



Sexual cannibalism in fishing spiders (*Dolomedes triton*): an evaluation of two explanations for female aggression towards potential mates

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(Received 8 June 2000; initial acceptance 15 August 2000;

final acceptance 16 October 2000; MS. number: A8805)

I manipulated food availability in juvenile and adult fishing spiders (*Dolomedes triton*) to test two hypotheses for sexual cannibalism. The adaptive foraging hypothesis posits that sexual cannibalism is an economic, adaptive foraging strategy on the part of the adult female. In contrast, the aggressive-spillover hypothesis suggests that precopulatory sexual cannibalism is misplaced aggression favoured in previous life-history phases. Several results indicated support for the adaptive foraging hypothesis. First, increased adult food availability produced marginally nonsignificant fecundity benefits in female's first egg sacs and highly significant fecundity benefits in female's second egg sacs. Second, while consumption of a male did not result in more offspring in either egg sac, it did significantly increase the probability a female would successfully hatch an egg sac. Finally, mating trials revealed mixed support for the adaptive foraging hypothesis as, for the most part, female mating behaviour (attack or mate) was not determined by the adaptive value a male represented (food item or sperm donor). Specifically, the likelihood of a precopulatory attack was not determined by male size, date (an indirect estimate of male availability) or female nutrient load. However, mated females did tend to attack courting males more often than virgin females. The aggressive-spillover hypothesis was supported by several findings. For juveniles, food availability had a significant positive effect on fixed female size (cephalothorax area at final moult) which, in turn, had a significant positive effect on fecundity. Thus, the spillover hypothesis' assertion that strong fecundity selection acts on juvenile feeding and fixed adult size was supported. The possibility that the spillover and adaptive foraging hypotheses are not mutually exclusive is discussed, especially in light of the presence of high levels of sexual cannibalism both before and after mating.

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Sexual cannibalism, or intraspecific, intersexual predation of a male during courtship, copulation, or shortly thereafter, is a phenomenon that has fascinated and perplexed mating systems ecologists for the past century (Polis 1981; Elgar 1992; Johns & Maxwell 1997). Sexual cannibalism is relatively widespread among invertebrates, and is particularly prevalent amongst arachnids (Elgar 1992). Many hypotheses have been put forth to explain the evolution and maintenance of this behaviour, however, little consensus has been reached. While post-copulatory sexual cannibalism, defined generally as cannibalism of the male by the female after sperm transfer, has received considerable experimental and theoretical treatment as a male strategy (Thornhill 1976;

Parker 1979; Buskirk et al. 1984; Andrade 1996) and female strategy (Elgar 1998), fewer studies have addressed precopulatory sexual cannibalism. Consumption of the male prior to sperm transfer cannot be construed as an adaptive male tactic, thus hypotheses have focused on explaining precopulatory sexual cannibalism from the female's perspective.

Elgar (1992) lists three possible explanations for precopulatory sexual cannibalism. First, Gould (1984) suggested that sexual cannibalism may simply be the nonadaptive product of mistaken identity if generally aggressive females attack males as prey items before 'realizing' their adaptive value as mates. Second, females may use discriminatory aggression towards potential mates as an extreme mechanism of mate refusal. Males of inferior phenotype (e.g. small males) may be attacked, while large males are the preferred mates. Finally, precopulatory sexual cannibalism may arise strictly as an adaptive female foraging strategy.

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The adaptive foraging hypothesis for sexual cannibalism was first formalized by Newman & Elgar (1991), and it is essentially an economic model suggesting that females adaptively weigh a courting male's value as a mate versus his value as a food item. The model assumes strong effects of adult feeding on fecundity and that fertilization success is a function of the number of times a female mates. According to the adaptive foraging idea, females should attack males when food is limited but mates are not. Thus, the hypothesis predicts that the likelihood of sexually cannibalistic attacks will (1) increase with decreasing food availability, (2) increase as variation in food availability increases, (3) be higher for nonvirgin females relative to virgins, (4) increase as male size increases and (5) decrease for virgin females as the breeding season progresses and male availability presumably declines.

Recently, Arnqvist & Henriksson (1997) found little support for the adaptive foraging hypothesis in the European fishing spider, *Dolomedes fimbriatus*, as adult feeding was not related to fecundity, and the likelihood of sexually cannibalistic attacks was not a function of male value as either a mate or a food item. The latter result was emphasized by the finding that despite multiple mating opportunities, many females cannibalized males to the extent that they remained unmated throughout the experiment. In addition, rather than being a result of adult feeding, variation in fecundity was best explained by fixed female size (measured as cephalothorax area and leg length). These measures are termed 'fixed' because they are set for life in arachnids at the final moult, and thus can only be influenced by feeding during immature stages.

The absence of obvious benefits to precopulatory sexual cannibalism, compounded by the documentation of a cost of sexual cannibalism in the form of the risk of remaining unmated, caused Arnqvist & Henriksson (1997) to suggest that the act of sexual cannibalism is not adaptive when viewed solely in the context of mating. Instead, this modern-day variant of the mistaken-identity hypothesis suggests that apparently nonadaptive levels of aggression towards mates are, in fact, the result of a 'spillover' of high levels of aggression towards food (hereafter referred to as voracity) that are favoured in previous life-history stages. In particular, they suggested that fecundity selection favouring juvenile voracity, which results in larger fixed adult size, might be so intense that it outweighs the costs of aggression at mating. Thus, this 'aggressive-spillover' hypothesis predicts that the most voracious juveniles will acquire the most food, attain the greatest fixed adult size, have the highest fecundity, and be the most likely to attack their mates. In other words, if juvenile voracity is positively correlated with adult aggression towards mates, and the subsequent fecundity benefits of juvenile voracity are great, then this might explain apparently costly levels of aggression at mating.

Constraints-oriented explanations such as Arnqvist & Henriksson's (1997) aggressive-spillover hypothesis are increasing in popularity as behavioural ecologists become more aware that behavioural correlations can play an important role in constraining adaptive behavioural

expression (Price & Langen 1992; Sih 1992; Riechert & Hedrick 1993; Partridge 1994; Sih & Gleeson 1995). If, for example, the expression of antipredator behaviour is positively correlated across high and low risk contexts, perhaps due to genetic or physiological constraints, then strong selection favouring optimal antipredatory responses at high risk might favour seemingly nonadaptive antipredatory responses at low risk. Hypotheses such as these presume that the genetic variance/covariance matrixes that underlie correlated traits are conserved to the extent that adaptive plasticity (e.g. negative behavioural correlations) across contexts does not readily evolve (Houle 1991; Arnold 1992).

Surprisingly few studies have tested directly a behavioural correlation explanation such as the aggressive-spillover hypothesis. A few notable exceptions exist. Several works addressing the fear-aggression continuum have shown that in taxa as diverse as fish and spiders, the most aggressive individuals in territorial disputes are often also the boldest individuals when confronted with predation risk (Huntingford 1976; Riechert & Hedrick 1993). Thus, aggression or boldness is positively correlated across contexts as different as territorial defence and predator avoidance, a situation in which plasticity of aggression might be more adaptive. Working with sticklebacks (*Gasterosteus aculeatus*), Bakker (1994) showed that this positive boldness correlation is heritable and that it is maintained across different life-history switch points (i.e. juvenile aggression correlates positively with adult aggression). The aggressive-spillover hypothesis merely extends this aggressive syndrome to include positive correlations between juvenile voracity and adult female aggression towards courting males.

The present study is an effort to clarify the validity of the adaptive foraging and aggressive-spillover hypotheses for sexual cannibalism using the North American fishing spider, *Dolomedes triton*. First, I report the results of a manipulation of juvenile and adult food availability. I employed experimental food regime differences as a surrogate for natural levels of variation in voracity and food availability that are suggested to account for sexual cannibalism by the aggressive-spillover hypothesis. By manipulating the juvenile food regime I was able to test several critical assumptions of the spillover hypothesis, namely that juvenile feeding determines fixed adult size and that fixed adult size determines fecundity. In contrast, the adaptive foraging hypothesis predicts that female fecundity is a function of food eaten as an adult. Second, by conducting mating trials I test the assertion of the adaptive foraging hypothesis that the likelihood of sexual cannibalism is a function of the male's value as a mate or a food item. Specifically, female attacks are predicted to be more likely under the following conditions: (1) large male size, (2) high male availability (i.e. early in breeding season), (3) low food availability and (4) nonvirgin mating status. In contrast, the spillover hypothesis suggests that the likelihood of sexual cannibalism arises from an individual female's overall level of aggression, and thus should show no adaptive pattern within the context of mating. Instead, the spillover hypothesis predicts that the likelihood of sexual

cannibalism can be predicted from the juvenile female's level of voracity, and thus from her fixed adult size. This prediction of a positive correlation between juvenile voracity, fixed adult size and the likelihood of sexually cannibalistic attack is not addressed in the current study, as voracity is not measured in the present work. Instead, this crucial prediction of the spillover hypothesis is the focus of ongoing experiments. Finally, while fecundity benefits from male consumption are potentially consistent with both hypotheses, the spillover hypothesis can account for costs of sexual cannibalism (incomplete fertilization) if the benefits of voracity in other contexts generally outweigh this risk.

Behaviour and Ecology of Fishing Spider Feeding and Mating

Fishing spiders (*Dolomedes* spp., Pisauridae: Araneae) are large, cursorial sit-and-wait predators most commonly associated with the edges of aquatic habitat (Carico 1973). In particular, *D. triton* is the most widely distributed species in North America, and is characteristically found along the edges of ponds or slow-moving streams. Fishing spiders forage by localizing vibratory prey stimuli and lunging at their prey (Bleckmann & Barth 1984). Prey items are most commonly insects trapped at the water surface (Carico 1973; Barth 1982; Zimmerman & Spence 1989), however fishing spiders are renowned for their ability, albeit infrequent, to attack and successfully subdue and consume aquatic vertebrate prey that often greatly outsize them (Bleckmann & Lotz 1987; personal observation).

The *Dolomedes* mating sequence is initiated when a searching male encounters female silken drag lines, which elicit a stereotypic courtship sequence of male leg waving and a slow regular tapping of the water surface or solid substrate (Carico 1973; Arnqvist 1992). If not immediately attacked, males proceed cautiously, approaching the female and continuing courtship movements. Males mount the dorsum of the female, lean forward usually between the female's legs II and III, and insert a single pedipalp charged with sperm into the female's epigynum, which is located at the ventral junction between the cephalothorax and abdomen. Sperm transfer takes only a few seconds after which the male jumps off and retreats. This process is often repeated and the male's second pedipalp is discharged. Mated females eventually produce an egg sac, which they carry in their mouthparts and defend throughout its development (approximately a 2-week period). Just prior to egg-sac hatching, females typically climb up in the vegetation and construct an elaborate nursery web for the emergent spiderlings.

Adult female fishing spiders are known to attack males at any point during this copulatory sequence. However, laboratory mating trials indicate that females of the European fishing spider, *D. fimbriatus*, most commonly attack during precopulatory courtship (75% of trials) and that males are killed in ca. 5–10% of these attacks (Arnqvist 1992; Arnqvist & Henriksson 1997). 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, aggression in the form of sexual cannibalism does appear to play a crucial role in the population ecology of *D. triton* and *D. fimbriatus*.

METHODS

As a surrogate for individual variation in female voracity resulting in differential feeding rates, I directly manipulated female access to food in the laboratory. To measure the relative effects of juvenile and adult feeding rate on fecundity I manipulated food availability for each age class using a 2×2 factorial design. The adaptive foraging hypothesis assumes that female fecundity is determined primarily by feeding rate during adulthood (i.e. that consuming one or more males increases fecundity). In contrast, the aggressive-spillover hypothesis posits that juvenile feeding rate determines fixed adult size, which in turn, is the main determinant of female fecundity.

General Protocol

Mature male and juvenile female *D. triton* that were approximately 2–4 weeks (1–2 moults) from maturity were collected in early May 1999 from ponds at the University of Kentucky's Ecological Research Facility, Lexington, Kentucky, U.S.A. (38°2'N, 84°36'W). Throughout the experiment males and immature females were kept in 425-ml transparent plastic cups filled with filtered water to a depth of 2.0 cm. Styrofoam floats (2.0 × 1.5 × 0.5 cm) were provided as a resting spot and underwater refuge. All spiders were weighed to the nearest milligram and images were digitally captured (Snappy 3.0) on the first day of the experiment. Females were weighed and imaged every 2 weeks thereafter. Morphological measures were made by digitizing relevant points on the spider image and connecting these points.

Following Arnqvist & Henriksson (1997), I measured fixed adult size as the area of the adult cephalothorax: area of an ellipse = $\pi \times (\text{cephalothorax width}/2) \times (\text{cephalothorax length}/2)$. Immature female spiders were randomly assigned to one of four food availability treatments ($N=15$ for each group): (1) low juvenile food, low adult food; (2) low juvenile food, high adult food; (3) high juvenile food, low adult food; (4) high juvenile food, high adult food. Upon adult emergence, females were moved to individual plastic containers (14 × 10 × 8 cm) filled with filtered water to a depth of 2.0 cm, and provided with Styrofoam floats (10 × 6 × 0.5 cm). Adult female containers were also provided with an inverted 212-ml plastic cup with opposing sides cut out. These 'spider dens' served as an additional refuge for females and males during mating trials, but did not preclude observation of copulations.

Food Regimes

Juvenile diets were initiated immediately upon collection and continued until adult emergence. Adult diets

Table 1. Least square means±standard error (N) for four diet regimes

Diet regime		Days on juvenile diet	Fixed adult size (mm ²)	Number of spiderlings
Juvenile	Adult			
Low	Low	20.40±2.26 (15)	37.24±2.00 (15)	386.00±67.80 (9)
Low	High	22.92±2.22 (12)	41.09±2.20 (12)	539.71±76.90 (7)
High	Low	17.07±1.26 (14)	43.32±2.10 (14)	562.67±67.80 (9)
High	High	14.92±1.30 (12)	43.41±2.10 (12)	685.60±91.00 (5)

Food contrasts indicate support for both the adaptive foraging and aggressive-spillover hypotheses.

began the first day of adulthood and continued until death. Adult females were not fed while they guarded their egg sacs (approximately a 2-week period) because during this time females will not release the egg sac to attack and consume food items. Low food availability consisted of one weekly feeding of one house cricket (*Acheta domestica*) weighing 50–75% of the spider's body mass, whereas high food availability consisted of three feedings per week of a cricket weighing 50–75% of the spider's body mass. Crickets were dropped upon the water surface in female containers. To minimize stress to the spiders, no cricket was offered if the previous food item had not been consumed.

Mating Trials

I paired virgin females 14 days into adulthood in their respective containers with a randomly selected male spider and observed them directly for a period of 2 h, or until mating had taken place. Males not displaying the typical leg waving and tapping courtship behaviours were replaced after 30 min. I scored reaction to male courtship (i.e. attack or mate), whether an attack resulted in a successful kill, and the number of palpal insertions achieved by the male. Females failing to mate were paired with a different male 1 week later. Mated females that had not yet produced an egg sac were paired 1 week later with a new male. Upon producing an egg sac females were left alone until the egg sac hatched. Two days after a hatching, I cut the nursery web out of the female's container and counted all spiderlings. Females that produced egg sacs that failed to hatch were not included in fecundity analyses.

Statistical Analyses

I performed statistical tests with SAS (1988). I analysed the effects of juvenile and adult food availability on fecundity via two-way analysis of variance (ANOVA). I analysed the likelihood of sexual cannibalism with binary logistic regressions for continuous variables (male size and date) and an analysis of maximum likelihood for the discrete variable female feeding regime. I performed a four-category *G* test for goodness of fit to examine the effect of mating status (virgin, nonvirgin) on the likelihood of sexual cannibalism. In this test I compared the observed frequency of attack tactics to an expected frequency derived from an estimate of the overall

probability of precopulatory attack irrespective of female mating status.

RESULTS

Food Regimes and Fecundity

Table 1 summarizes the effects of food regimes on juvenile growth, fixed adult size and fecundity. In accordance with the suggestion that juvenile feeding influences growth rate and development, low-food immature females pooled across adult diets ($N=27$) spent 21.5 days on their juvenile diets before moulting into adults, while their high-food counterparts ($N=26$) matured after only 16.1 days. This difference in development rate was statistically significant (*t* test with unequal variances: $t_{41,2}=2.10$, $P=0.04$). Despite being on their juvenile diets for a shorter period of time, high-food juveniles matured at significantly larger fixed adult body sizes than low-food juveniles ($t_{51}=2.11$, $P=0.04$).

There was no significant effect of diet manipulation on the probability that a female would have an egg sac hatch (juvenile food effect: $\chi^2_1=0.97$, $P=0.32$, adult food effect: $\chi^2_1=2.02$, $P=0.15$). However, as predicted by the aggressive-spillover hypothesis, a two-factor analysis of variance showed that high juvenile food availability had a statistically significant positive effect on the number of spiderlings produced in a female's first egg sac ($F_{1,26}=4.44$, $P=0.04$). Adult food availability also showed a tendency towards a positive effect on the number of spiderlings produced in the first egg sac, but this effect was not statistically significant ($F_{1,26}=3.27$, $P=0.08$). However, a similar analysis performed on a data set that excluded one outlying, well-fed juvenile that produced over 1000 offspring showed a reversal of this pattern with adult food being statistically significant ($F_{1,25}=5.51$, $P=0.03$), and juvenile food being marginally nonsignificant ($F_{1,25}=3.60$, $P=0.07$). There was no interaction between food regimes on the number of spiderlings produced.

To examine further the relationship between juvenile food availability, fixed adult size and fecundity, I performed an analysis of covariance (ANCOVA) with fixed adult size as the covariate. The model showed that fixed adult size was positively related to fecundity ($F_{1,24}=6.07$, $P=0.02$), but that beyond this size effect, there was no additional effect of juvenile food regime on fecundity ($F_{1,24}=2.13$, $P=0.16$). Interestingly, when fixed adult size

Table 2. Likelihood of a sexually cannibalistic attack given variables predicted to be important by the adaptive foraging model

Variable	Precopulatory attack			Postcopulatory attack		
	χ^2	<i>N</i>	<i>P</i>	χ^2	<i>N</i>	<i>P</i>
Male size	0.006	50	0.930	0.560	36	0.460
Date (male availability)	0.040	52	0.830	0.210	36	0.650
Female feeding regime (juvenile food effect)	0.090	52	0.760	0.020	36	0.880
Female feeding regime (adult food effect)	1.750	52	0.190	1.250	36	0.260

was controlled, the effect of adult feeding on fecundity became statistically significant ($F_{1,24}=4.61$, $P=0.04$).

Neither juvenile nor adult food availability affected the probability of hatching a second egg sac (hatching success ranged between 64 and 75% across treatments). However, two-factor analysis of variance showed that the number of offspring in a second egg sac was significantly increased by high adult food availability ($F_{1,17}=20.63$, $P=0.0003$), but not by high juvenile food availability ($F_{1,17}=1.72$, $P=0.21$).

Palpal Insertions and Fertilization Success

Arnqvist & Henriksson's (1997) sole finding that supported the adaptive foraging hypothesis was a significant rank correlation between the number of palpal insertions received by the female (0, 1, or 2) and the fertilization success of her first egg sac. In the current study, analysis of covariance controlling for fixed adult size showed a significant effect of the number of palpal insertions on spiderling production ($F_{2,49}=12.33$, $P=0.0001$). However, individual contrasts showed this effect to be solely the result of females receiving no insertions producing no offspring. Females accepting a single insertion ($N=26$) produced on average 432 offspring in their first egg sac, whereas females with multiple insertions ($N=10$) produced 333 offspring (Student's *t* test: $t_{34}=0.75$, $P=0.46$).

Likelihood of Sexual Cannibalism

With regard to sexual cannibalism, females have three behavioural options: (1) attack before mating, (2) accept one insertion then attack and (3) accept two insertions then attack. Thus, results will be presented for the likelihood of precopulatory attacks confined to each female's first virgin pairing (option 1, $N=52$), and for the likelihood of postcopulatory attacks confined to each female's first pairing that resulted in a mating (option 2, $N=36$). Few females accepted two insertions from the same male, and none of these females attacked after a second insertion (option 3). Overall, option 1 occurred 11/52 times (21%) and option 2 occurred 19/36 times (53%).

Likelihood statistics are summarized in Tables 2 and 3. Binary logistic regressions showed that the likelihood of virgin female attack (pre- or postcopulatory) was not affected by male size or time during the breeding season (an indirect indicator of male availability). Interestingly, a

Table 3. The observed and expected frequency distribution of four foraging tactics used by virgin and nonvirgin female fishing spiders, given an estimated experimentwide 29% probability of attack

Tactic	Virgin	Nonvirgin	Expected	Observed
1	Attack	Attack	1.76	1
2	Attack	No attack	4.32	2
3	No attack	Attack	4.32	9
4	No attack	No attack	10.59	9
Total			21.00	21

similar analysis on male size showed that large males tended to escape precopulatory attacks more often than small males ($\chi^2_1=3.66$, $N=50$, $P=0.06$). However, females did not preferentially mate with large males ($\chi^2_1=2.15$, $N=36$, $P=0.14$). Analysis of maximum likelihood showed no significant effect of either juvenile or adult feeding regimes on the likelihood of pre- or postcopulatory attacks. However, when pre- and postcopulatory attacks were combined, poorly fed adults did attack their mates more often than well-fed adults ($\chi^2_1=5.23$, $N=52$, $P=0.02$). Contrary to the aggressive-spillover hypothesis, fixed female size was not positively related to the likelihood of precopulatory attack within each juvenile diet regime (low-food juveniles: $\chi^2_1=0.47$, $N=24$, $P=0.49$; high-food juveniles: $\chi^2_1=1.52$, $N=25$, $P=0.22$).

A four-class *G* test for goodness of fit (see Table 3) showed that females employ the tactic of not attacking as a virgin but attacking as a nonvirgin (tactic 3) more often than can be explained by the expected frequency given an overall, experimentwide attack probability of 29% ($G_2=6.07$, $0.025 < P < 0.05$). No females switched postcopulatory tactics between their virgin mating and their first nonvirgin mating, thus precluding an evaluation of the likelihood of postcopulatory attacks given a female's mating history.

Costs and Benefits of Sexual Cannibalism

Twenty-eight per cent of females (15/53) failed to accept a palpal insertion despite multiple mating opportunities and thus remained unmated throughout the experiment. However, this 'cost' of remaining unmated cannot be attributed to sexual cannibalism in the present experiment as only 20% (3/15) of these unmated females behaved aggressively towards their potential mates. In fact, females accepting at least one insertion during the

experiment were marginally more likely to attack a mate (17/38, 45%) than the 15 females that remained unmated ($\chi^2_1=3.68$, $P=0.06$).

Cannibalizing at least one male significantly increased the probability of having an egg sac hatch (first egg sac: $\chi^2_1=8.09$, $P=0.004$; second egg sac: $\chi^2_1=4.31$, $P=0.04$). However, amongst females that hatched an egg sac, analysis of covariance controlling for fixed adult size ($F_{1,27}=4.10$, $P=0.05$), showed that females that killed and consumed at least one male did not produce more offspring than females that failed to cannibalize a male (first egg sac: $F_{1,27}=0.02$, $P=0.87$; second egg sac: $F_{1,19}=0.06$, $P=0.81$).

DISCUSSION

The aggressive-spillover hypothesis assumes that selection acting upon juvenile voracity favours high juvenile feeding rates and results in larger fixed adult body size and ultimately increased fecundity. Because the spillover hypothesis contends that precopulatory sexual cannibalism is a carry-over effect, it suggests that the likelihood of sexual cannibalism is predicted by an individual female's overall level of aggression rather than any adaptive benefit of male consumption per se. In contrast, the foraging hypothesis rests upon the assumption that adult feeding translates into fecundity benefits, as well as the prediction that females treat courting males according to their relative value as a sperm donor versus food item. Finally, the hypotheses differ in that the adaptive foraging explanation predicts benefits to sexual cannibalism, while the spillover hypothesis can explain apparently overzealous, maladaptive sexual cannibalism if benefits to the aggressive syndrome outweigh this potential cost to female fitness.

Food Availability and Fecundity

In support of the aggressive-spillover hypothesis, high juvenile food availability had several beneficial effects. First, well-fed juveniles matured faster than poorly fed juveniles. Thus, juveniles securing the most food may accrue a multitude of benefits inherent in early maturation (e.g. increased mate availability, reduced predation risk, broadening of diet, more time to produce multiple egg sacs). Further work will be required to determine whether these subtleties offer early maturing females a selective advantage.

High juvenile food availability also resulted in females of significantly larger fixed adult body size. This difference in fixed size accounted for a significant amount of the variation in fecundity attributable to juvenile food regimes. Thus, relatively modest increases in cephalothorax area can yield substantial increases in fecundity. While other works have noted a strong relationship between fixed size and fecundity in *Dolomedes* (Spence et al. 1996; Arnqvist & Henriksson 1997), this is the first study on fishing spiders to manipulate juvenile food availability, thus documenting the link between juvenile food, fixed size and fecundity.

It should be noted that these juvenile food effects on development time, fixed adult size and fecundity were all produced in the present study by manipulating only the latter 3 weeks of the juvenile life cycle (1–2 moults). In natural populations, juvenile *D. triton* typically experience a 2-year life cycle and are thought to go through 10–12 moults before adulthood (Carico 1973; Foelix 1982). Variation in juvenile food availability for the entire juvenile period should potentially yield even larger fecundity differences. Perhaps the most intriguing and persistent mechanism by which juvenile fishing spiders would consistently vary in their access to food is heritable variation in voracity. This is, of course, a key assumption underlying the aggressive-spillover hypothesis: voracious juveniles secure more food items (Hedrick & Riechert 1989; Uetz 1992), grow to larger fixed adult body sizes, and produce more offspring than their less voracious counterparts. Intense fecundity selection on juvenile voracity, particularly with no selection for juveniles to discriminate conspecifics from heterospecifics, could overwhelm any cost of indiscriminant aggression at mating and explain the maintenance of precopulatory sexual cannibalism.

In support of the adult foraging hypothesis, a high adult food regime yielded fecundity benefits, a finding in conflict with other recent works (Spence et al. 1996; Arnqvist & Henriksson 1997). Thus, both juvenile and adult food availability seem to impact fecundity in this study, whereas their interaction did not affect fecundity. Spence et al. (1996) addressed the relative importance of fixed adult size and adult food availability to fecundity. They describe an interaction between fixed size and adult food availability for a northern population of *D. triton* in which females of large fixed adult body size can only realize the fecundity benefits of their large size under conditions of high adult food abundance. Under experimental conditions of adult food limitation, a situation not naturally found in the field during the 2 years of their study, females were unable to translate fixed adult size into fecundity benefits. The present data (see Table 1) support their finding that fecundity in well-fed adults is determined by fixed adult size. However, in the present study, low-food adults also had their fecundity determined primarily by differences in juvenile food availability and fixed size. While these two studies differ in the magnitude of importance they place on juvenile food availability to fecundity, the recurring theme is that both juvenile and adult food appear to be important factors that ultimately determine fecundity.

In summary the fecundity results presented here support the contention that intense fecundity selection acts on juvenile female fishing spiders to secure prey items and maximize fixed adult body size. That said, adult food availability clearly plays a significant role in determining fecundity through its effects on offspring number, in particular its effect on fecundity via offspring number in second egg sacs. It may be naïve to expect food availability in one life-history phase to determine fecundity at the expense of the importance of food availability during other life-history phases. While statistical significance fluctuated given the specific test being done, at all times

both modes of food availability explained a substantial amount of variation in fecundity.

However, the aggressive-spillover hypothesis does not require that adult food availability have no effect on fecundity. In fact, a broader interpretation of the spillover hypothesis would suggest that fecundity benefits derived from juvenile voracity and adult voracity towards hetero-specific prey combine to outweigh the costs of sexual cannibalism. Regardless, as long as the fecundity benefits of voracity (juvenile or adult) outside of the mating context are large enough to outweigh any cost of the spillover of aggression to the mating female, the spillover hypothesis remains a viable explanation for aggression towards courting males.

Sperm Limitation

Fertilization success was not measured in the present study, therefore there is no way of knowing how many more offspring females could have produced if they had accepted more palpal insertions. None the less, evidence of sperm limitation was lacking in the present experiment. Females accepting multiple insertions realized no fitness benefits above and beyond that achieved by females accepting a single insertion. This assumption of the adaptive foraging hypothesis, that a direct relationship exists between number of insertions and fertilization success, is primarily a quantitative tool that allows the model to estimate expected reproductive output for females making decisions as to whether they should mate or cannibalize. Relaxation of this assumption strengthens the prediction of heightened sexually cannibalistic tendencies in mated females, but does not change any other qualitative predictions of the model (see Figure 2 in Newman & Elgar 1991). If a single insertion typically provides a female with enough sperm for her lifetime (Jackson 1980; Foelix 1983), then mated females should value all future suitors, including their first mate attempting to achieve a second palpal insertion, as food more so than as mates. Indeed, this is one of the trends seen in the present study (see below).

Newman & Elgar's (1991) adaptive foraging hypothesis for sexual cannibalism is strictly a material benefits model that attempts to explain female mating decisions (i.e. attack or mate) based on the premium females place on males as sperm donors or as food items. However, females may accept multiple mates for reasons other than attempts to maximize fertilization success. For example, much recent work addresses the hypothesis that females accept multiple mates, and thereby receive more sperm than they need to fertilize all of their available eggs, thus promoting sperm competition between males and cryptically choosing only the most competitive gametes (Eberhard 1998).

Likelihood of Sexual Cannibalism

Increasing male size and availability (date variable, Table 2) failed to enhance the probability of pre- or post-copulatory attacks. In line with Arnqvist & Henriksson

(1997), these data provide further evidence against the adaptive foraging hypothesis. There are several reasons one might not expect females to selectively attack large males despite the fact that they presumably represent the greatest nutritional reward. First, large males are better at escaping female attacks (present study; Arnqvist 1992; Arnqvist & Henriksson 1997). Thus, females may avoid attacking large males because they will incur greater resistance from such a male, or because females may expend more energy subduing a large male. Second, females may actively prefer to mate with large males in order to secure the indirect benefit of large body size for their offspring. However, no female mating preference for large males was noted in the present experiment. The latter suggestion, that females use precopulatory attacks/passivity as a drastic form of mate refusal/acceptance, is an often-cited possibility that has rarely been tested experimentally (Elgar & Nash 1988; Elgar 1992). Finally, as suggested by the aggressive-spillover hypothesis and as seen in the current study, females may react aggressively to males regardless of their size, and only large males survive these attacks.

Note that all three of these explanations for female aggression at mating result in directional selection on male body size; however, they make very different assumptions about female discriminatory abilities. The first two alternatives predict 'active' preferences for cannibalizing small males and for mating with large males respectively, while the third suggests no aggressive discrimination on the part of the female. A parallel dichotomy exists in the modern-day study of mate choice with the distinction some behaviourists draw between 'active mate choice' typified by adaptive female preferences for males of a certain phenotype, and indirect mechanisms of intersexual selection (Andersson 1994; Wiley & Poston 1996). The lack of evidence for adaptive female mating preferences for large males, combined with the lack of discrimination females show in choosing which males to attack, support an indirect mechanism of intersexual selection characterized by stereotypically high levels of aggression regardless of male size, and a large-male superiority in escaping female attacks.

If females make aggressive 'decisions' based on male material value (food or sperm), then as the season progresses and male availability declines, a virgin female should increasingly view a courting male as a mate, regardless of her nutrient load. However, no evidence of a seasonal decline in aggressive attacks was apparent in the present study. In nature, females may routinely encounter enough males early in the breeding season that the risk of progressing unmated into a time of the breeding season when males are limiting might be unrealistic. Unfortunately, little is known about the number of courting males that females may have to choose from in nature. It is known, however, that sex ratios at the beginning of the season may vary a great deal. Zimmerman & Spence (1992) documented a 1:1 sex ratio in 1986 followed by 2:1 sex ratio biased in favour of males in 1987. Thus, the limited available data suggest that males may be quite abundant at times, and may not represent a limiting resource to females early in the

season. Note that this line of thinking should remove the cost of aggression noted experimentally by [Arnqvist & Henriksson \(1997\)](#). If males are abundant during the period soon after females reach sexual maturity, then regardless of their aggressive behaviour females may never run the risk of remaining incompletely fertilized. In opposition to this suggestion is the finding of females in the field with incompletely fertilized egg sacs ([Arnqvist & Henriksson 1997](#)). To document whether or not females in nature are, in fact, running a high risk of remaining incompletely fertilized by behaving aggressively towards potential mates, future empirical and theoretical work should focus on the temporal patterns of male abundance and female aggression towards males throughout the breeding season.

Perhaps the most intuitive prediction of the adaptive foraging hypothesis is that if females cannibalize potential mates as an adaptive foraging strategy, then attacks should be more prevalent for food-limited females. However, surprisingly few studies have shown a positive relationship between female hunger levels and the likelihood of sexual cannibalism in arachnids (e.g. [Jackson 1980](#); [Breene & Sweet 1985](#); [Elgar & Nash 1988](#); [Arnqvist & Henriksson 1997](#); but see [Andrade 1998](#)). Similarly, in the present study, no effect of diet regime was found on the prevalence of pre- or postcopulatory attacks individually. However, poorly fed females did attack more often than well-fed females when pre- and postcopulatory attacks were combined. Thus, the prediction of the adaptive foraging hypothesis is supported if both types of sexual cannibalism are included. It would seem reasonable that if sexual cannibalism is an adaptive foraging strategy it could include attacks before and after sperm transfer. None the less, consistent with the spillover hypothesis' suggestion that females attack courting males indiscriminately, females do not appear to modulate their precopulatory aggressive behaviour according to their hunger level.

The adaptive foraging hypothesis asserts that females should use their own mating status (sperm needs) as a factor in determining whether they will eat, mate, or mate and eat a male. The current study provides two pieces of support for this idea. First, attacks after an insertion occurred more than 50% of the time, whereas attacks before an insertion occurred only 21% of the time. Thus, females seem much more likely to attack a male after they have obtained sperm. Second, the observed prevalence of the tactic of not attacking as a virgin but attacking as a nonvirgin exceeded that predicted by a distribution derived from the overall attack prevalence regardless of mating status. Thus, female mating status seems to be an excellent predictor of the likelihood of sexual cannibalism.

Finally, the aggressive-spillover hypothesis predicts that the likelihood of attack is a function of a female's overall level of voracity, and thus is predicted by her fixed size, rather than any indicator of male adaptive value. The current study offers little to test this idea because juvenile voracity was not measured and fixed size was artificially enhanced via variable juvenile food regimes. However, within juvenile food regimes, no correlation

was found between fixed size and the likelihood of sexually cannibalistic attack. Studies currently in progress will more adequately address this crucial assumption of the spillover hypothesis, namely that the most voracious juveniles will also be the adults that are most likely to attack their mates.

Costs and Benefits of Sexual Cannibalism

The aggressive-spillover hypothesis requires no net benefit to male consumption, but instead stresses that benefits of aggression in other contexts must outweigh the cost of eating rather than mating with males. Laboratory studies such as this one might overestimate the cost of cannibalism by providing females with artificially low numbers of potential mates, thus increasing the chances a female will remain incompletely fertilized. Despite this fact, in the present study, no evidence was found that aggression towards mates was responsible for females remaining unmated or incompletely fertilized. Future field surveys of egg sac fertilization rates, along with experimental manipulations of male availability, should allow a better approximation of the costs of aggression to female fertilization rates. Such experiments will also evaluate the intriguing possible trade-off between the benefits of juvenile voracity in terms of large adult size (measured as the number of eggs manufactured) versus the costs of this aggressive syndrome to the adult female (measured as the number of unfertilized eggs/number of eggs manufactured).

In contrast, the adaptive foraging hypothesis requires that sexual cannibalism has adaptive benefits. In the present study male consumption was not responsible for the production of more offspring. In fact, few studies have shown such a quantitative benefit of sexual cannibalism or less extreme courtship food gifts (but see [Andrade 1996](#)). While eating a male did not yield more offspring, it did increase the probability that a female would hatch an egg sac. Thus, males may represent an important qualitative addition to the female's diet. First, studies of nutritional ecology have shown that arachnids require a breadth of amino acids to maximize reproduction ([Riechert & Harp 1987](#)), and that some species will display prey selectivity in order to optimize the diversity of amino acids in their diet ([Greenstone 1979](#)). Second, males may be qualitatively important prey items if they are more efficiently converted to energy than other prey items ([Elgar & Nash 1988](#)). Finally, postmating feeding in spiders is known to be associated with the onset of the accumulation of larger egg yolk granules ([Foelix 1982](#)). Accordingly, males may represent adaptive foraging to females not in terms of the crude mass they offer, but instead as a source of nutrient diversity, which is most efficiently converted to energy, and is available at a crucial time in egg development.

The original inspiration for the aggressive-spillover hypothesis was [Gould's \(1984\)](#) suggestion that sexual cannibalism is maintained simply because generally aggressive females mistake the identity of courting males and attack them. Following [Arnqvist & Henriksson's](#)

(1997) suggestion that selection for a syndrome of aggression could explain apparently costly levels of aggression towards mates, I have presented data that support and link assumptions 2 and 3 of the spillover hypothesis: increasing juvenile food availability positively affects fixed adult size, which, in turn, positively affects fecundity. Future work will standardize an assay of female aggressive tendencies to address the critical final assumption, that intraindividual, positive behavioural correlations in levels of aggression across contexts (juvenile voracity and adult aggression towards courting males) result in behaviourally constrained, precopulatory sexual cannibalism.

In conclusion, none of the evidence presented for or against either hypothesis mutually excludes the other hypothesis. For example, the trend for poorly fed adult females to attack indiscriminately upon courtship, but to attack more often than their well-fed counterparts when postinsertion attacks are included, fits a hypothesis combining a spillover of genetically constrained, precopulatory aggression with adaptive postinsertion aggression, which corresponds to the predictions of the adaptive foraging hypothesis. Indeed, the optimal behaviour for a hungry, virgin female is to mate and then feed on the male. Thus, the two hypotheses might explain sexual cannibalism at different stages of the mating sequence. While the elaborate nature of male courtship in fishing spiders (Carico 1973; Bleckman & Bender 1987; Bleckman & Lotz 1987) suggests that male signals are finely tuned to female sensory biases, it remains a possibility that precopulatory attacks may result from female aggressive tendencies, which are favoured outside of the mating context, overwhelming their discriminatory capacities. Subsequent to that, following successful insertions, females may cannibalize mates according to the predictions of the adaptive foraging model. Inter-populational and interspecific variation in factors such as juvenile and adult food limitation may alter the relative importance of each mechanism. For example, severe food limitation in the juvenile phase may accentuate benefits of juvenile voracity, thus moderating the cost/benefit ratio of aggressive spillover. In contrast, food limitation during the adult phase should coincide with increases in sexual cannibalism according to the predictions of the adaptive foraging hypothesis. Sequential components of a complex behavioural continuum such as sexual cannibalism need not have the same mechanistic or evolutionary explanation.

Acknowledgments

This work benefited greatly from comments and suggestions made by Andy Sih and Goran Arnqvist. I thank Andy Sih, Rob Ziemba, Tracie Ivy and two anonymous referees for reading and commenting on the manuscript. Members of the Sih laboratory and Center for Ecology, Evolution and Behavior at the University of Kentucky discussed and critiqued the study's design, data analysis and interpretation on several occasions. I thank Sandra Deer, Jane Bishop, Jennifer Deer, Tracie Ivy, Gina Hupton and Penny for their love and moral support. Financial

support was provided by a National Science Foundation Graduate Research Training Fellowship, and the University of Kentucky's Graduate School, School of Biological Sciences, and Center for Ecology, Evolution and Behavior.

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