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ORIGINAL ARTICLE

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Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioral syndromes

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Abstract Precopulatory sexual cannibalism (predation of a potential mate prior to copulation) offers an extreme example of intersexual conflict, a current focus in behavioral ecology. The 'aggressive-spillover' hypothesis, posits that precopulatory sexual cannibalism may be a nonadaptive by-product of a general syndrome of voracity (aggression towards prey) that is expressed in multiple behavioral contexts. In this view, selection favoring high levels of voracity throughout ontogeny spills over to cause sexual cannibalism in adult females even when it is not necessarily beneficial. Using the North American fishing spider, *Dolomedes triton,* we present the first in depth test of this hypothesis. We found support for three aspects of the spillover hypothesis. First, voracity towards hetero-specific prey results in high feeding rates, large adult size, and increased fecundity. Second, juvenile and adult voracity are positively correlated (i.e., voracity is a consistent trait over ontogeny). Third, voracity towards hetero-specific prey is indeed positively correlated with precopulatory sexual cannibalism. Assays of antipredator behavior further revealed positive correlations between boldness towards predators, voracity and precopulatory sexual cannibalism. Overall, our results support the notion that precopulatory sexual cannibalism in *D. triton* is part of a behavioral syndrome spanning at least three major contexts: foraging, predator avoidance, and mating.

Keywords Aggressive-spillover hypothesis · Sexual cannibalism · Fishing spiders

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Introduction

Precopulatory sexual cannibalism, or predation of a potential mate prior to copulation, has been documented in a number of insect and arachnid families (Elgar and Schneider 2004; Elgar 1992), offering behavioral ecologists an ideal model system for at least two reasons. First, precopulatory sexual cannibalism provides a particularly dramatic example of intersexual conflict (Elgar and Schneider 2004; Elgar 1992; Choe and Crespi 1997). Unlike sexual cannibalism occurring during or after successful mating (e.g., Andrade 1996), precopulatory sexual cannibalism entails no male benefits. Thus, the research on precopulatory sexual cannibalism has focused on documenting female benefits of this behavior (Johns and Maxwell 1997).

In addition, precopulatory sexual cannibalism provides an example of the general view that mating behavior is best understood in conjunction with a range of other relevant selection pressures (Rowe et al. 1994; Jackson and Pollard 1997). For example, female mate choice is often influenced by predation risk and/or feeding rate (Real and Caraco 1986; Sakaluk 1990; Crowley et al. 1991; Sih 1994; Lima 1998). In systems characterized by precopulatory sexual cannibalism mating, foraging and predator–prey issues are uniquely inseparable as males are simultaneously potential mates and prey items, and females are simultaneously potential mates and predators.

Perhaps the most widely discussed explanation for precopulatory sexual cannibalism is the adaptive foraging hypothesis (Newman and Elgar 1991; Elgar 1992), which posits that precopulatory sexual cannibalism provides adult females direct, material benefits as part of an optimal foraging strategy. Newman and Elgar (1991) developed this hypothesis with an economic model showing that precopulatory sexual cannibalism can be explained, even for virgin females, as the result of adaptive tradeoffs between the nutrient payoff of feeding on a male and the fertility benefits of mating with a male. This intuitive, resource-optimization idea has, however, met with limited empirical support (Arnqvist and Henriksson 1997). In this particularly striking example, the authors showed in the European fishing spider (*Dolomedes fimbriatus*) that (1) female fecundity was unrelated to adult feeding history including precopulatory sexual cannibalism, and (2) attacks on males were not predicted by the level of sperm and food limitation experienced by a female (but see Johnson 2001; Johnson 2005a). Notably, despite multiple mating opportunities, some virgin females, in their laboratory experiment, attacked every single male provided, failed to mate, and thus produced no offspring. These authors concluded that (1) if females receive no fecundity benefits from adult feeding, and specifically feeding on males, then precopulatory sexual cannibalism cannot be explained as an adult foraging strategy, and (2) if aggressive behavior towards males causes some females to suffer sperm limitation, then precopulatory sexual cannibalism may have fertility costs rather than foraging benefits.

Arnqvist and Henriksson (1997) offered an alternative explanation for their results hypothesizing that precopulatory sexual cannibalism represents a spillover of aggression from the juvenile foraging context, where high levels of aggression might be selectively advantageous, to the adult mating context. The idea is that genetic constraints limit the range of behavioral plasticity in aggressiveness—some individuals tend to be highly aggressive, while others are less aggressive across a range of contexts. The result is positive behavioral correlations for aggression levels across ontogenetic stages (juvenile–adult), as well as across behavioral contexts (foraging–mating). Selection then acts on the suite of correlated aggressive behaviors rather than optimizing aggressive levels in each individual context. Sih et al. (2004a, b) used the term "behavioral syndrome" to describe suites of correlated behaviors. Thus, the aggressive-spillover hypothesis represents a particularly striking example of how a behavioral syndrome may produce behaviors that appear suboptimal when viewed in an isolated context.

The aggressive-spillover hypothesis

The aggressive-spillover hypothesis (Arnqvist and Henriksson 1997), predicts positive relationships between juvenile voracity (attack tendency), juvenile feeding rate, fixed adult body size (set for life at the adult molt and thus influenced exclusively by juvenile feeding), and fecundity. Arnqvist and Henriksson (1997) argue that adaptive foraging benefits and female fecundity are more tightly linked to juvenile feeding rate than adult feeding rate, including precopulatory sexual cannibalism. Given these conditions, it is further suggested that juvenile voracity is positively correlated with the expression of precopulatory sexual cannibalism which may entail fertility costs. The fecundity benefits of juvenile voracity are suggested to outweigh, on average, any fertility cost incurred by the most voracious and sexually cannibalistic females.

Recently, Johnson (2001) demonstrated a significant effect of juvenile food availability on fixed adult size and fecundity in the North American fishing spider *Dolomedes triton*. However, fecundity in *D. triton* is also influenced by adult foraging (Johnson 2005a; Johnson 2001; Kreiter and Wise 2001). We thus extend the original aggressive-spillover hypothesis to predict that adult voracity, adult feeding rate, egg sac mass, and fecundity will be positively correlated with each other, and that a general voracity syndrome in fishing spiders might span across both development (juvenile–adult) and behavioral context (feed–mate).

Here we use the North American fishing spider (*D. triton*) to provide the first in depth examination of the spillover hypothesis. Following Riechert and Hedrick (1993), we also examine the antipredator context to test the idea that boldness towards predators is a part of the proposed behavioral syndrome. In addition, we directly address the adaptive foraging hypothesis by testing the prediction that foraging history and mating status determine aggressive behavior.

Study system

The natural history (Carico 1973), sensory ecology (Bleckmann and Barth 1984; Bleckmann and Lotz 1987), population ecology (Zimmerman and Spence 1989, 1992), and behavioral ecology (Johnson 2005a, b; Kreiter and Wise 2001) of *D. triton* have been documented previously. With regard to precopulatory sexual cannibalism, experimental mating trials indicate that virgin females attack in approximately 20–30% of pairings, and are successful in up to 40% of these attacks (Johnson 2005b). Field studies of *D. triton* suggest that males represent a common contribution to the adult female diet (Zimmerman and Spence 1989), and that male population density declines drastically, soon after adult female emergence (Zimmerman and Spence 1992). Thus, sexual cannibalism plays an important role in the ecology of *D. triton*.

With regard to antipredator behavior, fishing spiders respond to disturbances by diving underwater and clinging to submerged substrate. Bishop (1924) and Carico (1973) reported submergence of 30 min in *D. triton*. Recent work suggests that, in fact, females can remain submerged for 90 min (Johnson, unpublished data). Submergence most likely involves lost foraging opportunities (*Dolomedes* primarily detect prey items through water surface vibrations).

Methods

Our experimental approach involved repeated assays on a set of 60 focal females quantifying each individual's behavior across ontogeny and in multiple behavioral contexts. The study began in the juvenile stage (1–1.5 months before sexual maturity), and continued through adulthood until death (approximately 5–6 months total). To measure morphology, spiders were digitally imaged upon collection and after every molt until adulthood. Photographs were taken while the spider floated motionless in a cup of water. Imaging conditions (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 photographing a piece of floating graph paper (2 cm×2 cm). Digitized images (Sigma Scanpro) provided measures of the length and width of the cephalothorax. We estimated relative fixed adult size as the area of the cephalothorax (area of an ellipse $= \pi \times$ [cephalothorax width/2] $\times$ [cephalothorax length/2]). In addition, all spiders were weighed to the nearest milligram upon collection, following each molt and prior to each behavioral trial (see below). An adult female's mass at any given time divided by her fixed adult size was used as an index of her body condition (see Jakob et al. 1996 for a discussion of other condition indices). Experimental females were maintained outdoors in individual, large (60 cm×41 cm×16 cm) plastic tubs. Containers were filled with filtered water to a depth of 2.0 cm. and each contained a large Styrofoam float (10 cm×6.0 cm×0.5 cm) and a 22-oz. upturned plastic flowerpot. These latter items combined with the size of the container allowed males some cover from females during courtship trials. When not being used in trials, adult males were maintained in the laboratory in individual 425 ml transparent cups filled with filtered water to a depth of 2.0 cm. Each cup contained a Styrofoam float (2.0 cm×1.5 cm×0.5 cm) that served as a resting spot and underwater refuge.

Foraging trials

Females underwent 30-min foraging trials twice weekly throughout the experiment. This feeding regime results in successful growth to adulthood and offspring production within the range of that seen in the field (Johnson, unpublished data). Foraging trials were conducted on females as juveniles and adults, but not when adult females were carrying egg sacs. Females rarely attack prey while carrying an egg sac in their mouthparts (Carico 1973; Johnson, personal observation). To begin each trial, a 4-week old cricket (*Acheta domesticus*) was introduced to the water surface at a point 30 cm directly in front of the female. We used the inverse of latency to attack as a measure of voracity in both juveniles and adults. The average latency scores for each female across multiple trials was used as an indicator of her voracity. Crickets that survived the trial (i.e., they were not captured or were captured and discarded while still alive) were removed at the end of a trial such that females failing to secure prey during a trial did not have another feeding opportunity until their next trial. Thus, hunger state (and presumably condition) was allowed to vary across females according to past foraging successes or failures as it would in nature. By not controlling hunger across this longitudinal experiment, we test for a syndrome of voracity in spite of hunger differences rather than in the absence of hunger differences.

Courtship trials

Courtship trials ran for 90 min and were conducted four times per week beginning on each female's third day following adult emergence and continuing until egg sac production (~7–10 days following mating, Johnson, unpublished data). During the first five of these trials for each female, males were allowed to court the female, but if mounting and copulation began it was immediately terminated. This was necessary to allow us to obtain repeated measures of each virgin female's propensity for attacking males. From the initial pool of 135 males collected that molted to adulthood successfully, males were chosen randomly with replacement. The exception to this being that a female never encountered the same male twice, and of course males that were killed in a trial could not be used again. Males were introduced to a point 30 cm in front of the female. These introductions did not result in an immediate attack by the female (no attacks occurred prior to courtship), thus the experimental introduction of males did not appear to inflate rates of sexual cannibalism. Males that did not initiate typical courtship leg waving and tapping behavior within the first 15 min of a trial were replaced. We used the inverse of the latency to attack a courting male as a measure of voracity in the mating context.

Egg sacs are carried by the female in her mouthparts and defended vigorously. As a result, egg sacs cannot be removed from the female's grasp without ripping the outer lining. We approximated the mass of the egg sac by subtracting the female's mass one day following egg sac hatching, from her mass while clutching the egg sac just prior to egg sac hatching. The number of spiderlings emerging from an egg sac was counted and used as a measure of fecundity.

Antipredator trials

Antipredator trials were performed twice weekly throughout the experiment and ran for 30 min. The goal here was to startle the spider and provoke submergence behavior by firmly tapping each spider's abdomen with a prod. The few females that still remained on the surface after this time were scored as unwilling to submerge and received a submergence duration score of 0 s. Females were scored as resurfacing when at least four legs had returned to the water surface. No additional startle was employed following a female's resurfacing. Nevertheless, females often went through two or more cycles of surfacing and resubmerging over the course of a trial. Therefore, boldness was defined as (1/proportion of a trial spent submerged).

Results

The benefits of feeding voracity

Means and standard deviations for our experimental variables are reported in Table 1. A key premise of the

Table 1 Summary statistics. See the text for predictions on correlations among these variables. Sample size for fecundity analysis is reduced to only those females successfully hatching an egg sac

	n	Mean	SD
Fixed adult size (cm^2) (cephalothorax area)	60	0.348	0.071
Condition (g/cm^2) (mass/cephalothorax area)	57	1.59	0.293
Egg sac mass (mg)	50	695.58	183.05
Offspring # (fecundity)	32	388.15	159.78
Juvenile latency to attack crickets (min) (juvenile voracity)	53	24.1	5.18
Adult latency to attack crickets (min) (adult voracity)	59	17.6	6.13
Latency to attack males (min) (precopulatory sexual cannibalism)	59	22.19	16.81
Proportion of antipredator trial spent submerged (min) (1/boldness)	59	0.521	0.241

aggressive-spillover hypothesis is that juvenile voracity has benefits, i.e., it is associated with high juvenile feeding success, which results in large fixed adult size and high fecundity. Our modification of the hypothesis notes that adult voracity might also have benefits, i.e., that adult voracity should drive high adult feeding success that also contributes to fecundity. Because the hypothesis makes these a priori, unidirectional predictions, all *p* values reported below are one-tailed.

As predicted, juvenile voracity (1/(latency to attack a prey item)) was strongly, positively correlated with juvenile feeding rate (proportion of foraging trials in which the spider fed arcsine transformed; r_{57}=0.921, t=16.32, p<0.0001). In turn, juvenile feeding rate was positively correlated with fixed adult size (measured as cephalothorax area; r_{53}=0.23, t=1.69, p=0.049), and fixed adult size was significantly, positively correlated with fecundity (measured as offspring number; r_{32}=0.50, t=3.16, p=0.002). Similarly, adult voracity towards hetero-specific prey (1/(latency to attack)) was significantly positively related to adult feeding rate (r_{57}=0.920, t=17.82, p<0.0001), adult feeding rate was positively related to egg sac mass (r_{50}=0.297, t=2.15, p=0.018), and egg sac mass was positively related to fecundity (r_{32}=0.722, t=5.71, p<0.0001). Thus high feeding voracity (juvenile and adult) clearly provides benefits in terms of enhanced fecundity for *D. triton* females.

Courtship trials and precopulatory sexual cannibalism

Across the entire experiment, females exhibited precopulatory attacks in 32% of courtship trials and males were killed in 50/109 (46%) of these attacks. The proportion of trials in which a female exhibited a precopulatory attack was an excellent indicator of that female's propensity to actually kill and cannibalize courting males (r=0.51, $F_{1,57}$=19.59, p<0.0001). The above propensity to attack males was not, however, related to the number of pedipalp insertions she ultimately received (r=0.136, $F_{1,56}$=1.05, p=0.31), or the likelihood that she would hatch an egg sac (χ^2=0.862, d.f. = 1, p=0.35).

Behavioral correlations across ontogeny and across contexts

Juvenile voracity and adult voracity were significantly, positively correlated (r_{52}=0.381, t=2.92, p=0.003), thus supporting the notion of an ontogenetic spillover of voracity from juvenile to adult. Univariate tests showed significant correlations between both juvenile and adult voracity and the tendency to engage in precopulatory attacks (juvenile voracity: r_{52}=0.348, t=2.61, p=0.006; adult voracity: r_{59}=0.39, t=3.28, p=0.001). A multiple regression model including juvenile voracity and adult voracity as independent variables explained a significant amount of variation in precopulatory attacks($F_{3,48}$ =7.65, p=0.001). Partial regression analyses showed that both juvenile and adult voracity had significant effects on precopulatory attacks even after accounting for the effects of the other variable (juvenile: r= 0.217, t=1.63, p=0.05; adult: r=0.367, t=2.76, p=0.004).

Finally, with regard to the possibility that boldness towards predators is part of a voracity/boldness syndrome, boldness (measured as 1/time spent submerged following a disturbance) was positively correlated with both precopulatory attacks (r_{59}= 0.243, t=1.89, p=0.032, and hetero-specific foraging voracity (juvenile and adult voracity combined: r_{60}= 0.317, t=2.54, p=0.007). Thus, spiders that exhibit high levels of voracity in foraging and mating contexts are also the quickest to return to the surface following a disturbance.

Tests of the adaptive foraging hypothesis

An underlying assumption of the adaptive foraging hypothesis is that males represent a valuable food source for females, i.e., that the tendency to engage in precopulatory sexual cannibalism should provide females with measurable fecundity benefits. Contrary to this assumption, offspring number was not predicted by the number of males consumed (0, 1, 2, 3, or 4) by an individual female after controlling for female condition at adult emergence (n=32, t=0.601, p=0.280).

A major prediction of the adaptive foraging hypothesis is that females that are in better condition (e.g., that are well fed) should be less motivated to attempt precopulatory sexual cannibalism. That is, we should see a negative correlation between female condition and tendency to attack males (or other prey). Our measure of female body condition was the ratio of mass and cephalothorax area; for a given fixed adult size, females in higher condition weigh more. Adult female body condition was not significantly negatively correlated to either precopulatory attacks (r_{50}=0.178, t=1.36, p=0.179) or feeding voracity on crickets ($r=0.09$, $F_{55}=0.433$, $p=0.51$). Indeed, for precopulatory attacks, the above data suggest a nonsignificant positive relationship, with females in the best condition displaying the most precopulatory attacks. This pattern was also apparent for precopulatory attacks and fixed adult body size alone (an indicator of juvenile feeding rate: $r_{59}=0.211$, $t=1.63$, $p=0.108$).

Discussion

Aggressive spillover

Our results support the idea that precopulatory sexual cannibalism represents a spillover of aggression from a broader syndrome of correlated behaviors. Corroborating a previous study (Johnson 2001), we documented a link between juvenile voracity, juvenile feeding rate, fixed adult size, and fecundity. Most notably, we present the first test of the spillover hypothesis' prediction that positive behavioral correlations exist across ontogeny and behavioral contexts. Strong positive correlations were apparent between juvenile voracity, adult voracity in the hetero-specific prey foraging context, adult voracity in the mating context (i.e., precopulatory sexual cannibalism), and boldness towards predators. Voracity in *D. triton* appears to spill over across both ontogeny (juvenile–adult) and behavioral contexts (foraging–mating-antipredator). Multivariate analyses suggest a stronger role for spillover across behavioral contexts (adult foraging voracity–precopulatory sexual cannibalism) than ontogeny (juvenile foraging voracity–precopulatory sexual cannibalism. However, the possibility of an even stronger positive relationship between juvenile voracity and precopulatory sexual cannibalism cannot be entirely ruled out as juvenile fishing spiders develop for 2 years before reaching maturity. Juvenile foraging trials in this experiment only quantified voracious behavior during the final 4–6 weeks of the juvenile period. Future work should aim to document voracity correlations across the entire juvenile life cycle.

Our data add to a growing number of studies that have examined correlated behavioral traits from an evolutionary/ecological viewpoint (reviewed in Sih et al. 2004a, b). A few previous studies have documented potentially costly correlations across behavioral contexts within a given ontogenetic stage. For example, Wilson et al. (1993) described a shy-bold continuum in juvenile pumpkinseed sunfish (*Lepomis gibbosus*) in which consistent individual differences in boldness affected predator risk, diet choice and parasitic infection. Similarly, Sih et al. (2003) demonstrated a positive activity correlation for larval salamanders (*Ambystoma barbouri*) in the presence and absence of predatory fish. Individuals with high activity levels in the absence of predation risk acquired more resources and developed faster. However, these same individuals were also more active and took greater risks in the presence of predators. Finally, Riechert and Hedrick (1993) showed that funnel web spiders (*Agelenopsis aperta*) that were most aggressive in contests with conspecific intruders were the same individuals that were boldest towards potential predators. This aggressive/bold syndrome was later shown to also correlate with wasteful killing (killing but not fully consuming prey) in the foraging context (Maupin and Riechert 2001).

Particularly lacking, however, are longitudinal studies that follow animals across ontogeny looking for behavioral correlations across different points in development (but see Bakker 1986; Bell and Stamps 2005). Our data on *D. triton* provided further evidence for: (1) the notion that behavioral type (here, feeding voracity) carries over between the juvenile and adult stages; and (2) the existence of a voracious/bold syndrome. We further show that these behavioral correlations also surface in the form of precopulatory sexual cannibalism in the mating context. Whether voracity in the mating context involves fertility costs is the subject of ongoing work.

Adaptive foraging

While our results fit the aggressive-spillover hypothesis, they did not support the adaptive foraging hypothesis. Voracity was not predicted by female condition and consuming males did not allow females to produce more offspring. Indeed, such negative findings are consistent with previous studies that have attempted to test the adaptive foraging hypothesis in spiders (Andrade 1996; Spence et al. 1996; Arnqvist and Henriksson 1997; Fahey and Elgar 1997; Elgar et al. 2000; Johnson 2001; but see Elgar and Nash 1988). Patterns of precopulatory sexual cannibalism in this experiment also did not accord with a recent variant of the adaptive foraging hypothesis—adult foraging compensation (Schneider and Elgar 2002). This idea suggests that precopulatory sexual cannibalism is the by-product of a female's need to compensate for poor feeding rate as a juvenile. The compensation hypothesis predicts precopulatory sexual cannibalism to be most frequent among females with the poorest juvenile feeding history and thus the smallest fixed adult size. We found no evidence to support this idea in the present experiment. In fact, the present data indicate a nonsignificant positive relationship between fixed size and precopulatory sexual cannibalism such that females with the highest juvenile feeding rate were most likely to exhibit precopulatory sexual cannibalism. This result is more consistent with predictions of the aggressive-spillover hypothesis than any form of adaptive adult foraging.

Boldness and voracity

Also intriguing are our data that suggest a link between voracity and boldness towards predators. While it has been argued that aggression and fear are distinct motivational states governed by separate genetic mechanisms and hormonal axes (Riechert and Maynard-Smith 1989), it is interesting to note that several studies have found behavioral correlations between aggressive and bold behavior (Wilson et al. 1993; Huntingford 1976). Because, to date, these studies represent a very limited number of taxa any general link between fear and aggression remains to be established. While the potential fertility costs of overzealous precopulatory sexual cannibalism behavior are extreme and obvious, a spillover of voracity/boldness to the antipredator context could also be very costly. Future works should address the possibility that feeding benefits (e.g., increased developmental rate or fecundity) can, on average, outweigh the costs of inappropriately high levels of boldness towards predators (e.g., Sih et al. 2003).

Implications

We suggest that behavioral syndromes such as the one documented here may be very common. If so, this will require a dramatic shift in the way we think about and study animal behavior, similar to that occurring in the field of behavioral endocrinology (Ketterson and Nolan 1999). We cannot atomize the behavioral repertoire of an animal and expect to fully understand why it behaves the way it does. Future studies should examine the same individuals in multiple developmental and behavioral contexts to address the extent to which seemingly different behaviors (e.g., juvenile foraging behavior and parental care) are correlated in their expression. In many situations we may find evidence of both context-specific benefits and behavioral spillover. For example, it is quite likely that precopulatory sexual cannibalism may yield context-specific foraging/fecundity benefits in some ecological contexts (e.g., under extreme food limitation).

In conclusion, the existence of a voracious syndrome of behaviors throughout development and across multiple behavioral contexts may go a long way to help explain curious behaviors such as precopulatory sexual cannibalism. Our data suggest that future work cannot ignore the potential of behavioral correlations. Next steps in this and the other systems should include (1) the search for potential costs of syndromes, (2) evidence that syndromes are heritable, (3) mechanistic studies aimed at deciphering what common factors (e.g., shared genes or hormones) are responsible for coupling certain behaviors and how they might be decoupled, and (4) ecological studies on how fluctuations in the availability of critical resources (e.g., food or mates) impact the evolution and maintenance of syndromes. Progress such as this will significantly advance our understanding of the potential that behavioral syndromes have for influencing the dynamic process of behavioral evolution.

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