

The Role of Body Size in Mating Interactions of the Sexually Cannibalistic Fishing Spider *Dolomedes triton*

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Abstract

Some arachnids display extreme sexual size dimorphism (SSD) with adult females being several times larger than adult males. One explanation for SSD in species that exhibit pre-copulatory sexual cannibalism (female attack, kill and consumption of the male prior to mating) is that smaller males may be less likely victims of predatory attacks by females. However, in some sexually cannibalistic species SSD is relatively moderate (i.e. males are similar in size to females) suggesting benefits of large male body size. Here, I report the results of an experiment designed to explore the ramifications of body size in mating interactions of the sexually cannibalistic, North American fishing spider (*Dolomedes triton*). Results suggest that male size does not influence courtship behavior, the likelihood of being attacked, or the male's ability to secure a mounting. However, large males were superior at gaining copulations once mounted. Sexual cannibalism may also be predicated on female size. Female condition (mass/cephalothorax area) did not explain any of these behaviors from the copulatory sequence, however, females with a smaller cephalothorax area were more likely to attack courting males. Finally, analysis of the ratio of female size to male size showed that when SSD is weak males are more likely to escape attacks and mate successfully. Results are discussed in light of several hypotheses for sexual cannibalism, and the benefits of large male body size illustrated here are put forth as potential explanations for the relatively moderate extent of SSD found in this sexually cannibalistic species.

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Introduction

The striking disparity in adult body size between males and females of many species (i.e. sexual size dimorphism: SSD) has inspired a wealth of explanations

(reviewed in Andersson 1994), and continues to be an active area of inquiry in a wide variety of taxa (anurans: Monnet & Cherry 2002; Cox et al. 2003; birds: Kissner et al. 2003; mammals: Kennedy et al. 2003; and arthropods: see references below). Spiders are one group in which SSD is often extreme with adult females of some species being 10 times larger than adult males (Elgar et al. 1990; Elgar 1992). Recently, the extreme SSD found in some spider taxa has been the topic of a debate between models positing selective benefits for 'dwarf males' (Vollrath & Parker 1992, 1997), and others noting the fecundity benefits of being a 'giant female' (Head 1995; Prenter et al. 1998, 1999; Hormiga et al. 2000).

The 'dwarf-male' model suggests that extreme SSD is frequently observed in arachnid systems because females are generally sedentary relative to males that experience high mortality through mate searching. This male-biased mortality will shift the operational sex ratio in favor of females. Such a shift should result in a scramble competition (Thornhill & Alcock 1983) for relatively abundant females, rather than direct competition between males for access to a limited number of females. Under these circumstances, sexual selection on males should favor early maturation (protandry) and small male size, rather than the large male body size typically favored when males compete directly, sometimes physically battling each other for females. In contrast, the 'giant female' models argue that, across species, fecundity selection and variation in female size best explain the extent of SSD, whereas variation in male size often shows little effect on SSD (Prenter et al. 1999; Hormiga et al. 2000). In addition, proponents of the latter model point out that life-history comparisons do not support the dwarf-male model when they are corrected for phylogenetic relatedness (Prenter et al. 1998).

The extent of SSD within any given species, however, should reflect selection acting on both male size and female size. In addition, body size within each sex will most often be the net result of a multitude of conflicting selection forces that sometimes favor drastically different optimal body sizes. Thus, realistic, taxon-specific selection pressures on body size (in both directions and for both sexes) need to be considered on top of these types of general models to fully understand SSD. One factor suggested to select for small male body size in a subset of spider taxa is the risk of pre-copulatory sexual cannibalism (i.e. female attack, kill and consumption of the male prior to mating). Cambridge (1871), Darwin (1871) and later Robinson & Robinson (1980), suggested that small male spiders would benefit if their small size makes them less likely prey items for the female. This benefit could arise in one of two ways: smaller males may escape the notice of predatory females, or females may refuse to prey on diminutive males if they are inadequate prey items (Elgar 1992; Elgar & Fahey 1996).

Regardless of the exact mechanism, this hypothesis predicts that smaller males will avoid pre-copulatory sexual cannibalism, and should subsequently secure more matings and sire more offspring relative to larger males. However, contrary to this idea, SSD is much less pronounced in some species where females commonly attack males upon courtship (Elgar & Nash 1988). Thus, despite a high risk of pre-copulatory sexual cannibalism, some male spiders do not show an extreme reduction in body size.

Several factors may favor large male size, and thus reduced SSD, despite the risk of pre-copulatory sexual cannibalism. First, large body size is generally associated with increased foraging success in arachnids (Vollrath 1987). For example, large juvenile males may have higher prey capture rates leading to growth/survival benefits. This benefit should be accentuated in cannibalistic systems where larger juveniles commonly feed on the smaller members of their cohort. Thus, larger juvenile males will have access to more prey items (both hetero-specific and con-specific), and will also be subject to fewer con-specific predators. Secondly, in systems characterized by direct male–male competition, sexual selection may favor large males that out-compete smaller males for access to females. Elgar & Fahey (1996) show such a benefit in the highly size dimorphic orb-web spider *Nephila plumipes*. In this species, selection to avoid sexual cannibalism favors small males, whereas male–male competition favors large male body size. The result in this species is a great deal of variation in male body size. Third, large male size may actually be adaptive in terms of pre-copulatory sexual cannibalism if large size is associated with increased escape success. Indeed, several studies addressing the relation between male size and pre-copulatory attacks have found a large-male escape advantage (Arnqvist 1992; Arnqvist & Henriksson 1997; Johnson 2001). Finally, when the above benefits of male size exist, females may derive an indirect genetic benefit by mating with large males and/or rejecting/attacking small males (Elgar & Nash 1988).

Study System

Here, I explore the ramifications of male body size in the sexually cannibalistic North American fishing spider *Dolomedes triton* (Araneae; Pisauridae). Fishing spiders are relatively large, cursorial ambush predators most commonly associated with the edges of aquatic habitat. The natural history (Carico 1973), sensory ecology (Bleckmann & Barth 1984; Bleckmann & Lotz 1987), population ecology (Zimmerman & Spence 1989, 1992) and behavioral ecology (Johnson 2001; Kreiter & Wise 2001) of *D. triton* have been well documented previously. In terms of sexual cannibalism, adult female *D. triton* routinely attack males at any point during the courtship-copulation sequence. Experimental mating trials indicate that pre-copulatory attacks by virgin females occur in approx. 20–30% of pairings, and these attacks are successful up to 40% of the time (Johnson 2001; Johnson unpubl. data). In addition, field studies of *D. triton* suggest that males represent a common contribution to the adult female diet (Zimmerman & Spence 1989), and that male population density declines drastically, soon after adult female emergence (Zimmerman & Spence 1992). Thus, sexual cannibalism appears to play an important role in the ecology of *D. triton*.

The family Pisauridae is one of only two spider families in which pre-copulatory sexual cannibalism is known to be frequent (see Table 7.4 in Elgar 1992). Orb-web building spiders from the family Araneidae, perhaps the family most frequently associated with pre-copulatory sexual cannibalism, are also the most sexually dimorphic group of spiders (see Fig. 3b in Vollrath & Parker 1992

for a graphical comparison of SSD between Araneids and Pisaurids/Lycosids). In contrast, adult female *D. triton* are typically only 1.28–1.34 times the size of adult males (Carico 1973; Johnson unpublished data). Thus, fishing spiders offer the opportunity to examine an exception to the rule that SSD should be extreme in spiders that commonly display pre-copulatory sexual cannibalism. Here I ask the question: why are male *D. triton* relatively large when they run a substantial risk of pre-copulatory attacks? Specifically, I examine the ramifications of male body size throughout the courtship-copulation sequence to see if this sexually cannibalistic mating system favors either extreme in adult body size.

Methods

One hundred-twenty males in their final juvenile molt were collected in Apr., 2001 from a single pond in Central Kentucky. Males were maintained in the laboratory for 2 wk in individual 425 ml. transparent, plastic cups. Each cup was partially filled with water and provided with a Styrofoam float (2.0 × 1.5 × 0.5 cm.). During this holding period males were fed weekly one juvenile house cricket, *Acheta domesticus*, weighing approximately three-fourth of the spider's body mass.

Body size was estimated in the present study as each adult's cephalothorax area. This measure is often termed fixed adult size because dimensions of the cephalothorax are set for life at the adult molt in the majority of spiders (Vollrath 1987). Digital images were taken while each spider floated motionless in a cup of water. Image components (e.g. amount of water in the cup, distance of camera from spider etc.) were standardized and each day the imaging set-up was calibrated by imaging a piece of floating graph paper (2 × 2 cm). Images were later digitized providing measures of the length and width of the cephalothorax. From these measures I calculated the area of the cephalothorax as the area of an ellipse [$=\pi \times (\text{cephalothorax width}/2) \times (\text{cephalothorax length}/2)$]. Adult males were categorized according to their cephalothorax area as either 'large' (top one-third of the population size distribution, $n = 40$), 'intermediate' (middle one-third of the population size distribution, $n = 40$), or 'small' (bottom one-third of the population size distribution, $n = 40$). Individuals in the intermediate size class were returned to the field and the large and small males were included in the experiment. In addition, males were weighed to the nearest milligram weekly and immediately prior to each mating trial.

Females in the final molt before adulthood ($n = 33$) were collected from the same population in mid-May, 2001, weighed, imaged and maintained outdoors in individual, large (60 × 41 × 16 cm.), transparent, plastic containers. These containers were filled with water to a depth of 2.0 cm. and each contained a large Styrofoam float (10 × 6.0 × 0.5 cm). Females were fed one adult cricket three times per week until they reached their adult molt. This food regime has been used previously (Johnson 2001), and has proven to promote successful reproduction. Two days following their adult molt females were fed one adult cricket. Two days following this feeding, females had their first mating trial.

Males were randomly chosen from each size group to be used in the experiment and no male was used more than once. Males were introduced to the female's container as far from the female as possible. Females experienced a sequential pair of mating trials in which the size class of male offered was alternated daily (i.e. small-large, $n = 16$ or large-small, $n = 17$). Males not initiating courtship within 15 min of introduction to the container were replaced with a male of the same size class. I then observed mating trials for 90 min recording the occurrence of (1) male courtship (defined as characteristic leg waving and/or tapping the water or solid substrate), (2) female pre-copulatory attack, or (3) male mounting, (4) mating, and (5) female post-copulatory attack.

Statistical Analyses

Traditional chi-square analyses were used to examine differences in the likelihood of a behavior occurring across groups. In addition, the effect of male size class manipulation is analyzed with McNemar's test for significance of changes (see Sokal & Rohlf 1995, p.779). This analysis allows for the repeated testing of the same individuals and is designed to indicate whether or not the independent variable (here, the size of male presented) is responsible for a change in behavior across the paired trials. For example, the test indicates whether or not a change in female behavior across trials (e.g. attack small male, but do not attack large male) is more or less prevalent than the reverse (attack large male, but do not attack small male). Thus, the null hypothesis that the frequencies of the two types of behavioral changes are equal is tested. In addition, multiple logistic regression was used to simultaneously account for several male and female size variables in a further attempt to understand these behaviors.

Results

This population of fishing spiders exhibits a substantial amount of variation in both adult male body mass and cephalothorax area (reported as $\bar{x} \pm SE$), and these factors are highly correlated with each other (see diamond symbols in Fig. 1). Six males (one small and five large) died before females matured and mating trials could be run. Of the males available to be used in the experiment, small males ($n = 39$) weighed 141.37 ± 5.39 mg. and had a cephalothorax area of 0.163 ± 0.004 cm². In contrast, males from the largest one-third of the population size distribution ($n = 35$) weighed 314.68 ± 9.02 mg. and had a cephalothorax area of 0.304 ± 0.007 cm². For both measures this difference is statistically significant (mass: $t = 17.23$, $df = 72$, $p < 0.0001$; cephalothorax area: $t = 18.38$, $df = 72$, $p < 0.0001$).

The Effect of Male-Size Class

Males typically began courting within the first 5 min of a pairing and male size class did not influence the likelihood of courtship behavior ($\chi^2 = 0.95$, $df = 1$,

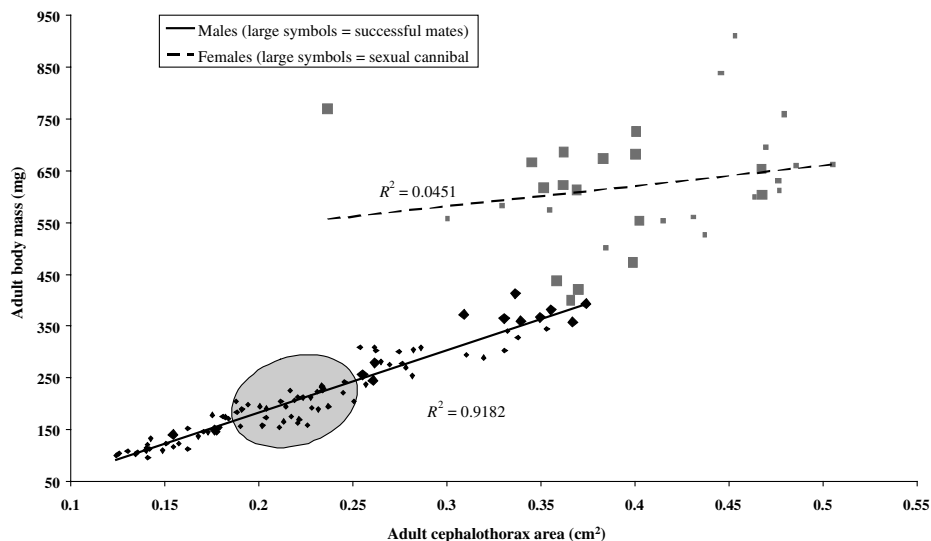


Fig. 1: Population size distribution of male (solid line, diamond symbols) and female (dashed line, square symbols) *Dolomedes triton* sampled in this experiment. Males from the intermediate one-third of the population size distribution (within shaded circle) were not used in the experiment

$p = 0.33$). The sequence of male-size class experienced by females (small-large, $n = 16$ vs. large-small, $n = 17$) had no effect on the occurrence of behaviors measured: (1) pre-copulatory attacks ($\chi^2 = 0.72$, $df = 1$, $p = 0.40$), (2) successful kills given an attack ($\chi^2 = 0.02$, $df = 1$, $p = 0.91$), (3) mountings ($\chi^2 = 0.09$, $df = 1$, $p = 0.77$), or (4) matings given a successful mount ($\chi^2 = 0.71$, $df = 1$, $p = 0.40$). Therefore, I pooled females from the two sequence types and performed a paired contingency analysis with these 33 females.

Females showed no tendency to switch their attack behavior based on male size class (see Table 1). The tactic of attacking small males but not large males did not occur more often than the tactic of attacking large males but not small males ($G = 1.36$, $df = 1$, $p > 0.1$). Interestingly, females displayed tactics that failed to discriminate between male size classes more often than would be expected given the overall probability of attack on each size class [$p(\text{attack small}) = 0.30$, $p(\text{attack large}) = 0.21$]. Also from Table 1, it is apparent that kills/attack are not biased towards small males ($G = 0.34$, $df = 1$, $p > 0.5$), nor are mountings biased in favor of large males ($G = 0.69$, $df = 1$, $p > 0.1$). However, females do tend to mate with large males but not small males more often than they mate with small males but not large males ($G = 2.93$, $df = 1$, $0.05 < p < 0.1$).

The above analysis treats single behaviors as part of a paired tact taken by individual females. Thus, behaviors are only considered from the female vantage point and each female was used as the experimental unit. However, the likelihood of a pre-copulatory kill, mounting and mating may be controlled by male

Table 1: The observed and expected number of females exhibiting four distinct strategies (e.g. attack males of both size classes, attack one size class but not the other, or attack neither size class)

Event	Large	Small	Observe	Expect
1. Attack (n = 33)	Yes	Yes	5	2.12
	Yes	No	2	4.88
	No	Yes	5	7.87
	No	No	21	18.12
2. Kill/Attack (n = 17)	Yes	Yes	2	1.00
	Yes	No	1	2.00
	No	Yes	2	3.00
	No	No	7	6.00
3. Mount (n = 33)	Yes	Yes	1	1.64
	Yes	No	5	4.36
	No	Yes	8	7.36
	No	No	19	19.64
4. Mate/mount (n = 15)	Yes	Yes	1	0.86
	Yes	No	5	5.14
	No	Yes	1	1.14
	No	No	7	6.86

behavior just as much as female behavior. Accordingly, I compared these measures across male size classes for all virgin males. For this dataset, male size class had no effect on the likelihood of a kill ($\chi^2 = 1.03$, $df = 1$, $p = 0.31$) or a mounting ($\chi^2 = 0.16$, $df = 1$, $p = 0.69$). However, the likelihood of mating given a successful mounting was contingent on male size class. Large virgin males were significantly more likely to successfully mate during a mount (11 of 13; successful males are the enlarged diamonds in Fig. 1) relative to the mating success of small virgin males that obtained a mount (two of 13; $\chi^2 = 12.46$, $df = 1$, $p = 0.0004$).

The irregularity with which small males were able to successfully copulate precluded a formal comparison of the effect of male size on post-copulatory attacks and kills. Post-copulatory attacks occurred following six of 11 (55%) of successful matings with large males and four of these six (67%) post-copulatory attacks were successful. Neither of the small males that succeeded in mating were attacked after copulation.

Other Effects of Body Size

A multiple logistic regression model including female size (cephlothorax area), female condition (mass/size), male size, and the ratio of female size to male size showed some interesting results. Perhaps surprisingly, female condition did not predict any of the behaviors measured (attacks, kills/attacks, mounts, matings/mount). However, females of inferior size were more likely to attack a male before mating ($\chi^2 = 10.40$, $df = 1$, $p = 0.001$, enlarged squares in Fig. 1 represent females that cannibalized the male). The ratio of female size to male size

predicted the likelihood of a kill given a pre-copulatory attack such that males that approximated the female's size were significantly more likely to escape an attack than were males that were dwarfed by the female ($\chi^2 = 6.08$, $df = 1$, $p = 0.01$). In addition, successful matings were significantly more likely from pairs in which the ratio of female size to male size was small ($\chi^2 = 6.76$, $df = 1$, $p = 0.009$).

Discussion

A substantial amount of within-sex and between-sex size variation was found in both adult body size (cephalothorax area) and adult body mass for this population of fishing spiders. In terms of cephalothorax area, large males are as large as smaller females. In contrast, small males may often be forced to court small females that are twice their size, or perhaps court large females that are four times their size (Fig. 1).

When viewed as a paired tactic by females, the occurrence of pre-copulatory attacks by females was not based on the size class of the courting male. In fact, females were much more likely to behave the same way towards males from different size classes than they were to switch behaviors between males (see Table 1). Indiscriminate female behavior towards males of extremely different sizes suggests that female phenotype, rather than male phenotype, determines the likelihood of attack. Such a finding is consistent with a recent model for sexual cannibalism termed the aggressive spillover hypothesis, which was inspired by work done on the European fishing spider, *Dolomedes fimbriatus* (Arnqvist & Henriksson 1997; see below).

The only female size variable that predicted pre-copulatory attacks was adult size (cephalothorax area). Once again, dimensions of the cephalothorax are set for life at the adult molt, and thus can only be enhanced by juvenile processes such as juvenile foraging success and growth up until adult emergence. As such, there is no evidence that pre-copulatory attacks are motivated by a lack of adult foraging success (Newman & Elgar 1991). Instead, it appears that females with the smallest fixed size, those that presumably had the poorest juvenile foraging success, are the most likely to attempt sexual cannibalism. Thus, sexual cannibalism may be a component of a strategy of foraging compensation employed by adults having experienced a poor history of foraging success through development (Schneider & Elgar 2002; Moya-Laraño et al. 2003). According to this idea, and consistent with the present data, pre-copulatory sexual cannibalism should be employed most often by females that emerge at relatively small adult body size.

This interaction between juvenile feeding (fixed size) and adult feeding (adult mass) has been studied in *D. triton* previously (Spence et al. 1996; Johnson 2001). Johnson (2001) provides support for the possibility that adult foraging success can effectively compensate for poor juvenile foraging and small fixed size. Results from this manipulation of juvenile and adult food availability suggested that both juvenile and adult foraging have positive effects on fecundity. In particular,

poorly-fed juvenile females from that study that were shifted upon adulthood to a high-food regime far exceeded the fecundity of females held on a low-food regime throughout both juvenile and adult stages (Johnson 2001).

As noted by Schneider & Elgar (2002), the finding that sexual cannibals are most often the females of the smallest fixed size is the exact opposite of that predicted by a recent hypothesis for sexual cannibalism. Arnqvist & Henriksson (1997) hypothesized that pre-copulatory attacks stem, not from any adaptive foraging response by females, but instead from a spillover of aggression from advantageous contexts such as the juvenile foraging context, to potentially costly contexts such as the mating context. One prediction of this 'aggressive-spillover' hypothesis is that pre-copulatory attacks should be most common in the largest adults who were the most voracious and successful juvenile predators. The present data, as well as one previous laboratory study (Johnson 2001) provide no support for this prediction.

The frequency of successful kills per attack in this study (13 of 26) was significantly higher than in earlier work on this population of *D. triton* (Johnson 2001), as well as that reported for a European congener (Arnqvist & Henriksson 1997). However, male-size class had no effect on the male's ability to escape an attack. This contrasts with previous suggestions that superior speed and agility in large *Dolomedes* males allows them to escape more female attacks (Arnqvist & Henriksson 1997; Johnson 2001). However, disregarding the male-size classifications imposed in this experiment, SSD (i.e. male size relative to the attacking female's size) was an important determinant of male escape ability. Apparently, when the largest males face an extremely large female, escape success remains poor despite large male size. Conversely, small males paired with relatively small females are often able to avoid pre-copulatory attacks. Thus, the heightened capture success seen in this experiment is likely the by-product of using males from the extreme ends of the size distribution. Males of average size, which were not used in this experiment, should have a better chance of being large enough relative to their attacker to escape the majority of pre-copulatory attacks.

Finally, copulation offers a point at which large males are strongly favored in this mating system. The results from this experiment suggest that small males rarely complete copulation successfully. This effect is particularly strong when the size dimorphism between a male-female pair is large. In other words, small males struggle in all cases, but completing a mating with a relatively large female may be impossible for a small male. Females may exacerbate this bias against small males if movements during copulation (e.g. the raising of the legs high) make it even more difficult for a small male to reach the female's genitalia. Regardless of whether females are actively taking part in this mating bias, matings with small males were rare, and when they did occur in this study they involved a small, presumably less fecund, female.

In sum, small male fishing spiders do not benefit in any recognizable way during the course of the mating sequence in this sexually cannibalistic mating system. Instead, small males suffer greater mortality in pre-copulatory attacks and are largely excluded from the gene pool through their poor mating performance.

The question then is no longer ‘why are males not smaller when they are at risk of sexual cannibalism’, but instead ‘why are males not bigger if size largely determines mating success’? Male body size is likely constrained by food availability. In addition, the benefits of early emergence may be great in systems such as this where competition between males is more often via mate location and less often dependent on a male’s ability to directly battle other males for access to a female. Nonetheless, multiple adult males are often found cohabiting with penultimate stage and recently matured females (personal observation). It is not known if males ever come into conflict over females, but if they do the benefits of delayed maturation and large size might begin to approximate the benefits of early emergence at inferior sizes. Thus, optimal adult male body size in this species is most likely a delicate balance between the costs and benefits of early emergence at small size, the availability of resources allowing for growth to large sizes, and the costs and benefits of taking longer to mature at a large size. Results from the present study suggest that large males are better able to escape female attacks and more adept at gaining copulations.

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