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Males Can Benefit from Sexual Cannibalism Facilitated by Self-Sacrifice

Highlights

- Male self-sacrifice behavior is adaptive in the dark fishing spider
- Postcopulatory sexual cannibalism results in fecundity benefits for both sexes
- Cannibalized males benefit via increased offspring number, size, and survivorship
- Benefits result from the consumption of the male, not from an alternative prey item

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In Brief

Schwartz et al. show that obligate male death and subsequent sexual cannibalism in the dark fishing spider, *Dolomedes tenebrosus*, result in large and significant increases in the number, size, and survivorship of offspring. This empirical study provides support for the hypothesis that self-sacrifice behavior is adaptive via paternal effort.



Males Can Benefit from Sexual Cannibalism Facilitated by Self-Sacrifice

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SUMMARY

In a number of species, males are cannibalized by females after mating (reviewed in [1, 2]), and some males actually appear to facilitate their own cannibalism (reviewed in [3]). Such self-sacrifice can evolve if being eaten sufficiently enhances either fertilization success (mating effort) or offspring number or fitness (paternal effort). While there is some support for the mating-effort hypothesis, few studies have found support for paternal effort. We used two experiments to test the paternal-effort hypothesis in the dark fishing spider, *Dolomedes tenebrosus*. Males of this species provide themselves as a material contribution: they spontaneously die during copulation and are subsequently eaten by females. In support of the paternal-effort predictions, when females were allowed to consume their mating partner, we found large and significant increases in (1) the number, (2) the size, and (3) the survivorship of the offspring. Similar benefits were not seen when females were allowed to consume a cricket in lieu of a male, suggesting that it is the consumption of the male's body per se that is responsible for these fitness benefits. Together, our results suggest that *D. tenebrosus* males can benefit from self-sacrifice behavior through paternal effort. Such behavior may be particularly likely to evolve when high rates of postcopulatory cannibalism trap males into investing in their first mate instead of investing in acquiring additional matings and/or if strong first-male sperm precedence reduces the benefits of both investing in additional matings and paternity protection.

RESULTS AND DISCUSSION

Conflict between the sexes can occur when the mating decisions of individuals of one sex impose costs on individuals of the other sex [4, 5]. Males, for example, commonly evolve traits that increase their success in mating or sperm competition with other males, and many of these traits simultaneously impose costs on females. In response, females can evolve traits to miti-

gate these costs [6]. While less commonly studied, female reproductive traits can impose costs on males, like the killing and consumption of males during reproductive interactions. Such sexual cannibalism, which can occur prior to or following copulation, is rare within most animal groups, but in some taxa, such as gastropods, copepods, insects, and arachnids, sexual cannibalism is quite common (see [1, 7]). Males always benefit from avoiding cannibalism prior to mating and will usually benefit from avoiding cannibalism following mating, particularly when it allows them to acquire additional mates [8]. Indeed, males appear to have evolved a variety of counter-adaptations to sexual cannibalism, such as feigning death [9], sedating females [10], tying up females in silk [11], and providing nuptial gifts [12].

Surprisingly, males of some species, instead of resisting sexual cannibalism, actually appear to facilitate their own cannibalism by females [13, 14], resulting in a monogynous mating system (a mating system in which males mate with only one female but in which females may mate with more than one male). Early discussions surrounding the evolution of male complicity in cannibalism predicted that male self-sacrifice should evolve if being eaten enhances the number of offspring a male produces with their sole mate and if males have a low probability of surviving to find additional mates [8]. Under these conditions, males may benefit from investing maximally in the only female they are likely to mate with, including investing their soma (paternal effort; Table 1). A small number of subsequent studies failed to find evidence that postcopulatory cannibalism increases female fecundity (reviewed in [18]), although cannibalism does increase female fecundity in some non-sacrificing species (reviewed in [2] and see Table 1 in [19]). Because of the sparse evidence for the paternal-effort hypothesis, and because males in self-sacrificing species are almost always substantially smaller than females and thus unlikely to be a substantial energy resource [7, 20, 21], recent discussions have tended to focus on how self-sacrifice might evolve in response to sperm competition [3, 22, 23]. This focus has resulted in evidence that self-sacrifice increases male success in sperm competition in some species (mating effort; Table 1). However, given the limited number of relevant empirical tests, it seems premature to generally reject the paternal-effort hypothesis. First, males in a variety of non-cannibalistic taxa are known to provide nutritional resources that increase female fecundity [26], sometimes at a substantial cost to a male's future mating opportunities [27]. Second, males can invest limiting nutrients [28, 29] or defensive compounds [30] in females rather than energy. Thus, it may be irrelevant

Table 1. The Adaptive Male Sacrifice Hypotheses

Hypothesis	References
Paternal Effort	
The self-sacrificing male invests his somatic nutrients into his own offspring by:	[5, 7, 8, 15–17]
(1) Increasing offspring quantity	
(2) Increasing offspring quality	
Mating Effort	
The self-sacrificing male increases the proportion of eggs he fertilizes under sperm competition by:	[7, 13, 16, 17, 24, 25]
(1) Transferring more sperm	
(2) Reducing female receptivity	
Male self-sacrifice (complicity in cannibalism or spontaneous death associated with copulation) facilitates sexual cannibalism, resulting in reproductive benefits for the self-sacrificing male. Males can benefit from self-sacrifice via paternal effort or mating effort. Note that these hypotheses are not mutually exclusive.	

that males in self-sacrificing species are substantially smaller than females.

We tested whether males might receive benefits associated with increased offspring quantity and quality (i.e., paternal-effort hypothesis) through self-sacrifice in the sexually dimorphic dark fishing spider, *Dolomedes tenebrosus*. Male *D. tenebrosus* are 7%–13% the mass of females ([14]; this study) and exhibit an unusual mating strategy in which they appear to passively facilitate their own cannibalism: they obligately die upon sperm transfer and are subsequently cannibalized by their larger, female partner [14, 31]. Prior research has shown that the consumption of a male *D. tenebrosus* does not reduce the probability that a female will re-mate [31].

Across two experiments, in which females were allowed to consume their mating partner or were prevented from consuming their mating partner (experiment 1: cannibalism versus no cannibalism) or in which females were allowed to consume their partner, consume nothing, or consume a cricket (experiment 2: cannibalism versus no cannibalism versus cricket), we show that the obligate death and subsequent consumption of male *D. tenebrosus* leads to fitness benefits for both males and females. When allowed to cannibalize their mating partner, *D. tenebrosus* females produced nearly twice as many offspring (Figures 1A and 1D and Tables 2 and 3), produced offspring that were approximately 14%–20% larger (Figures 1B and 1E and Tables 2 and 3), and produced offspring that survived approximately 44%–63% longer compared to females that were prevented from cannibalizing their mates (Figures 1C and 1F and Tables 2 and 3).

Our results suggest that the fitness benefits associated with sexual cannibalism in *D. tenebrosus* result from the consumption of the male per se, not simply a prey item during a critical window postcopulation. Cannibalistic females produced more and larger spiderlings than females who consumed a cricket postcopulation (Figures 1D and 1E and Table 3), and the spiderlings of cannibalizing females survived significantly longer compared to either the no-cannibalism or cricket-treatment spiderlings (Figure 1F and Table 3). In addition, we did not find any correlations

between the number of spiderlings or spiderling mass with any of the other variables in experiment 1 (female mass, male mass; Table S1) or experiment 2 (female mass, male mass, cricket mass; Table S2). Although many studies across a diverse set of taxonomic groups have failed to find evidence of increased offspring quantity or quality due to precopulatory or postcopulatory sexual cannibalism (see Table 1 in [19]), results similar to ours have been observed in some mantids [19, 32] and some spiders [33–35]. For example, in the orb weaver *Argiope bruennichi*, males are 8%–14% the mass of females [34, 36, 37], and their consumption by females results in larger clutches, heavier eggs, and increased offspring survival [34]. However, unlike in *D. tenebrosus*, it is not clear whether *A. bruennichi* males exhibit self-sacrifice behavior (complicity in cannibalism or spontaneous death associated with copulation; see [21, 34, 37]) or whether the fitness benefits observed were the result of the consumption of a male, per se.

We found that *D. tenebrosus* females consumed a large portion of their partner's body: 87% of the male's mass (before trial: 92.5 ± 3.4 mg; after trial: 12.5 ± 1.1 mg; $n = 105$). Consumption estimates did not differ between males cannibalized prior to (0.87 ± 0.01 , $n = 47$) or following (0.87 ± 0.01 , $n = 58$) copulation (Mann-Whitney U test: $U = 1326.00$, $z = -0.239$, $p = 0.811$, $r = -0.023$). Although we did not calculate the proportion consumed for the crickets, our observed efficacy of male consumption is higher than that observed in other spiders (51% of a *Hogna helluo* male [38]). Prior work has suggested that the ratio of lipid to protein in male spiders, as compared to crickets, is not as consistent with the requirements of females for egg production [38]. Nonetheless, in the orb-weaving spider *Argiope keyserlingi*, the consumption of either a high-protein prey or a conspecific male resulted in increased egg energy density (kJ/g), which has been suggested to translate into enhanced offspring development and survivorship [39]. Quantifying lipid-to-protein ratios in male *D. tenebrosus* was beyond the scope of this study, but future work exploring the mechanism underlying the fitness benefits of male cannibalism are now needed.

Conclusions

In *D. tenebrosus*, males spontaneously die following mating and are inevitably cannibalized by their mates [14], thus limiting males to a single lifetime mating. Our previous results found that the consumption of the male does not reduce a female's probability of re-mating, so males do not appear to facilitate their own cannibalism in order to increase their success in mating or sperm competition [31]. However, it remains possible that spontaneous male death increases sperm transfer. Our current results show that the consumption of the male substantially increases female fecundity and offspring quality, so males may at least partially facilitate their own cannibalism in order to increase the number and quality of the offspring they produce.

Males do not simply provide the energy in their bodies to females. Females in our experiment were well fed prior to and following their mating trials, so the energy in a male's body made a relatively minor contribution to a female's energy budget. Furthermore, females that were allowed to eat their mate after mating showed substantially higher fecundity and offspring quality than females that were allowed to eat a male-sized cricket after mating. These results thus suggest that male bodies include

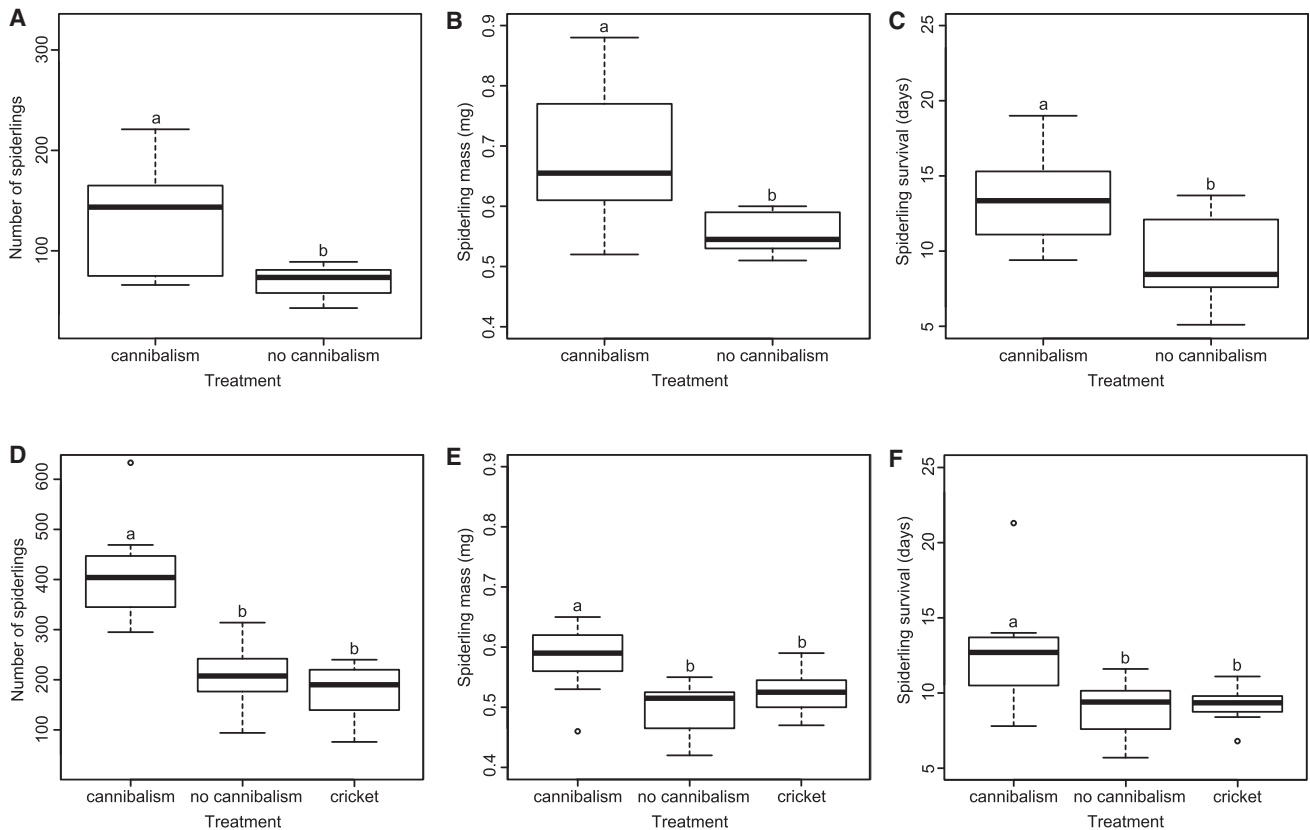


Figure 1. Spiderling Number, Size, and Survival

(Left column) Females that cannibalized their mating partner produced significantly more spiderlings than females that did not cannibalize; (A) experiment 1: cannibalism versus no cannibalism and (D) experiment 2: cannibalism versus no cannibalism versus cricket.

(Middle column) Females that cannibalized their mating partner produced significantly larger spiderlings than females that did not cannibalize; (B) experiment 1: cannibalism versus no cannibalism and (E) experiment 2: cannibalism versus no cannibalism versus cricket.

(Right column) Females that cannibalized their mating partner produced spiderlings that survived significantly longer than females that did not cannibalize; (C) experiment 1: cannibalism versus no cannibalism and (F) experiment 2: cannibalism versus no cannibalism versus cricket.

Spiderling numbers, size, and survival were also significantly increased for females that cannibalized than for females that consumed crickets (D–F). See Table 2 for statistical details of top row (A–C, cannibalism $n = 10$, no cannibalism $n = 6$) and Table 3 for bottom row (D–F, cannibalism $n = 9$, no cannibalism $n = 12$, cricket $n = 12$). Top row (A–C): different letters above boxes indicate a significant ($p < 0.05$) difference between medians. Bottom row (D–F): different letters above boxes indicate a significant ($p < 0.0167$) pairwise difference between medians. Box plots show median, interquartiles, and range (see also Tables S1 and S2).

limiting nutrients that are important for female egg production and offspring survival. We do not yet know what these limiting nutrients might be.

It is somewhat puzzling that *D. tenebrosus* males would show complicity in cannibalism in order to invest in offspring number and quality. First, males would appear to have substantial opportunities to mate with multiple females if they did not spontaneously die; male encounter rates with females are quite high under natural conditions [14], suggesting that the costs of searching for additional mates are low. Additionally, females will clearly mate with multiple males if given the opportunity [31]. Second, the adult sex ratio is strongly male biased [14], a scenario in which selection is expected to favor investment in paternity protection, not investment in females or offspring [22].

We suggest two non-mutually exclusive alternative explanations for monogyny and paternal investment in *D. tenebrosus*. First, high ancestral rates of postcopulatory cannibalism may have trapped males into investing in their first mate instead of investing in acquiring additional matings. If ancestral females were

highly successful in eating males after mating, then male investment in what was likely to have been their only mate may have been favored. In line with this hypothesis, in order to maximize the payoff of this investment, males may have evolved self-sacrifice behavior to ensure that their female mating partners eat them. Self-sacrifice, even if it results in just a small increase in the probability that a male will be eaten, would be favored by selection. Second, strong first-male sperm precedence may have obviated the benefits of investing in acquiring additional matings or in protecting paternity, making investment in offspring quantity and quality more advantageous. Given that additional mates are also likely to be previously mated, acquiring additional mates in a system with first-male sperm precedence would tend to yield relatively few extra offspring. Furthermore, when there is strong first-male sperm precedence, males do not need to invest in protecting paternity with their first mate, as long as their first mate is a virgin. Interestingly, male *D. tenebrosus* prefer virgin females to previously mated females [14], but sperm-precedence patterns have yet to be directly tested. While sperm-precedence patterns

Table 2. Experiment 1

Variables	Treatment		Test Statistic			Effect Size
	Cannibalism (n = 10)	No Cannibalism (n = 6)	U	z	p	r
Female mass (mg)	755 (670–875)	665 (529–830)	21.00	−0.976	0.368	−0.24
Male mass (mg)	92 (58–123)	49 (43–109)	15.00	−1.627	0.118	−0.41
Time to egg sac (days)	36 (16–77)	53 (26–95)	23.00	−0.761	0.492	−0.19
Time to hatching (days)	27 (25–30)	28 (25–30)	26.00	−0.439	0.713	−0.11
Number of spiderlings ^a	144 (74–174)	74 (54–83)	11.00	−2.061	0.042 ^a	−0.52
Spiderling mass ^a (mg)	0.66 (0.60–0.79)	0.55 (0.53–0.59)	7.00	−2.495	0.011 ^a	−0.62
Spiderling survival ^a (days)	13 (11–16)	8 (7–13)	10.00	−2.169	0.031 ^a	−0.54

Comparison between treatments in which *Dolomedes tenebrosus* females were and were not allowed to cannibalize their mating partner postcopulation. Values are medians and interquartile range. P values are from Mann-Whitney *U* tests (see also Figures 1A–1C and Table S1).

^aSignificant differences ($p < 0.05$).

alone do not help explain male self-sacrifice in *D. tenebrosus*, first-male sperm precedence may have facilitated the evolution of self-sacrifice and paternal investment in a system with high rates of postcopulatory sexual cannibalism.

EXPERIMENTAL PROCEDURES

Immature male and female *D. tenebrosus* were collected at night during April and May of 2010 (experiment 1: cannibalism versus no cannibalism) and 2013 (experiment 2: cannibalism versus no cannibalism versus cricket) in Lancaster County, Nebraska, USA. Details regarding spider housing, maintenance, and mating trials can be found in the Supplemental Information.

In experiment 1, we randomly assigned females to one of two treatments postcopulation: (1) cannibalism or (2) no cannibalism. For all females, regardless of the treatment, the curled body of the male was removed from the female. Immediately following the male's removal, females were provided

either (1) the same male's body (cannibalism) or (2) nothing (no cannibalism). The same protocol was used for experiment 2, with the addition of a third treatment, (3) cricket. Females in the cricket treatment were provided a freshly killed cricket approximately the mass of the removed male (± 3.1 mg). Males and crickets were provided to females using large forceps (30.5 cm), and all females readily accepted and consumed their postcopulation food item.

Following mating, females were maintained in their individual containers on a diet of two crickets three times per week with water ad libitum and monitored daily for egg sac production. When an egg sac hatched, all spiderlings were counted and two subsets of ten spiderlings were selected at random for additional measurements. The first subset was weighed together three times (Ohaus Explorer balance 0.0001 g), and the average mass was divided by 10 to obtain an approximated individual mass. The second subset was used in a survival assay. Spiderlings were placed in individual 60 × 15 mm plastic Petri dishes (Fisherbrand, ThermoFisher Scientific) with no food or water and monitored daily until death.

Table 3. Experiment 2

Variables	Treatment			Test Statistic			Effect Size
	Cannibalism (n = 9)	No Cannibalism (n = 12)	Cricket (n = 12)	H	df	p	
Female mass (mg)	775 (655–1192)	723 (656–985)	710 (584–825)	1.339	2	0.512	N/A
Male mass (mg)	90 (62–109)	73 (63–96)	69 (62–80)	1.150	2	0.563	N/A
Time to egg sac (days)	41 (36–57)	68 (37–100)	50 (34–66)	2.291	2	0.318	N/A
Time to hatching (days)	27 (26–29)	28 (27–30)	28 (27–32)	2.260	2	0.323	N/A
Number of spiderlings ^a	404 (324–458)	208 (175–243)	190 (131–222)	19.187	2	<0.001 ^a	N/A
Spiderling mass ^a (mg)	0.59 (0.55–0.63)	0.52 (0.46–0.53)	0.53 (0.50–0.55)	10.918	2	0.004 ^a	N/A
Spiderling survival ^a (days)	13 (10–14)	9 (8–10)	9 (9–10)	9.844	2	0.007 ^a	N/A
	Post Hoc Comparisons between Treatments			U	z	p	r
Number of spiderlings	cannibalism versus no cannibalism ^b			2.00	−3.695	<0.001 ^b	−0.81
	cannibalism versus cricket ^b			0.00	−3.838	<0.001 ^b	−0.84
	no cannibalism versus cricket			51.50	−1.184	0.242	−0.24
Spiderling mass (mg)	cannibalism versus no cannibalism ^b			11.50	−3.031	0.001 ^b	−0.66
	cannibalism versus cricket ^b			20.50	−2.386	0.015 ^b	−0.52
	no cannibalism versus cricket			48.50	−1.366	0.178	−0.28
Spiderling survival (days)	cannibalism versus no cannibalism ^b			14.50	−2.809	0.003 ^b	−0.61
	cannibalism versus cricket ^b			16.00	−2.701	0.006 ^b	−0.59
	no cannibalism versus cricket			69.00	−0.173	0.887	−0.04

Comparison between treatments in which *Dolomedes tenebrosus* females were allowed to consume their mating partner, nothing, or a cricket postcopulation. Values are medians and interquartile range.

^aSignificant differences ($p < 0.05$). P values are from Kruskal-Wallis tests.

^bSignificant differences ($p < 0.0167$). Bonferroni correction ($0.05/3 = 0.0167$). P values are from Mann-Whitney *U* tests (see also Figures 1D–1F and Table S2).

To determine the efficacy of male consumption, we used unpublished data from a previous study in which females were allowed to mate and cannibalize freely (see [31]), and we measured male mass (mg) before and after mating trials in which females cannibalized males. Dividing the postcannibalism mass by the live mass enabled us to calculate the proportion consumed.

We conducted all statistical tests using SPSS version 11.0 [40] and the R statistical software [41] version 3.1.2 with consultation from Zar [42], Field [43], and Field et al. [44]. Details of all statistical analyses can be found in the Supplemental Information.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and two tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.08.010>.

AUTHOR CONTRIBUTIONS

Conceptualization, S.K.S., W.E.W., and E.A.H.; Methodology, S.K.S., W.E.W., and E.A.H.; Investigation, S.K.S.; Formal Analysis, S.K.S.; Writing – Original Draft, S.K.S.; Writing – Review & Editing, S.K.S., W.E.W., and E.A.H.; Funding Acquisition, W.E.W. and E.A.H.

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