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Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints

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Summary

Several hypotheses have been proposed for the evolution of sexual cannibalism by females. Newman and Elgar (1991) suggested that sexual cannibalism prior to mating by virgin female spiders may have evolved as a result of female foraging considerations. According to this model, an adult female's decision to mate or cannibalize a courting male should be based on an assessment of the male's value as a meal versus his value as a mate. The current study provides an empirical test of the assumptions and predictions of this model in the sexually cannibalistic fishing spider. Adult females were subjected to different food treatments, and exposed to adult males in the laboratory. However, only one of the assumptions of the model and none of its five predictions were upheld. We failed to find any effects of female foraging, female mating status, female size, male size or time of the season on females' behaviour towards courting males. Females behaved stereotypically, and many females were left unmated despite numerous mating opportunities. We also demonstrate costs of sexual cannibalism in a natural population. We propose that the act of sexual cannibalism in the fishing spider is non-adaptive, and develop a model for the evolution of premating sexual cannibalism in spiders based on genetic constraints. According to this hypothesis, sexual cannibalism by adult females may have evolved as an indirect result of selection for high and non-discriminate aggression during previous ontogenetic stages. Genetic covariance between different components of aggressive behaviour may constrain the degree to which (1) juvenile and adult aggression and/or (2) aggression towards conspecifics and heterospecifics can vary independently. We briefly review the support for our model, and suggest several critical tests that may be used to assess the assumptions and predictions of the model.

Keywords: Araneae; evolutionary constraints; genetic constraints; mating behaviour; sexual cannibalism; spiders

Introduction

Sexual cannibalism is a matter of some controversy, and various hypotheses have been proposed to account for the evolution of this dramatic behaviour. Sexual cannibalism is said to occur when a female kills and consumes her mate during some stage of courtship and/or mating. It occurs frequently in spiders and several other invertebrates (Thornhill, 1976; Polis, 1981; Elgar, 1992), and it is thought to play a significant role in the evolution of sexual behaviour and sexual dimorphism in many species (Robinson, 1982; Ridley, 1983; Austad and Thornhill, 1986; Elgar *et al.*, 1990; Barth and Schmitt, 1991; Elgar, 1991; Prenter *et al.*, 1994; Andrade, 1996). Thornhill (1976) and Parker (1979) originally proposed that sexual cannibalism after sperm transfer evolved as an extreme form of paternal investment; that is, males offer their body as a blood meal to females,

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thereby increasing the quantity or quality of the offspring. This suggestion was subsequently formalized by Buskirk *et al.* (1984), who showed that sexual cannibalism after mating may be adaptive for males if (1) males have a very low probability of remating with other females and (2) the act of cannibalism significantly increases offspring number or quality. Further, Andrade (1996) showed that sexual cannibalism during or after mating may be adaptive in terms of sperm competition avoidance.

However, even though the paternal investment hypothesis has received much attention, it has been rejected as a general explanation of the evolution of sexual cannibalism for three reasons. First, and most importantly, sexual cannibalism most frequently occurs *before* copulation (see Elgar, 1992). The paternal investment and sperm competition avoidance hypotheses are clearly not applicable in these cases, since the male is consumed prior to sperm transfer. Second, male mating behaviour seems poorly designed for sexual cannibalism in most sexually cannibalistic species (Polis and Farley, 1979; Gould, 1984; Breene and Sweet, 1985; Birkhead *et al.*, 1988; Arnqvist, 1992; Elgar, 1992; Lawrence, 1992; but see Forster, 1992; Sasaki and Iwahashi, 1995; Andrade, 1996). Third, males are potentially able to mate with multiple females even in species classically characterized as sexually cannibalistic (Breene and Sweet, 1985; Birkhead *et al.*, 1988).

Newman and Elgar (1991) presented a model that accounts for premating sexual cannibalism. While previous models focused on male interests, this model dealt only with female interests. Newman and Elgar (1991) showed that, given a number of assumptions, cannibalism prior to copulation by unmated (virgin) females may evolve solely as a result of female foraging considerations. The act of sexual cannibalism may be said to be adaptive for females but not for males, and the model thus predicts an intense sexual conflict where males attempt to copulate and then escape while the optimal female option may be to consume the male prior to sperm transfer. However, there have been very few experimental studies of sexual cannibalism, and many empirical observations are more or less anecdotal (Elgar, 1992). This study represents an experimental test of the assumptions and predictions of the model of Newman and Elgar (1991). Experiments were performed with the fishing spider, a highly cannibalistic species (see below). We also present a new and essentially non-adaptive hypothesis for the evolution of premating sexual cannibalism, based on spillover effects of aggression among ontogenetic stages.

The fishing spider

Fishing spiders (*Dolomedes* spp., Pisauridae: Araneae) are large semi-aquatic 'sit-and-wait' predators that feed primarily on arthropods trapped at the water surface, but also prey on vertebrates such as small fish and tadpoles (Schmidt, 1953, 1957; Carico, 1973; Williams, 1979; Bleckman and Lotz, 1987; Zimmermann and Spence, 1989). Males exhibit an elaborate pre-copulatory courtship display, involving vibratory signalling and leg-waving, during which they approach females with great caution (Roland and Rovner, 1983; Bleckman, 1985; Bleckman and Bender, 1987; Arnqvist, 1992). If the female remains passive when approached, the male mounts her and transfers sperm. Males may insert one or two pedipalps during a mating, and each palpal insertion typically lasts only a few seconds (Schmidt, 1957; Carico, 1973; Arnqvist, 1992). Matings are terminated by males, who make a sudden jump followed by a rapid retreat. Females carry and tend their egg sac, and construct and guard a nursery web at the time of spiderling emergence. Most females in natural populations only produce a single egg sac during their life (Zimmermann and Spence, 1992; G. Arnqvist, personal observation).

Female fishing spiders are sexually cannibalistic, and laboratory studies of *D. fimbriatus* demonstrate that virgin females may attack and attempt to cannibalize males during any part of courtship and mating (Gerhardt, 1926; Schmidt, 1953, 1957; Arnqvist, 1992). Females' most common response to male courtship is to attack from a distance, and males in the laboratory suffer approximately a 5% risk of being cannibalized prior to sperm transfer in any given mating attempt (Arnqvist, 1992). Field studies of *D. triton* have verified that males are common prey of females, and that sexual cannibalism has dramatic consequences for population dynamics (Zimmermann and Spence, 1989, 1992). The sex ratio at the time of adult emergence is close to 1:1, and males emerge prior to females. However, the male population declines dramatically at the time of female emergence (Zimmermann and Spence, 1992). This pattern also occurs in *D. fimbriatus* (G. Arnqvist, personal observation).

The model

The model of Newman and Elgar (1991) was developed for orb-web spiders and is based on stochastic dynamic programming. Female fitness is determined by the number of palpal insertions and the body mass she achieves during the time period from final moult to egg production. Both of these state variables are assumed to be affected by a female's decision to either mate or cannibalize a courting male. Thus adult females may be said to balance the male's economic value as a meal versus his value as a sperm donor.

Assumptions. The model makes two basic assumptions: (1) female fecundity is a product of the amount of food consumed *as an adult* prior to egg laying and (2) the fertilization rate of eggs produced is a function of the number of palpal insertions received (figs 1 and 2 in Newman and Elgar, 1991). We test both assumptions.

Predictions. The model makes several explicit predictions. (1) Female mating status should affect the likelihood of premating sexual cannibalism. Virgin females should be less likely to attempt cannibalism prior to sperm transfer compared to mated females. (2) When food availability increases, a courting male's value as a meal decreases relative to his value as a mate. Thus the higher the availability of other prey items, the more likely virgin adult females should be to mate rather than cannibalize males prior to mating. (3) When variance in food availability increases, females should be more likely to cannibalize males prior to mating. (4) Large males are relatively more profitable as prey compared to small males, and virgin females should thus be more likely to attempt premating cannibalism with large males. The model thus predicts selection for small male size, since females should be most willing to mate with small males. (5) Virgin females should be less prone to cannibalize males prior to mating when the expected encounter rate with males decreases, due to an increased risk of remaining unmated or only partially inseminated. We evaluate experimentally how each of these five factors affects female premating sexual cannibalistic behaviour in the fishing spider.

Methods

A total of 60 female and 55 male *D. fimbriatus*, penultimates and adults, were collected from an alluvial meadow by the Vindelälven river (64° 22′ N, 19° 28′ E) on 25 May and 8 June 1992. All individuals were brought to the laboratory (20°C, natural light regime) and placed individually in plastic aquaria (0.45 × 0.25 m) filled with water to a depth of 8 cm. A piece of floating styrofoam (0.17 × 0.05 m) provided a foraging and resting site. Adult females carrying egg sacs were also collected from the field on 24 June and 3 July. These females were kept individually in the laboratory for 10 days to allow egg maturation, after which they were preserved in 70% ethanol for subsequent determination of female size, egg size, egg number and fertilization rate of eggs (see below).

Males were fed *ad libitum* throughout the experiments with water striders (*Gerris odontogaster*). Females were fed larval field crickets (*Gryllus bimaculatus*). Females were randomly assigned to two different food treatments factors (2 × 3) starting 8 June, according to the following scheme. Females were fed either small (< 30 mg) or large (> 30 mg) crickets. Further, each female was fed either once every day, once every second day or once every third day. The two factors thus represent different amounts of food provided (prey size) and different levels of daily feeding rate (feeding rate) respectively. Some females in the highest food treatments did not consume all crickets offered. To avoid crowding, only two live prey were allowed in each aquaria at any given time, causing some deviation from the original food treatment design. However, all prey items were weighed and the total mass of food each female consumed could thus be calculated. This enabled us to use (1) the total cumulated amount of food consumed prior to the experiments and (2) the daily food consumption rate prior to experiments (cumulated weight of consumed prey items divided by the number of days from start of the experiments) as additional dependent variables in the subsequent statistical analysis (see below).

Female responses towards courting males were observed and recorded in three rounds of behavioural arena trials, executed 13–25 June, 25 June–5 July and 5–8 July. In each round, one (round 1) or two (rounds 2 and 3) males were introduced into each female in her aquarium for 45 min, and the spiders were observed visually and videotaped for subsequent behavioural analyses from slow-motion replays. Males were numbered individually, and used for behavioural trials in numerical order (a round robin design). Thus any given male was used once or twice within each round, and three repeated measures (rounds 1–3) of each female's response to courting males were obtained. No male was exposed to the same female more than once. Males were weighed prior to round 1 to provide a measure of male size. Female cephalothorax area was used as a measure of female size (estimated as the area of an ellipse: $\pi \times$ [cephalothorax width/2] $\times$ [cephalothorax length/2]). Female mating status prior to each trial was used as a categorical state variable with three levels: virgin, one palpal insertion received and two or more palpal insertions received. Female mating status was either known prior to each trial (individuals collected as penultimates) or was subsequently determined at the end of the experiments from individual mating history and the fertilization rate of the egg batch (individuals collected as adults).

In each trial, we recorded the following variables: female response to courting male (aggressive attack or passivity), attack distance, attack success (male caught and cannibalized or male escaped) and whether copulation occurred or not. If more than one male–female interaction occurred per trial, the first was used for statistical analysis. Female response to courting males (attempt to cannibalize or passivity) was used as the dependent variable to analyse the effects of various factors on female behaviour.

Females that produced and nursed an egg sac in the laboratory were preserved with their egg sac 10 days after egg laying, at which time the spiderling embryo is clearly visible in fertilized eggs. Eggs were measured with a micrometre eyepiece (15 eggs from each egg sac), and the average egg area ($\pi \times$ [egg width/2] $\times$ [egg length/2]) from each female was used as a measure of egg size. Unmated *D. fimbriatus* females only rarely nurse their unfertilized egg batches, but instead typically consume their own eggs after oviposition (Schmidt, 1957; Arnqvist, 1992), thus limiting our sample size on female fecundity. Only females that had not yet produced eggs were used in the behavioural trials.

All statistical analyses were performed with SYSTAT (Wilkinson, 1987; Steinberg and Colla, 1991). Since the dependent variable in analyses of female response to male courtship is binary, univariate and multivariate binary logistic regression analyses were used. Logistic regression involves the method of maximum likelihood (using iteratively reweighted least squares), and is appropriate to estimate regression models when the dependent variable is categorical (Hosmer and

Lemeshow, 1989). Regression models were tested with the log likelihood ratio test of H_0: all regression coefficients (except the intercept) are equal to zero. This test is analogous to an overall *F*-test in least-squares regression analysis. Logistic regression model correctness was evaluated graphically by plotting various regression diagnostics versus the estimated logistic probabilities of the model (Hosmer and Lemeshow, 1989). In all univariate tests of factors affecting female behaviour towards courting males, the statistical power of each test was estimated (Cohen, 1988). The statistical power of a test represents the probability of obtaining a significant result, given a specific probability level of α, a given sample size and a certain magnitude of the true effect (effect size; Cohen, 1988).

Results

When introduced into female aquaria, female drag-lines invariably released male courtship behaviour. Males courted females by vibratory and visual signals, and approached females cautiously. Females either attacked courting males from a distance (78% of all interactions), in which case they killed and consumed the male if caught (11% of the attacks), or they remained passive. In the latter case, the male typically mounted the female and attempted palpal insertion (for details, see Schmidt, 1957; Arnqvist, 1992).

Factors affecting female fecundity

Fourteen females produced egg sacs which they nursed for at least 10 days. Female size was strongly positively related to the number of eggs produced. However, neither the total amount of food consumed as an adult prior to egg laying, nor the average daily food consumption rate, were significantly related to fecundity (Table 1). Thus adult female cephalothorax size was very important for fecundity, whereas adult female food consumption did not have any detectable effects, contrary to the assumptions of the model. The number of eggs laid did not differ between females that cannibalized a male prior to egg laying and those that did not (ANCOVA with female size, effect of consumption of male: $P = 0.195$, $n = 14$).

A joint analysis of covariance of laboratory females ($n = 14$) and females collected in the field with egg sacs ($n = 18$) confirmed that adult female size strongly affects fecundity ($P < 0.001$; Table 2) (Fig. 1). Further, the relationship between cephalothorax size and fecundity did not differ between the two groups of females, either in slope ($P = 0.981$) or intercept ($P = 0.533$) (see Ta-

Table 1. Multiple regression analyses of the effects of (A) fixed female size and the total cumulated amount of food consumed prior to egg laying and (B) fixed female size and the food consumption rate (amount of food consumed per day) prior to egg laying, on the number of eggs laid by females kept in the laboratory ($n = 14$ in all cases)

Variable	β	S.E.	t	P
A				
Cephalothorax area	21.75	8.18	2.66	0.022
Cumulated amount of food consumed	−0.18	0.62	−0.28	0.772
($F = 4.272$, d.f. = 2, $P = 0.042$)				
B				
Cephalothorax area	20.38	7.33	2.78	0.018
Food consumption rate	0.99	12.94	0.08	0.940
($F = 4.199$, d.f. = 2, $P = 0.044$)				

Table 2. Analysis of covariance of the effects of fixed female size and adult environment (field-collected *vs* laboratory-reared) on the number of eggs laid by *D. fimbriatus* females ($n = 32$)

Source	d.f.	Mean-square	*F*	*P*
Cephalothorax area	1	257847.83	44.46	< 0.001
Adult environment	1	2309.73	0.40	0.533
Cephalothorax area × adult environment	1	3.30	0.001	0.981
Residual	28	5799.70		

ble 2), indicating that the non-significant effects of female food consumption on fecundity did not result from unnaturally high levels of food supplies in the laboratory. In univariate regressions between cephalothorax area and number of eggs, size explained more of the variance in fecundity in field females ($n = 18$, $R^2 = 0.84$, $P < 0.001$) than in laboratory females ($n = 14$, $R^2 = 0.43$, $P = 0.011$), again suggesting that the strong effect of size on fecundity in the laboratory did not result from unnatural food supplies. The mean (± s.d.) number of eggs per egg sac was 436.6 ± 116.1 and 383.6 ± 131.2 for the field and laboratory females, respectively. The variance in number of eggs per egg sac did not differ between the field and laboratory females (Bartlett's test for homogeneity of variances: $\chi^2 = 0.215$, d.f. = 1, $P = 0.643$).

Egg size was not related to any other variable (see also Marshall and Gittleman, 1994). Neither the total amount of food consumed ($r = 0.35$), food consumption rate ($r = 0.12$), number of eggs laid ($r = -0.18$) or female size ($r = -0.06$) correlated with egg size ($n = 14$ females). Further, egg size did not differ between females that cannibalized a male prior to egg laying and those that did not ($t = 1.793$, $n = 14$, $P = 0.098$).

The number of palpal insertions a female received in the laboratory was highly correlated with the fertilization rate of the female's subsequent egg batch (Spearman rank correlation: $r_S = 0.945$,

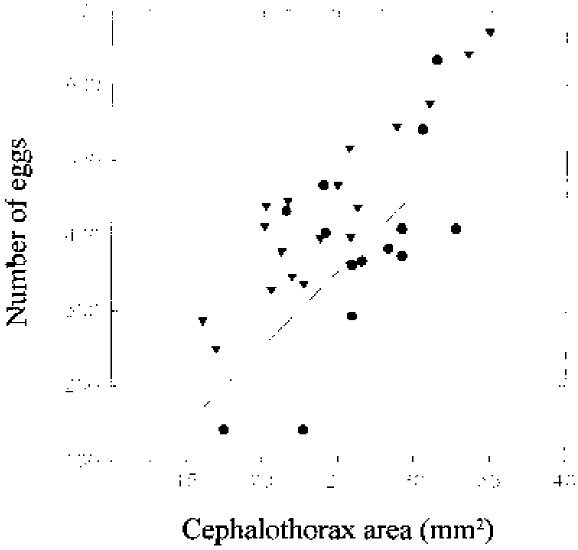

Figure 1. The relationship between cephalothorax area and number of eggs laid by *D. fimbriatus* females. Circles and solid regression line represent females reared in the laboratory, and triangles and dotted regression line represent females collected with egg sacs in the field (see Table 2 for statistical evaluation).

$n = 13$, $P < 0.001$), in agreement with the assumption of the model. Females that did not achieve any palpal insertions all laid completely unfertilized egg batches ($n = 6$), females that achieved one palpal insertion had an average fertilization rate of 34.9% ($n = 6$, range 13.7–54.8%) and the single female that achieved two palpal insertions had a fertilization rate of 96.8%.

The distribution of fertilization rates of females collected with egg sacs in the field appeared to be bimodal (Fig. 2). Thirty-three percent of these females had fertilization rates between 30 and 50% and the remaining 67% all had fertilization rates between 70 and 99%. Three measures of distributional bimodality confirmed this interpretation. First, the kurtosis of the distribution of arcsine transformed fertilization rates was $g_2 = -1.566$, strongly indicating a mechanism generating bimodality (Wyszomirski, 1992). Second, a bimodality analysis based on maximum-distance generated a best partitioning of the distribution when divided into two subgroups. The squared Fisher distance value at this point was $FD^2 = 62.341$, again strongly suggesting bimodality (Phillips *et al.*, 1989). Finally, a clustering test comparing between- and within-cluster sums of squares of all possible cluster pairs was performed (Engleman and Hartigan, 1969; Hartigan, 1975; McLaughlin, 1989), allowing objective determination of whether the data form one or two clusters. The test was performed on untransformed, arcsine-transformed, square-root-transformed and log-normal-transformed fertilization rates. In all cases, the test yielded a best partitioning of the distribution when divided into the two clusters mentioned above, and the null hypothesis of a random sample from a common distribution could be rejected at $\alpha = 0.05$ in all cases (e.g. $C = 15.44$, $n = 18$, $P < 0.001$, for untransformed data). Average fertilization rates were 39.2% for the lower cluster and 94.4% for the upper cluster. The average cephalothorax area did not differ significantly between females in the two clusters ($t = 0.342$, d.f. $= 16$, $P = 0.737$).

Factors affecting female behaviour towards courting males

Female mating status. According to the model of Newman and Elgar (1991), female mating status should be a major determinant of female behaviour towards males. However, we failed to find any

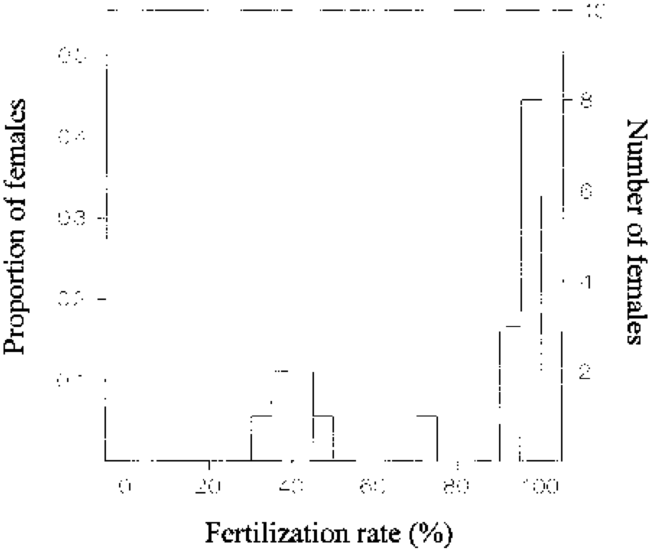

Figure 2. Frequency distribution of fertilization rate of egg batches of females collected in the field with egg sacs. Note the apparent bimodality of the distribution ($n = 18$).

role of female mating status, as measured by the number of palpal insertions achieved (0, 1 or 2) prior to trial, on their aggressiveness towards males in any of the three rounds (Table 3).

Male size. There was no effect of male size on the probability of female cannibalistic behaviour (Table 3). Thus contrary to the predictions of the model, females' decision to mate or attempt to cannibalize courting males was not related to male size. Female attack distance was not related to male size ($F = 0.085$, d.f. = 1, $P = 0.771$), but female attack success was negatively related to male size in all three rounds of behavioural observations (round 1: LLR = 5.590, d.f. = 1, $P = 0.018$, $n = 49$; round 2: LLR = 4.526, d.f. = 1, $P = 0.033$, $n = 43$; round 3: LLR = 5.533, d.f. = 1, $P = 0.021$, $n = 40$). Thus when attacked by females, large males were better able to escape and avoid being cannibalized.

Food availability. Prey size or feeding rate did not significantly affect female behaviour towards courting males in any of the three rounds (Table 4). Further, neither total cumulated amount of food that a female consumed prior to exposure to the male, nor female daily food consumption rate prior to exposure, had any significant effects on female behaviour (Table 3). Thus females' decisions to mate or attempt to cannibalize courting males were not significantly related to any measure of food consumption in the laboratory.

Female size. Female cephalothorax size was not significantly related to female behaviour in any of the three rounds of behavioural observations (Table 3).

Time during season. Since the risk of remaining unmated increases during the season as the number of available males decreases, virgin females should be less likely to attempt to cannibalize courting

Table 3. Results of univariate binary logistic regression analyses of the effects of various factors on female aggression towards courting males, in each of the three rounds of behavioural observations

Factor	Round	*n*	LLR[a]	d.f.	*P*	Power[b]
Female mating status (no. of palpal insertions)	1	42	0.088	1	0.766	0.64
	2	46	0.616	1	0.432	0.68
	3	37	0.264	1	0.607	0.59
Cumulated amount of food consumed	1	43	0.171	1	0.679	0.65
	2	46	0.001	1	0.970	0.68
	3	37	0.463	1	0.496	0.59
Daily food consumption rate	1	43	0.159	1	0.690	0.65
	2	46	0.000	1	0.987	0.68
	3	37	0.738	1	0.390	0.59
Female cephalothorax size	1	39	0.051	1	0.822	0.61
	2	42	1.494	1	0.222	0.64
	3	35	0.476	1	0.494	0.56
Male weight	1	43	0.118	1	0.732	0.65
Difference between rounds[c]	1–3	126	2.504[c]	2	0.286	0.86

[a] LLR represents the log likelihood ratio of the full logistic regression model versus a model including only the constant.
[b] Estimates of the statistical power of single tests (Cohen, 1988).
[c] Difference between rounds tested with χ^2-based contingency table test.

Table 4. Binary logistic regression analyses of the effects of prey size and feeding rate on female cannibalistic behaviour towards courting males, in each of three rounds of behavioural observations

Variable	β	S.E.	t	P	n	LLR[a]	d.f.	P
Round 1								
Prey size	1.21	1.96	0.616	0.538				
Feeding rate	0.95	1.49	0.63	0.526				
Prey size × feeding rate	−0.72	0.92	−0.79	0.432				
					43	0.945	3	0.815
Round 2								
Prey size	−2.16	2.61	−0.83	0.407				
Feeding rate	−1.73	1.85	−0.93	0.350				
Prey size × feeding rate	0.62	1.06	0.58	0.562				
					46	3.667	3	0.300
Round 3								
Prey size	−2.93	3.08	−0.95	0.342				
Feeding rate	−2.44	2.30	−1.06	0.289				
Prey size × feeding rate	1.84	1.52	1.21	0.227				
					37	2.245	3	0.523

[a] LLR represents the log likelihood ratio of full model versus model including only the constant.

males towards the end of the season (Newman and Elgar, 1991). Contrary to the predictions of the model, the frequency of female cannibalistic behaviour did not decrease in the successive rounds (Table 3). In fact, there was a slight tendency in the opposite direction; virgin females attacked from a distance and attempted to cannibalize courting males in 72% of the interactions in round 1 ($n = 43$), 76% in round 2 ($n = 46$) and 86% in round 3 ($n = 37$).

Power analysis. The statistical power of logistic regression models was estimated by the algorithms of Whittemore (1981), and the power of chi-squared based tests was estimated as suggested by Cohen (1988). All estimations were based on $\alpha = 0.05$ and 'medium' effect sizes (odds ratio $\theta = 2$ in logistic regression models and $W = 0.3$ in chi-squared tests) (see Cohen, 1988). The estimated power for single tests ranged between 0.56 and 0.86, and the average power of single tests was 0.65 (Table 3). Assuming true effects on female behaviour of the magnitude on which the power analyses are based for all factors examined, the combined power (the probability of obtaining at least one significant result) at $\alpha = 0.05$ is > 0.99.

Discussion

Evaluation of the model

Only one of the two assumptions of Newman and Elgar's (1991) model was upheld in the fishing spider. In agreement with the model, the fertilization rate was related to the number of palpal insertions a female achieved. However, we found no effects of adult feeding on the number or size of eggs produced in our experiment. Instead, female adult cephalothorax size, which reflects juvenile growth, was the major determinant of fecundity. This result may seem surprising, but the pattern is far from unique among spiders (see discussion below).

Consuming a male did not increase offspring quantity (number) or quality (size) in the fishing spider. Similarly, Spence *et al.* (1996) found that consuming a male did not affect female fecundity in the congeneric *D. triton*. Elgar and Nash (1988) found that adult female *Araneus diadematus* allowed to consume a male gained more weight than females prevented from consuming males. They did not, however, measure fecundity.

None of the five predictions of Newman and Elgar's (1991) model for female sexual cannibalistic behaviour was upheld. We found no effects of female mating status, male size, female food availability/consumption, female size or time of the season on females' decision to mate or attempt to cannibalize courting males. The statistical power analyses show that this cannot be ascribed to insufficient statistical power in our experimental tests. Adult females clearly did not balance the male's economic value as a meal versus his value as a sperm donor in the adaptive manner predicted by the model. Rather, females behaved stereotypically and aggressively, and many females in the laboratory were left unmated at the time of egg laying despite numerous mating opportunities.

There have been few studies of species known to exhibit premating sexual cannibalism where female aggressive behaviour towards males has been related to environmental or internal conditional variables. Jackson (1980) found no effect of 1 month's starvation on female behaviour towards courting males in the jumping spider, *Phidippus johnsoni*. Elgar and Nash (1988) also failed to find any predictors of female aggressive behaviour towards courting males in the orb-weaving spider, *Araneus diadematus*; neither female weight, male weight or male age affected female aggression. Breene and Sweet (1985) concluded that female hunger did not seem to affect the cannibalistic behaviour in the black widow spider, *Latrodectus mactans*, but this study was not designed specifically to asses the role of hunger on cannibalistic behaviour. Thus, collectively, these studies provide no support for the key prediction in the model of Newman and Elgar (1991), that females of sexually cannibalistic spiders should assess a male's value as a meal versus his value as a mate and adjust their behaviour accordingly. In contrast, studies on cannibalistic praying mantises indicate that starved females are more aggressive towards males than well-fed females in these insects (Liske and Davis, 1987; Birkhead *et al.*, 1988; Hurd *et al.*, 1994; Kynaston *et al.*, 1994).

Some studies suggest that female aggressive behaviour may be more plastic in spider species where sexual cannibalism is absent or insignificant. Dodson and Beck (1993), for example, found that mated and virgin adult female crab spiders, *Misumenoides formosipes*, behaved differently towards courting males. Similarly, Watson (1990, 1993) found that adult female sierra dome spiders, *Linyphia litigiosa*, adjust their behaviour towards males according to their mating status as well as their recent foraging success.

Newman and Elgar (1991) and Elgar (1992) suggested that females may suffer a certain risk of remaining incompletely inseminated as a result of aggression towards courting males. In the fishing spider, the distribution of fertilization rates of females caught in the field with eggs was bimodal. Further, the average fertilization rates of the two groups of females (39% and 94%, respectively) corresponded to the average fertilization rates of females in the laboratory that had achieved one (35%) and two (97%) palpal insertions. Our interpretation of this pattern is that a significant proportion of females in the field failed to achieve complete insemination; this is, to our knowledge, the first demonstration of a cost of sexual cannibalism to females in a natural population. Completely unmated female fishing spiders are known to consume or abandon their unfertilized egg batches (Schmidt, 1957; Arnqvist, 1992; Zimmermann and Spence, 1992). Thus our method probably underestimates the risk of remaining incompletely mated, since we would also expect some females in natural populations to produce but not nurse their unfertilized eggs. Interestingly enough, female *D. triton* have been observed to abandon their eggs in the field (Zimmermann and Spence, 1992).

In conclusion, our results do not support the model of Newman and Elgar (1991) and alternative explanations are needed, especially since our data demonstrate high costs associated with sexual cannibalism.

Alternative hypotheses

Elgar and Nash (1988) suggested that premating sexual cannibalistic behaviour may have evolved as a mechanism of female choice of large males. However, two lines of evidence suggest that this behaviour has not evolved in the context of mate discrimination. First, as we demonstrate, sexual cannibalism may be associated with very high costs to females. It is highly unlikely that any genetic benefits obtained by means of mate discrimination could balance the risk of incomplete insemination or total infertility (Parker, 1984; Elgar, 1992). Second, female aggressive behaviour towards courting males was not related to male size either in *D. fimbriatus* (this study) or *A. diadematus* (Elgar and Nash, 1988). Hence, females do not seem to be actively more willing to mate with large males in sexually cannibalistic spiders, and any non-random mating by size among males that may occur as a result of female aggression is more likely to represent a side-effect (e.g. large males are better able to escape attacks) of a behaviour that has evolved for reasons other than intraspecific mate discrimination (see below) (Kirkpatrick, 1987).

Since sexual cannibalism in fishing spiders mainly occurs prior to mating, one hypothesis which could account for the behaviour is that of ‘mistaken identity’ (see Elgar, 1992). According to this view, sexual cannibalism is an infrequent and indirect result of the ‘predatory nature’ of females, and the behaviour would not have evolved in response to selection on either males or females (Gould, 1984; Jamieson, 1986). However, this hypothesis has never been stated formally, and Elgar (1992) considered ‘mistaken identity’ to be a less probable hypothesis for the evolution of sexual cannibalism. Below, we present an explicit verbal model for the evolution of sexual cannibalism based on genetic constraints, which is partly related to the ideas of ‘mistaken identity’. The model is developed to account for premating sexual cannibalism in spiders, but it may apply to other taxa and situations as well.

A non-adaptive model for the evolution of sexual cannibalism

The simple model described below is non-adaptive in the sense that the act of sexual cannibalism is not beneficial *per se* for either sex. We propose that premating sexual cannibalism by adult females is an indirect result of a behaviour that is adaptive in previous life-history stages. The model is based on four assumptions. First, food consumption is positively related to aggression. Second, juvenile growth and adult female size are closely related to juvenile food consumption. Third, female adult size (measured by cephalothorax size as opposed to weight) is a major determinant of female fitness. Fourth, female aggressive behaviour is genetically constrained during ontogeny. Given these assumptions, there will be intense selection on females to be aggressive and non-discriminating with regards to taxonomic affiliation of prey during the juvenile stages. Aggressive female pre-adults will consume more food, grow larger and subsequently lay more eggs. However, due to genetic constraints, the high levels of general aggression will tend to spill over into the adult stage, and adult females will generally be more aggressive and exhibit less discrimination between conspecific and heterospecific prey than would be optimal at this life-history stage. Under this scenario, sexual cannibalism by virgin adult females may have originated, and be maintained, by selection on juveniles, even though there may be serious costs at the adult stage (i.e. risk of not achieving sufficient palpal insertions).

Aggression, juvenile foraging and adult size. In most spiders, a higher level of aggression (e.g. shorter latency to attack prey) will generally increase prey capture rates (Hedrick and Riechert, 1989; Uetz, 1992). Further, there is ample evidence that adult size is closely related to juvenile foraging in spiders. Spiders seem to be especially plastic in growth, and adult size varies greatly in many species as a result of juvenile foraging (Nakamura, 1987; Vollrath, 1987; Uetz, 1992). For example, Beck and Connor (1992) showed that weight gain in the last juvenile instars of the crab spider *Misumenoides formosipes* was related to variation in foraging success, and nearly all of the variation in adult size was attributable to juvenile variation in weight gain.

Female size and fitness. One critical assumption of our model is that female size correlates with fecundity. Female size is, however, an ambiguous concept and it has been measured in several ways in spiders. It is crucial to distinguish between measures of fixed adult size and more plastic measures of size. The former represents measures of sclerotized parts (e.g. cephalothorax width, leg length) which are not affected by female foraging as adults (Foelix, 1982). These size measures are set at the last moult and thus primarily reflect the history of juvenile food consumption. The latter represents measures of size which are also affected by foraging by adults (e.g. weight, abdominal length). There are two reasons why fixed measures are strongly preferable. First, the use of plastic measures brings about autocorrelation between variables in correlative analyses between size and fecundity, since pre-oviposition weight is not independent of egg number. Second, plastic measures confound adult and juvenile food intake. Unfortunately, plastic size measures are often used to evaluate the relationship between female size and fecundity (e.g. Fritz and Morse, 1985; Suter, 1990; Higgins, 1992).

There is a general consensus regarding a close relation between female 'size' and fecundity in spiders (Enders, 1976; Vollrath, 1987; Uetz, 1992; Marshall and Gittleman, 1994). In assuming that *adult* female foraging is key to fecundity, the model of Newman and Elgar (1991) predicts a relatively weak association between fixed adult size and number of eggs. However, fixed adult female size typically explains a very large proportion of both intraspecific (Table 5) and interspecific (Marshall and Gittleman, 1994) variance in fecundity in spiders. Further, food consumption exerts strong effects on subsequent adult fecundity in experimental studies when experimental treatments are started at pre-adult stages (e.g. Riechert and Tracy, 1975; Wise, 1979; Nakamura, 1987; Suter, 1990; Beck and Connor, 1992). When food abundance is varied for adults only, the effects seem to be absent or at least much less prominent (e.g. Kessler, 1971; Spence *et al.*, 1996; this study). In conclusion, these studies all confirm that while foraging success is intimately related to fecundity, food consumption in the pre-adult stages (and thus subsequent adult fixed size) appears relatively more important than adult food consumption for determining female fecundity (Beck and Connor, 1992; Higgins, 1992; Spence *et al.*, 1996; this study).

Table 5. Estimates of the proportion of variance in fecundity accounted for by fixed female size (R^2 values in regressions between cephalothorax size and number of eggs laid), and approximate difference in fecundity between 'small' and 'large' females in a number of spider species

Species	R^2	Difference in fecundity	Source
Dolomedes fimbriatus	0.84	5 fold	This study
Dolomedes triton	0.25	3–4 fold	Spence *et al.* (1995)
Meta segmentata	0.85	4 fold	Rubenstein (1987)
Nephila clavipes	–	3 fold	Higgins (1992)
Misumenoides formosipes	0.44	4–5 fold	Beck and Connor (1992)
Misumena vatia	–	3 fold	Fritz and Morse (1985)
Lycosa palustris	0.38	3 fold	Petersen (1950)
Peucetia viridans	0.67	8 fold	Killebrew and Ford (1985)
Linyphia litigiosa	0.49	2–3 fold	P. Watson (personal communication)

Another characteristic of natural spider populations is the large range in fecundity associated with variation in adult size. The fecundity of 'large' females is typically 3–5 times as high as that of 'small' females (Table 5). Thus an increase in juvenile growth results in a dramatic increase in adult fecundity, which may be further augmented by size-related guarding success of offspring (Morse, 1988). The difference in relative reproductive fitness between small and large females will thus be very high, resulting in intense selection for high juvenile growth rate (Marshall and Gittleman, 1994).

Genetic constraints on aggressive behaviour. Two major shifts in selection on aggression are likely during the ontogeny of female spiders. First, selection for high food consumption rate should be more intense in the pre-adult stages than in the adult stage. There are likely to be costs involved in aggression towards potential prey, such as risk of injury or death. However, since the potential rewards are higher for pre-adults (see above), the optimal level of aggression should be higher among pre-adults than among adults. Second, selection should favour females discriminating between conspecifics and heterospecifics in the adult stage, but not in the pre-adult stages. For a juvenile, killing and consuming conspecific rather than heterospecific prey entails no costs, and may even be beneficial (Polis, 1981; Elgar and Crespi, 1992). In contrast, cannibalistic behaviour may be associated with high costs in the adult stage, if adult females suffer a certain risk of remaining incompletely inseminated as a result of aggression towards courting males (Newman and Elgar, 1991; Elgar, 1992; this study).

It is widely recognized that phenotypic evolution may be constrained by the genetic 'architecture' of a trait or a set of traits (for reviews, see Maynard Smith *et al.*, 1985; Arnold, 1992), and that morphological traits are typically intercorrelated both across traits and within traits during ontogeny (Werner and Gilliam, 1984; Werner, 1992). Recent research indicates that behavioural traits may often be subjected to similar constraints – for example, due to genetic correlations between different behaviours (e.g. Garland, 1994). There are at least three sets of potential genetic constraints that may be important for the evolution of sexual cannibalism. First, if there is genetic covariance between juvenile and adult general levels of aggression, this could cause non-adaptively high levels of aggression among adults. Studies of the three-spined stickleback have shown that aggressive behaviour during the juvenile and adult stages is phenotypically and genotypically correlated, especially in females (Bakker, 1986, and references therein). Further, Stevens (1994) has demonstrated that cannibalistic predatory behaviour in juvenile and adult *Tribolium* flour beetles is highly genetically correlated.

Second, if aggression towards heterospecifics and conspecifics is genetically correlated, this could cause non-adaptively high levels of aggression towards courting males by adult females. If pre-adult females evolve to be highly aggressive towards all potential prey, aggression towards conspecifics in adult females could result as an indirect response. Only a few studies have investigated such constraints in modulation of various aggressive behaviours. Again, studies of the three-spined stickleback have shown that a whole suite of different aggressive behaviours (both intra- and interspecific) are phenotypically and genotypically correlated, and that this is due to a common hormonal basis for these behaviours (Bakker, 1986; Tulley and Huntingford, 1988, and references therein). Similarly, studies of the behavioural genetics of the funnel-web spider, *Agelenopsis aperta*, by Riechert and co-workers (Riechert and Maynard Smith, 1989; Hedrick and Riechert, 1989; Riechert and Hedrick, 1990, 1993; Riechert, 1993a,b,c), reveal that aggression towards heterospecific prey and conspecifics is phenotypically correlated at both the individual and population levels. The 'level of aggression' of an individual is composed of a set of intercorrelated traits, all of which are related to overall aggression, and this suite seems to be inherited jointly. Thus a limited set of pleiotropic genes seem to be responsible for both inter- and intraspecific aggression in *A. aperta*, and the mechanism behind this behavioural integration was again suggested to be a common hormonal regulation. Finally, Finley and Haley (1983) reported high genetic correlations between different components of aggressive behaviour in the lobster, *Homarus americanus*.

Third, aggression is determined to a large extent by sex-linked loci in *A. aperta* (Riechert and Maynard Smith, 1989). Since males are generally the heterogametic sex in spiders (a X_n0_n system) (Wise, 1983), females may in effect receive double doses of gene products regulating aggression. Such sex-linked inheritance of aggression may contribute to the evolution of sexual cannibalism in the following way. In many spider species, sexual selection for large adult males arises either through large male superiority in male–male competition (intrasexual selection; Vollrath, 1980, 1987; Rubenstein, 1987; Watson, 1990; Dodson and Beck, 1993) or via a size-related ability to escape female aggressive attacks (intersexual selection; Elgar and Nash, 1988; this study). Aggressive spillover in adult females may result from a genetic correlation in aggression between the sexes; the same genes that cause high levels of aggression and growth in pre-adult males may cause non-adaptively high levels of aggression in adult females, since females receive a double dose of the gene products that regulate aggression. According to this yet unexplored scenario, premating sexual cannibalism by adult females may in part be a non-adaptive genetic corollary of selection for aggression in pre-adult males, and males would be caught in an ‘evolutionary trap’ dictated by the genetic design of the regulatory system for aggression.

In conclusion, the assumptions of our model are well supported by the avaliable literature. There is most likely an intense selection for high female aggression, and a lack of selection to avoid conspecific prey, during the pre-adult stages in many spider species. Given genetic constraints on aggressive behaviour, sexual cannibalism by virgin adult spider females may thus be a non-adaptive and indirect result of aggressive spillover. Assuming a cost of sexual cannibalism (Newman and Elgar, 1991; Elgar, 1992; this study), this scenario will lead to a situation where aggression should evolve to an intermediate level, representing a balance between conflicting selection for aggressiveness during the pre-adult and adult stages.

The above constraints represent evolutionary limitations brought about by current genetic covariance between different components of aggressive behaviour (i.e. the first horizon of genetic constraints, *sensu* Arnold, 1992). Of course, one possible evolutionary outcome of this scenario is increased female discriminatory abilities; that is, reduced genetic and phenotypic covariances between the aggressive behaviours involved (a breakdown of genetic constraints) (Elgar, 1992). However, this may not be accomplished easily; the evolution of the pattern of genetic covariation for a set of traits may in itself be constrained (i.e. the second horizon of genetic constraints, *sensu* Arnold, 1992). As stressed by Houle (1991), the evolvability of genetic covariances between traits critically depends on the functional genetic and physiological ‘architecture’ of the traits, and certain genetic correlations may indeed be evolutionarily conservative (Arnold, 1992). Little is known about the regulation of aggression in spiders. If various components of aggression are at least in part determined by, for example, a single common hormone (see Riechert and Maynard Smith, 1989), evolutionary constraints on aggressive behaviour may indeed be conservative. Breaking such constraints may require the evolution of a novel endocrine regulatory system for aggression or, alternatively, the evolution of novel neural processing pathways of perceived sensory information.

Tests of the model. The use of constraints as components of evolutionary hypotheses has been criticized because of the paucity of possible empirical tests (e.g. Reeve and Sherman, 1993). This is largely because most arguments have been cast in non-genetic terms (Arnold, 1992). To meet this criticism, we outline a number of tests that may be used to assess the assumptions of our hypothesis. We also state explicit and testable predictions.

In sexually cannibalistic species, it is important to evaluate the relative contributions of juvenile and adult foraging to adult fecundity, by independently varying food consumption for juveniles and adults. We predict juvenile feeding rate to explain a larger part of variance in adult female fecundity compared to adult feeding rate. In contrast, the model of Newman and Elgar (1991) critically depends on a major role of adult feeding rate.

We suggest a quantitative genetic approach to test the magnitude of genetic constraints on aggressive behaviour in sexually cannibalistic species. This would involve standard estimations of genetic correlations between traits, either by comparisons between relatives or by population-level artificial selection experiments (Falconer, 1989). In either case, it is essential to use standardized methods that permit measurement of the behavioural phenotypes of single individuals rather than pairs of individuals (see Riechert and Maynard Smith, 1989).

It is also possible to measure directly natural selection on traits involved in natural populations of sexually cannibalistic species by using longitudinal studies, where behavioural and morphological phenotypes of individual females are related to relative fitness (fecundity) (Lande and Arnold, 1983; Endler, 1986). We predict positive selection for aggression in juveniles, because aggressive individuals should have higher growth rates and thus larger adult size and fecundity. In contrast, selection on aggression may be negative in adults, primarily due to incomplete fertilization of egg batches. Positive phenotypic correlations should be observed between (1) aggression towards heterospecifics as juveniles, (2) aggression towards males as adults, (3) fixed female adult size and (4) the number of eggs laid. This suite of traits should also be negatively correlated with the fertilization rate of the eggs.

In his review, Elgar (1992) noted that sexual cannibalism is widespread within some spider families (e.g. Araneidae, Pisauridae, Theridiidae) but almost completely absent in others. If sexual cannibalism before mating evolved as a result of genetic constraints on aggressive behaviour, we would expect the taxonomic distribution of sexual cannibalism to reflect differences in design or function between taxa. This hypothesis may be tested using comparative data (Harvey and Pagel, 1991). Taxa which exhibit sexual cannibalism should differ from those which do not in one or several of the following characteristics: the relationship between (1) aggression and food consumption, (2) food consumption and adult size and/or (3) adult fixed size and fecundity. All of these factors may reduce selection for high aggression in juveniles. (4) Variance in fecundity may be lower in species not exhibiting sexual cannibalism, reducing the opportunity for selection on aggression. (5) Finally, taxa may differ in the regulatory system for aggressive behaviour, and/or in the neural system triggering such behaviour. This would mean that the degree to which aggressive behaviour is genetically constrained may vary among species. The phenotypic and/or genetic covariance between different components of aggressive behaviour may be lower in taxa not exhibiting premating sexual cannibalism, allowing aggression towards heterospecifics and conspecifics, as well as aggression during different ontogenetic stages, to evolve more independently in these taxa. Indeed, the few studies available seem to indicate that female aggressive behaviour of non-cannibalistic spiders may be less rigid than that of sexually cannibalistic species (see above).

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