, Fromhage L. 2010 Monogamous mating strategies in spiders. In Animal behaviour:


