

Cohabitation of juvenile females with mature males promotes sexual cannibalism in fishing spiders

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Precopulatory sexual cannibalism, or female predation of a potential mate before mating, illustrates an extreme intersexual conflict. Unlike sexual cannibalism occurring after mating, precopulatory sexual cannibalism cannot be construed as a male strategy. Thus, research on the adaptive significance of this phenomenon has focused on female benefits. In the present study, I test the idea that precopulatory sexual cannibalism represents an adaptive female trade-off between the material costs and benefits of mating with a male (forgoing food, securing sperm) and preying on a male (forgoing sperm, securing food). I pay particular attention to the rarely tested prediction that precopulatory sexual cannibalism by virgin females should increase as each female's expectation of future mating opportunities increases. I use the phenomenon of cohabitation between adult males and juvenile females nearing sexual maturity as a means to manipulate female expectation of future mate availability. Results indicate that feeding on a male has significant positive effects on several measures of female fecundity. However, the likelihood of precopulatory attacks was not explained by a female's recent feeding history. Finally, as predicted, juvenile female cohabitation with mature males (expectation of future mating opportunities) heightens the prevalence of precopulatory attacks by virgin females, suggesting that juvenile experience can alter a female's propensity for sexual cannibalism. This is the first study to suggest that juvenile experience can alter a female's propensity for sexual cannibalism. This finding emphasizes the point that studies of sexual selection and mating systems need to consider the effects of juvenile experience on adult behavior. *Key words:* adaptive foraging, fishing spiders, juvenile experience, male-female cohabitation, precopulatory sexual cannibalism. [*Behav Ecol*]

The trade-off between foraging behavior and predation risk has been a core idea in the development of behavioral ecology (Krebs and Davies, 1991). More recently, studies have begun to include mating decisions into an integrative optimality approach to animal behavior (Jackson and Pollard, 1997; Rowe et al., 1994). Thus, understanding the manner in which an animal juggles these three requirements—*foraging, mating, and avoiding predation*—is a central goal of modern behavioral ecology. Precopulatory sexual cannibalism (pre-SC), or female predation of a potential mate before mating, provides an ideal model system for this integrative approach (Elgar, 1992). In systems characterized by pre-SC, the distinction among mating, foraging, and antipredator behaviors is blurred as males are forced to solicit copulations from potential predators, and females have the option of mating with or trying to prey upon a male. Thus, pre-SC illustrates an extreme case of intersexual conflict that, unlike postcopulatory sexual cannibalism (see Andrade, 1996), cannot be construed as a male mating strategy.

Pre-SC may also be costly for females. The cost of attacking a potential mate may be particularly high for virgin females in terms of lost mating opportunities. As a result, research on the adaptive significance of pre-SC (for review, see Elgar, 1992; Johns and Maxwell, 1997) has focused on female benefits that could outweigh such risks. Here I focus on the material costs and benefits to females of pre-SC. Specifically, I examine the trade-off for females between mating with a male (forgoing

food, securing sperm) and preying on a male (forgoing sperm, securing food).

A material benefits, trade-off hypothesis for pre-SC (elsewhere referred to as feeding opportunism [Andrade, 1998] and adaptive foraging [Johnson, 2001; Schneider and Elgar, 2002]) was first suggested by the finding that females of the orb-web spider, *Araneus diadematus*, that consumed a single male added significantly to their body weight (Elgar and Nash, 1988). This hypothesis was later developed as an economic model to determine whether potential costs to the virgin female associated with pre-SC (lost mating opportunities) could be outweighed by material benefits (enhanced fecundity) gained by eating a male (Newman and Elgar, 1991). The model thus predicts that the two most important factors determining the prevalence of pre-SC are the degree to which nonmale food sources are available (i.e., food limitation), and the number of males that a female can expect to encounter during the breeding season (i.e., sperm limitation).

Two features of the current state of this hypothesis are noteworthy. First, this intuitive idea has met with little support (Arnqvist and Henriksson, 1997). Feeding history (a proxy for food limitation) rarely explains the prevalence of pre-SC attacks, and the fecundity benefit of feeding on a male, shown originally in *A. diadematus* (Elgar and Nash, 1988), has not been replicated in other spiders (Arnqvist and Henriksson, 1997; Johnson, 2001). The trade-off hypothesis for pre-SC seems unlikely if attacks are not based on hunger and eating a male provides no material benefit (Arnqvist and Henriksson, 1997). Second, almost all tests of this hypothesis have been limited to food manipulations. Although occasional reference is made to the prediction that pre-SC should be more frequent in mated females relative to sperm-limited, virgin females (Johnson, 2001; Wojcicki, 1992), no study has examined variation in pre-SC by virgin females as a function

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of mating expectations. In the current study, I present the first test of the prediction that, among virgin females, pre-SC attacks should be more frequent when female expectation of mate availability is high, and less frequent when female expectation of mate availability is low.

A key question for testing such a prediction is: how might virgin female assessment of male availability vary naturally? Differences in male availability are likely to affect the frequency of female encounters with males before sexual maturity. In many protandrous spiders, adult males cohabit with juvenile females nearing sexual maturity (Carico, 1973), and this may provide an index of expected mate availability for females.

Here I use the semiaquatic North American fishing spider (*Dolomedes triton*) to test the material benefits, trade-off hypothesis for pre-SC. The natural history of this sexually cannibalistic species has been reviewed elsewhere (Carico, 1973; Johnson, 2001). In *D. triton*, precopulatory attacks by virgin females occur in approximately 20–30% of pairings, and up to 46% of these attacks can result in a successful kill (Johnson, 2001; Johnson JC, unpublished data). In addition, field studies suggest that sexual cannibalism plays an important role in the ecology of *D. triton* (Zimmerman and Spence, 1989, 1992).

Mature male *D. triton* are often found cohabiting in close proximity to females nearing adulthood (i.e., within 20 cm), and it is not uncommon to find two or three males cohabiting with a single female (Johnson JC, personal observation). I use this species to test the prediction that a female's expectation of future mating opportunities will affect her propensity for pre-SC. I do this by manipulating juvenile female cohabitation experience and subsequently measuring each adult female's propensity for pre-SC. In addition, I test the prediction that pre-SC attacks are most prevalent by hungry mated females, and the assumption that feeding on a male improves female reproductive success.

METHODS

Juvenile spiders ($N = 100$ males 1–2 weeks from adulthood and $N = 80$ females approximately 3–6 weeks from adulthood) were collected from a large pond (approximately 60 m²) outside of Lexington, Kentucky, during the first week of April 2002, immediately weighed (± 1 mg) and digitally imaged. Additional images were obtained after each spider's molt. Spiders were imaged while they floated motionless in a cup of water. Image components (e.g., amount of water in the cup, distance of camera from spider) were standardized, and each day the imaging set-up was calibrated by photographing a piece of floating graph paper (2 × 2 cm). Images were later digitized (Sigma Scanpro), 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 = $(\pi \times [\text{cephalothorax width}/2] \times [\text{cephalothorax length}/2])$. Cephalothorax area at adulthood is often termed "fixed adult size" because it is set for life at the adult molt. As such, this measure is only influenced by feeding in previous ontogenetic stages and can thus be used as an indirect indicator of juvenile foraging success. Each female's mass divided by her fixed adult size was used as an index of her body condition (for a discussion of other condition indices, see Jakob et al., 1996).

Foraging trials

Experimental females ($n = 60$) were maintained outdoors in individual, large (60 × 41 × 16 cm) plastic tubs. 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 offered one adult house cricket (*Acheta domesticus*) three times weekly from the time of collection until the production of an egg sac. Prey items were available for 30 min, after which they were removed if not eaten. This level of food availability is suitable to promote successful reproduction (Johnson, 2001). Foraging success was measured as the proportion of trials in which a female successfully fed on a prey item. The few instances of wasteful killing (i.e., killing but not consuming prey) were scored as failing to feed.

Cohabitation manipulation

Each juvenile female nearing sexual maturity (host) was housed with either a recently matured male ($n = 19$), a much smaller juvenile female ($n = 20$), or no other spider ($n = 21$). The cohabitation manipulation began a minimum of 10 days before female maturation. To prevent cannibalism of the cohabitant (guest) by the host female, guests were housed in a 16-oz, transparent, plastic cup with the bottom cut out. Mesh sheets were fastened to both open ends of the cup with rubber bands, and the cup rested on its side partially submerged in the water of the host female's container. Thus, both airborne and waterborne chemicals were continuously exchanged between host and guest, but full physical contact was prevented. There was, however, some direct contact as the two spiders were often found clinging to opposite sides of the cup's mesh covering such that their legs touched. In addition, every fifth day I placed hosts in guest's containers and vice versa for 2 h. This had the dual effect of (1) allowing hosts direct contact with their guest's physical environment (e.g., silken draglines left on the Styrofoam), and (2) allowing guests to leave silken draglines on the water and Styrofoam float of their host's container. Guests were rotated every second day to another female's container within the same treatment group. In this way, females housed with males were exposed to a series of males, ensuring that they experienced an environment indicative of a high abundance of potential mates. Females of the no-guest control group were housed with an empty cup.

Females were fed 2 days after their adult molt. Two days after this feeding, mating trials began. Adult females were paired with an adult male for 1 h or until mating had taken place. Males were introduced as far from the female as possible, and I recorded the occurrence of precopulatory attacks, both successful and unsuccessful. Cohabitants and their cups were removed before mating trials but replaced in the interval between mating trials. Males used in the cohabitation trials were never used in mating trials, thus females were never paired with males with whom they had cohabited. Mating trials were repeated every other day until a female produced an egg sac.

Egg sacs are produced approximately 7–10 days after a mating (Johnson JC, unpublished data), 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 of the egg sac. I estimated the mass of the egg sac as the female's mass just before egg sac hatching while clutching the egg sac minus the female's mass 1 day after egg sac hatching. Egg sacs were considered to have hatched successfully if live offspring emerged from them. The number of live emergent spiderlings was used as a measure of fecundity. Because females and/or emerging spiderlings can consume unfertilized eggs, I did not have an estimate of the number of infertile eggs in hatched egg sacs. A subset of females produced second egg sacs, so I performed separate fecundity analyses including and excluding offspring from second egg sacs.

Table 1
Summary statistics for response variables measured

	Fixed adult size (cm ²)	Adult condition (g/cm ²)	Offspring no. egg sac 1	Offspring no. egg sac 1 + 2	Egg sac mass (mg)	Egg sac mass (mg)/offspring
<i>N</i>	59	56	32	32	50	32
Mean	0.348	1.590	388.16	448.34	246.96	0.731
SE	0.009	0.039	28.24	35.46	13.74	0.086

Fixed adult size is measured as cephalothorax area and adult condition is measured as mass/cephalothorax area.

Statistical analysis

Given the a priori, unidirectional predictions made by the trade-off hypothesis, all tests reported are one-tailed. Several measures of female reproductive success can be used to examine the effects of female foraging on crickets and pre-SC. Here I report the results of three multiple linear regression models by using mass of the egg sac, offspring number, and the ratio of egg sac mass to offspring number as the dependent variables. Fixed adult size, female feeding history on crickets, and the proportion of mating trials in which females exhibited successful pre-SC were used as independent variables in all three of these models. I also report results from a logistic regression by using hatching success of the first egg sac as the categorical variable with the same three independent variables. Finally, I test the prediction that sperm-limited virgin females should attack males less often than do mated females by using a paired analysis (McNemar’s test for significant changes in correlated proportions; Sokal and Rohlf, 1995) of each female’s pre-SC behavior as a virgin and as a nonvirgin.

RESULTS

Effects of adult size, foraging on crickets, and pre-SC on female reproductive success

Summary statistics are presented in Table 1. Fixed adult size, adult feeding on crickets, and pre-SC (range = 0–4 males eaten) explained a significant amount of variation in the mass of the female’s first egg sac ($F_{3,46} = 3.69, p = .018$). Of these three independent variables, pre-SC was the only variable with a significant positive effect on the mass of the egg sac (Table 2). Although offspring number in the first egg sac was significantly predicted by the model ($F_{3,28} = 3.33, p = .034$), offspring number in the first and second egg sacs combined did not show such a relationship ($F_{3,28} = 1.56, p = .221$). This distinction arose from the fact that fixed adult size had a significant positive relationship with offspring number in the first egg sac, but this effect is much weaker when offspring from the second egg sac are included. Notably absent from either analysis on offspring number was an effect of adult feeding on crickets or pre-SC (Table 2).

Variation in the ratio of the mass of the first egg sac to the number of offspring in that egg sac was also significantly predicted by this model ($F_{3,28} = 3.07, p = .044$). Fixed adult size was significantly negatively related to this ratio; pre-SC was significantly positively related to this ratio; and adult feeding on crickets had no significant relationship with this ratio (Table 2). Finally, logistic regression indicated that hatching success of the first egg sac was significantly predicted by the model ($\chi^2 = 16.73, df = 3, p = .001$). Adult feeding on crickets and pre-SC contributed to increased hatching success (Table 2).

Food effects on pre-SC attacks

Across the entire experiment, females exhibited pre-SC attacks in 30% of virgin mating trials and males were killed in 42/103 (40%) of these attacks. The proportion of trials in which a female exhibited a pre-SC attack was a significant predictor of that female’s propensity to actually kill and cannibalize courting males ($r = .49, F_{1,59} = 18.00, p < .0001$). Contrary to the predictions of the trade-off hypothesis for pre-SC, female attacks on males were not associated with a poor feeding history. Instead, limiting the analysis to each female’s first pairing with a male, pre-SC attacks were most common among females with the highest recent feeding success on crickets ($r = .404, t_{57} = 3.45, p < .001$). In addition, adult female condition (mass/cephalothorax area) at the time of

Table 2
The effects of fixed adult size (cephalothorax area), adult feeding on crickets (proportion of foraging trials in which the spider fed), and pre-SC (proportion of mating trials in which the spider fed on its mate) on several measures of female reproductive success

	(<i>r</i>)	<i>t</i>	<i>P</i> _{1-tailed}
Egg sac mass, <i>n</i> = 50			
Fixed adult size	0.196	1.38	0.090
Adult foraging success (crickets)	−0.009	−0.062	0.475
Pre-SC	0.346	2.43	0.009
Offspring number egg sac 1, <i>n</i> = 32			
Fixed adult size	0.465	2.73	0.006
Adult foraging success (crickets)	0.032	0.185	0.427
Pre-SC	0.109	0.622	0.269
Offspring number egg sacs 1 ± 2, <i>n</i> = 32			
Fixed adult size	0.308	1.68	0.052
Adult foraging success (crickets)	0.052	0.274	0.393
Pre-SC	0.124	0.658	0.258
Egg sac mass/offspring number, <i>n</i> = 32			
Fixed adult size	−0.373	−2.17	0.019
Adult foraging success (crickets)	−0.033	−0.188	0.426
Pre-SC	0.434	2.46	0.010
Hatching success of egg sac 1, <i>n</i> = 32			
Fixed adult size	—	−0.936	0.174
Adult foraging success (crickets)	—	2.53	0.006
Pre-SC	—	1.71	0.044

Bold type highlights statistically significant results.

her first pairing with a male was positively related to the prevalence of pre-SC attacks ($r = .231$, $t_{57} = 1.76$, $p = .042$).

The effect of cohabitation and mating status on pre-SC attacks

There was no significant difference between the prevalence of pre-SC attacks by virgin females housed with an empty cup control and those housed with the smaller-female control ($t_{37.8} = 0.07$, $p = .473$). Therefore, I combined these control females that had no exposure to males and compared their pre-SC behavior with that of females housed with adult males. Virgin females allowed to develop in the company of mature males were significantly more likely to exhibit pre-SC attacks than were virgin females not experiencing males during development ($t_{38.3} = 1.963$, $p = .03$). Contrary to the predictions of the trade-off hypothesis, attacks were much more likely from virgin females relative to mated females. By using McNemar's test for significant changes of correlated proportions, regardless of the cohabitation treatment, females were significantly more likely to employ the tactic of attacking when virgin but not when nonvirgin (32/54, 59%) than they were to employ the tactic of attacking when nonvirgin but not when virgin (4/54, 7%; $G = 24.54$, $df = 1$, $p < .0001$).

DISCUSSION

The results presented here provide (1) mixed support for the assumption that adult female foraging, and pre-SC specifically, increases female fecundity, (2) no support for the prediction that females that have eaten little should be more likely to engage in pre-SC than well-fed females, and (3) the first evidence of support for the prediction that a virgin female's propensity for pre-SC varies along with her expectation of mate availability. Below I discuss each of these results in more detail.

Effects of adult size, foraging on crickets, and pre-SC on female reproductive success

The use of multiple indicators of female reproductive success (Tables 1 and 2) provided insight into how females may derive benefits of adult food intake (including pre-SC). Mass of the egg sac was significantly enhanced by pre-SC but not by adult feeding on crickets. This is a surprising result given that the crickets used in this experiment were three to four times heavier than adult male *D. triton*. Elgar and Nash (1988) suggested that foraging on a conspecific male may allow females to convert prey mass to energy more efficiently than does foraging on heterospecifics. In general, diet diversity in spiders is thought to benefit development speed, fecundity and survivorship (see Sigsgaard et al., 2001). Thus, pre-SC could represent qualitative diversification of the diet, explaining why pre-SC is correlated with increases in egg sac mass, whereas foraging on crickets is not.

Interestingly, neither adult female foraging on crickets nor pre-SC had any positive influence on offspring number, a result that appears to contradict the foraging side of the trade-off hypothesis. Instead, fixed adult size, a morphological measure that indicates successful juvenile foraging and growth, was a strong predictor of offspring number (see also Johnson, 2001). Adult female foraging (including pre-SC) did, however, promote reproductive success in more subtle ways. First, pre-SC proved to increase the amount of egg sac mass devoted to each egg. This relationship did not hold for foraging on crickets. One could argue that this ratio is the best indicator of female fitness, short of offspring vigor, because it reflects the amount of resource provided per

offspring. *D. triton* offspring, similar to many spiderlings, rely exclusively on nutrients obtained from their egg yolk until they reach a size that permits them to subdue live prey items (Carico, 1973). The ratio of egg sac mass to offspring number is one possible indicator of the head start a female provides each of her offspring through egg mass provisioning.

Second, in line with previous work on this species (Johnson, 2001), adult foraging on crickets and pre-SC increased the likelihood that a female's egg sac would hatch successfully. Egg sac failure in the field has been reported previously in *D. triton* (Zimmerman and Spence, 1992). Such failures have been associated with females who have not mated (see Arnqvist and Henriksson, 1997), but it remains a likely possibility that factors other than infertility (e.g., diet diversity, egg sac parasitism) may explain some instances of egg sac failure. Although egg sac mass, offspring number, and offspring vigor are undoubtedly good measures of female fitness in many circumstances, the ability to hatch an egg sac regardless of the number, size, and vigor of those offspring may be the most important reproductive challenge a female has to overcome.

Food effects on pre-SC attacks

This experiment represents a third independent study of this population that fails to support the prediction that pre-SC attacks are motivated by adult feeding history (Johnson, 2001; Johnson JC and Sih A, in preparation). In addition, studies of other *D. triton* populations (Spence et al., 1996), a European congener (Arnqvist and Henriksson, 1997) and a variety of other spider taxa (Jackson, 1980; Breene and Sweet, 1985; Elgar and Nash, 1988) have found similar results. Instead, in the present study, pre-SC was practiced most often by females having experienced the highest adult foraging success, a result opposite to that predicted by the trade-off hypothesis. This finding is consistent, however, with Arnqvist and Henriksson's (1997) hypothesis that pre-SC represents a spillover of aggression from the beneficial heterospecific foraging context to the mating context. The positive behavioral correlations suggested by this aggressive-spillover hypothesis (i.e., aggressiveness towards prey and aggressiveness towards mates) have been more formally documented in a recent study of this same population of *D. triton* (Johnson JC and Sih A, in preparation).

The effect of cohabitation on pre-SC attacks

The present study demonstrates that cohabitation between mature males and juvenile females can be used as a way to manipulate female expectation of future mate availability. Here I have provided the first experimental evidence showing that pre-SC attacks by virgin females are influenced by a juvenile female's experience of mate availability. This may be a frequent mechanism by which females assess whether pre-SC is a risk-free foraging strategy in their current environment. Past attempts to find a relationship between food limitation and pre-SC may have failed because variation in female "expectations" of mate availability were masking an effect of food limitation. Future empirical tests of the trade-off hypothesis need to simultaneously manipulate both food availability (including pre-SC) and female experience of mate availability.

If female experiences of mate availability through prereproductive interactions with adult males routinely affect the prevalence of pre-SC, then past studies may have drastically underestimated the occurrence of pre-SC in nature. Experimental studies of pre-SC routinely collect animals as juveniles nearing sexual maturity and house them individually until adulthood to ensure that they are virgins when mating trials are conducted (see Johnson, 2001). One unfortunate by-product of

this protocol is that it imposes an experience of artificially low mate availability on females. The prevalence of pre-SC we see in experimental studies using such isolation protocols before mating trials may be a fraction of what would be observed if females had been allowed to mature under natural conditions of male-female cohabitation and interaction.

In conclusion, the present study emphasizes the broader point that many forms of juvenile experience and development, in general, can have profound influences on adult behavior (Stamps, 2003). Juvenile female experience with adult males may be a particularly fertile area for future research. For example, recent work in the wolf spider, *Schizocosa uetzi*, suggests that juvenile female exposure to males of a certain phenotype (e.g., brown leg coloration) makes females more likely to mate with males of that phenotype and less likely to attack males of that phenotype upon adulthood (Hebets, 2003). Thus, juvenile female development in the company of mature males can have any number of effects on adult behavior, depending on whether it is being used by females as an indicator of mate availability, as suggested herein for *D. triton*, or as an indicator of mate suitability as suggested for wolf spiders. Expanding the scope of behavioral studies to account for the influence of juvenile development on adult behavior should yield many more novel findings such as these.

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