

Males under attack: sexual cannibalism and its consequences for male morphology and behaviour in an orb-weaving spider

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ABSTRACT

During their quest to maximize fertilization success, males may be under sexual selection through male–male competition, female choice and/or sexual conflict over mating frequency. In many orb-weaving spiders, mating interactions are characterized by sexual cannibalism, which has been hypothesized to drive the evolution of male morphology and mating behaviour in this group. Here, we investigate sexual selection on male body size, leg length and copulation duration due to sexual cannibalism in the highly sexually dimorphic orb-weaving spider *Argiope aurantia*. In a controlled laboratory experiment, we analysed male–female interactions for 99 pairs, with the aid of detailed video recordings. We measured selection on males during five selection episodes during the courtship and mating sequences. We found significant selection during the insertion of the first pedipalp, where 23% of males were killed. Larger males with longer legs for their size were more likely to be attacked, but male morphology had no effect on the likelihood of survival. Instead, males that stayed inserted longer (median insertion duration = 3.5 s) were more likely to be killed by the female. However, we did not detect any trade-off between fertilization success and survival during the first insertion. Males that achieved two insertions increased their fertilization success by about 25% compared with males that inserted only once. Our results suggest that sexual cannibalism is not an important contributor to the maintenance of the sexual dimorphism in size or shape (relative leg length) in this species. However, sexual cannibalism does select for very short copulation duration and rapid sperm transfer.

Keywords: Araneidae, *Argiope aurantia*, copulation duration, sexual cannibalism, sexual selection, sexual size dimorphism, shape dimorphism.

INTRODUCTION

Sexual selection is a powerful process shaping the morphology and behaviour of organisms (Andersson, 1994), leading for example to the evolution of impressive weaponry

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(e.g. Silverman and Dunbar, 1980), elaborate courtship displays (e.g. Petrie *et al.*, 1991), complex genitalia (e.g. Simmons, 2001) or even self-sacrifice in males (Andrade, 1996). One potentially very potent factor resulting in selection on males in the context of reproduction is sexual cannibalism. Sexual cannibalism occurs when the female kills and devours the male before, during or immediately after copulation (Elgar, 1992). It is known from a variety of invertebrate taxa, where females are usually larger than males, but occurs most frequently in praying mantids and spiders, and especially in highly dimorphic orb-weaving spiders (Elgar, 1992; Johns and Maxwell, 1997).

The fitness consequences of sexual cannibalism for males depend on the timing of cannibalism. If males are killed before copulation while they are approaching or courting the female, they achieve zero fitness. If males are cannibalized during or after copulation, after at least some sperm has been transferred, the net effect of sexual cannibalism on males will depend on the balance of the costs and benefits they incur (Buskirk *et al.*, 1984; Johns and Maxwell, 1997; Andrade, 2003). Costs may consist of reduced sperm transfer before being killed and of losing any further reproductive opportunities. Benefits result if the contribution of the male's soma increases the quantity and/or quality of the female's offspring, or if the male increases his paternity, because the female may actually copulate longer with him or is less likely to re-mate (Andrade, 1996). Therefore, sexual cannibalism can be adaptive for males, and this has been demonstrated for the redback spider *Latrodectus hasselti* (Andrade, 1996, 2003; Andrade and Banta, 2002). Male *L. hasselti* exploit the cannibalistic tendencies of females by enticing the females to eat them (Forster, 1992; Andrade, 1998). Similar self-sacrificial behaviour may also occur in other species (Grasshoff, 1964; Blanke, 1975; Downes, 1978; Sasaki and Iwahashi, 1995; Knoflach and Van Harten, 2001). However, in most species sexual cannibalism is probably maladaptive for the male and males typically approach females cautiously and try vigorously to escape after mating (Robinson and Robinson, 1980; Gould, 1984; Birkhead *et al.*, 1988; Elgar, 1992; Lawrence, 1992; Prenter *et al.*, 1994; Elgar and Fahey, 1996; Arnqvist and Henricksson, 1997; Maxwell, 1998; Uhl and Vollrath, 1998; Elgar *et al.*, 2000; Johnson, 2001; Schneider and Elgar, 2001; Schneider *et al.*, 2001).

Sexual cannibalism has been hypothesized to drive the evolution of various morphological and behavioural traits in male orb-weaving spiders (Araneoidea) (reviewed in Robinson, 1982; Elgar, 1992). For example, male body size has been considered to be under selection due to sexual cannibalism, because it might affect the risk of being attacked and/or the ability to escape. Small male body size has been suggested to be advantageous in highly sexually dimorphic species, because small males might fall below a certain threshold above which females would detect approaching males or consider them as valuable prey. Sexual cannibalism may thus contribute to the maintenance of extreme sexual size dimorphism in some species (Darwin, 1871; Elgar, 1991; Newman and Elgar, 1992; Elgar and Fahey, 1996; but see Uhl and Vollrath, 1998; Schneider *et al.*, 2000). In contrast, large size may be favoured in the less dimorphic common garden spider *Araneus diadematus*, a species of the subfamily Araneinae, in which mating takes place on a mating thread outside the female's web. Large males are better at escaping the female and achieve more pedipalp insertions (Elgar and Nash, 1988).

Leg length in males also appears to be important in the context of sexual cannibalism. Males typically use their legs to quickly jump off the female after copulation (Robinson and Robinson, 1980; Elgar *et al.*, 1990; Prenter *et al.*, 1995). In many Araneinae, males also use their legs to bring the female into the right position for intromission. Comparative data

suggest that relatively longer legs may be favoured through a better ability to escape the female in species in which males are relatively small compared with females (Elgar *et al.*, 1990), although direct evidence of such an effect is lacking. The significance of leg length during mating interactions involving cannibalistic females is unknown for other orb-weaver taxa. However, it is often reported that males lose legs while escaping the attacking female (e.g. Robinson and Robinson, 1980; Sasaki and Iwahashi, 1995). Thus, longer legs may actually be disadvantageous in some cases, because they offer a larger target for the female.

Sexual cannibalism may also influence the duration of copulation. Within spider families where sexual cannibalism is relatively common, copulation duration is shorter in cannibalistic genera than in non-cannibalistic ones (Elgar, 1995). This pattern could arise for two reasons. First, males staying longer in copula may face an increased risk of being cannibalized (Schneider and Elgar, 2001). Second, females may use cannibalistic attacks to control the copulation duration and, therefore, paternity of their mates (Elgar *et al.*, 2000). Copulation duration is often positively correlated with fertilization success (e.g. Elgar *et al.*, 2000; Schneider *et al.*, 2000). Thus, in species in which males control the duration of copulation, males may often face a trade-off between current and future reproductive investment.

In this study, we examined whether copulation duration, male body size and male leg length are under selection due to sexual cannibalism in the orb-weaving spider *Argiope aurantia* (Araneidae: Argiopinae). *Argiope aurantia* is a large orb-weaving spider species with pronounced sexual size dimorphism. Males are much smaller than females. The factors involved in the evolution and maintenance of extreme sexual size dimorphism, which occurs frequently in spiders, are a focus of current research (e.g. Vollrath and Parker, 1992; Coddington *et al.*, 1997; Prenter *et al.*, 1998, 1999; Legrand and Morse, 2000; Schneider *et al.*, 2000; Higgins, 2002; Moya-Laraño *et al.*, 2002; Walker and Rypstra, 2003). Yet our understanding of the adaptive significance of sexual size dimorphism in spiders is still poor and studies investigating the effect of sexual cannibalism on male size have so far focused almost exclusively on one genus, *Nephila* (Elgar and Fahey, 1996; Uhl and Vollrath, 1998; Schneider *et al.*, 2000; Schneider and Elgar, 2001; but see Elgar *et al.*, 2000). For example, almost nothing is known to date about the selective processes that determine male body size in *Argiope*, which belongs to a lineage in which extreme sexual size dimorphism has evolved independently from *Nephila* (Hormiga *et al.*, 2000). In *Argiope keyserlingi*, females apparently allow smaller males to achieve longer copulations through sequential mate choice by timing the cannibalistic attack (Elgar *et al.*, 2000). However, on average smaller males did not achieve longer copulations than larger males, and cannibalism is clearly not adaptive for males in this species (Elgar *et al.*, 2000). The significance of this type of female choice for body size evolution, therefore, remains unclear.

Male spiders generally have relatively longer legs than females, probably as a result of sexual selection (Prenter *et al.*, 1995; Foelix, 1996). Thus, to fully understand sexual dimorphism in spiders, it is important to determine the adaptive significance of leg length independent of body size. Longer legs are thought to confer an advantage, for example, during mate search in a three-dimensional habitat and during antagonistic interactions among males (Bridge *et al.*, 2000; Legrand and Morse, 2000). Sexual cannibalism might select for relatively longer or shorter legs (see above). To our knowledge, no study has yet directly examined selection on leg length independent of body size in any spider.

In this paper, we try to answer the following questions: (1) Is male body size under selection due to sexual cannibalism? (2) Is leg length in males under selection independent of

body size? (3) Is the duration of copulation under male control and, if so, are shorter copulations favoured because of an increased likelihood of survival? To answer these questions, we videotaped all interactions on females' webs and analysed five selection episodes according to the approach, courtship and mating sequences occurring in this species.

STUDY SYSTEM

In male spiders, the pedipalps (the pair of extremities posterior to the fangs) are morphologically derived to function as copulatory organs. Each palp inserts into one of the female's paired genital openings, which lead to separate sperm storage organs. Male *A. aurantia* always try to insert both palps into the same female to complete copulation. If a male encounters the web of a mature female, he slowly crosses the web to reach the female, who rests at the hub of the web. Once in contact with the female, the male commences his tactile courtship, which typically consists of very rapid tapping of the four anterior legs against the female's legs and body with intervening walkabouts over and around the female (for a detailed description of the courtship behaviour of this species, see Robinson and Robinson, 1980). A receptive female responds to the male's efforts by assuming a characteristic acceptance posture. She lifts the anterior part of the body so that her body is held at an angle to the web plane and the first one or two pairs of legs may be lifted off the web. The male has to move under the female's body to reach the genital openings, which are situated anteriorly on the ventral surface of the opisthosoma, and he then inserts his first palp (Robinson and Robinson, 1980). After only a few seconds, the male typically tries to escape the female by quickly jumping off. If he escapes, the male usually re-approaches by climbing back on his security thread. He has to court the female again to achieve a second insertion with the other palp. The female frequently attacks the male during pedipalp insertion (Foellmer and Fairbairn, 2003).

A unique feature of *A. aurantia* is that immediately after insertion of the second palp, males become motionless and die within minutes (Foellmer and Fairbairn, 2003). Male self-termination probably evolved in a context other than sexual cannibalism. If male *A. aurantia* encounter a juvenile female just one moult from adulthood during their mate search, they often cohabit with the female and wait for her to undergo the maturation moult to pursue an alternative mating strategy. They try to copulate with the female during her moult, when she is defenceless (opportunistic mating) (Robinson and Robinson, 1980). Males do not face cannibalistic attacks during opportunistic mating, but experience fierce competition over access to the female. Dead males probably act as whole-body mating plugs, preventing other males from inserting their palps (Foellmer and Fairbairn, 2003). Therefore, because males die spontaneously after inserting their second palp, they can achieve a maximum of only two insertions.

METHODS

Rearing

We reared individuals in the laboratory from egg sacs built by females that we collected in an old field on Île Perrot near Montreal, Quebec. Spiders were kept under controlled conditions (light:dark = 16:8, temperature = 26:20°C) in glass terrariums with chicken wire as web supports. We transferred penultimate females into individual aluminium screen

cages ($45 \times 45 \times 15$ cm) where they moulted to maturity and remained until after the mating trial. We transferred adult males into individual plastic vials (50×23 mm) after they had left their moulting webs to search for females. All individuals were provided with water by gently spraying the webs. Young instars were fed freely flying *Drosophila melanogaster*, which they had to catch with their web. From approximately the fifth instar on, the diet was supplemented with small *Tenebrio molitor* larvae. We fed penultimate and adult females with two large *T. molitor* larvae three times per week. Adult males do not build catching webs but may scavenge prey present in the female's web. We provided them with bits of fresh liver once a week.

We determined whether the use of laboratory-reared individuals in our study would affect the power to detect any body size effect by testing whether the size range of our experimental males corresponded to the size range found in the source population (systematic sampling of adult individuals found within a 1030 m^2 area during the mating season in 2000). Mean prosoma width of experimental males and females was greater than that of field-caught individuals [males: $t = -16.1$, $P < 0.001$, d.f. = 139.4 (equal variances not assumed); females: $t = -8.6$, $P < 0.001$, d.f. = 237.3 (equal variances not assumed)] (Fig. 1). This indicates that laboratory-reared individuals benefited from the constant supply of prey and ambient temperatures. Sexual size dimorphism (female/male prosoma width ratio) was very similar (experimental spiders = 1.9, source population = 2.0). Prosoma width of experimental males was more variable than that of males measured in the natural population (Levene's test: $F = 17.7$, $P < 0.001$). Thus, the variation in the experimental population should be sufficient to detect selection on male morphology.

Experimental design

We measured the following traits for adults: male and female prosoma width (at the broadest point), male opisthosoma length, body length and the average combined patella-tibia length for each pair of legs. Male prosoma length was estimated as body length minus

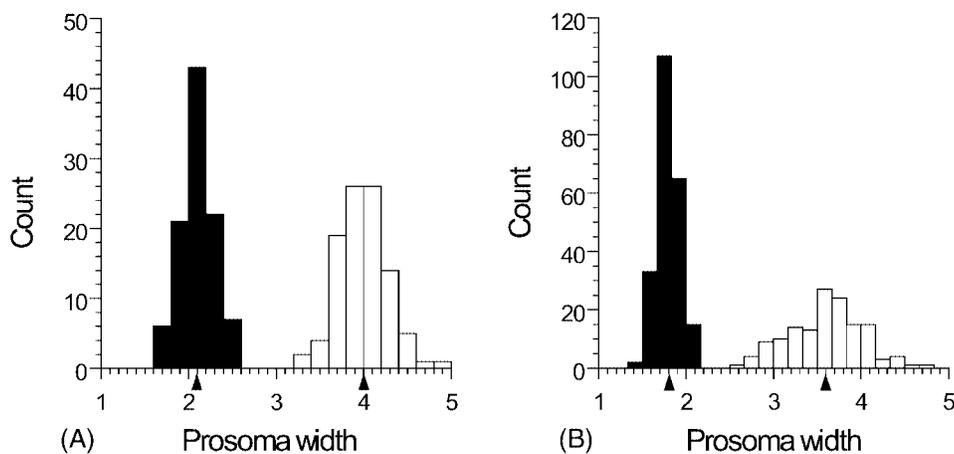


Fig. 1. Frequency distributions of prosoma width (A) for males ($n = 99$) and females ($n = 99$) used in the experiment and (B) for males ($n = 224$) and females ($n = 143$) from the source population. ■, males; □, females. The arrowheads point to the respective means of the distributions.

opisthosoma length. All measurements were taken from the dorsal aspect under a dissecting microscope with individuals held gently between two lids of Petri dishes balanced with cotton. The repeatability of male prosoma length was 0.88; that of all other measurements was > 0.97 ($n = 10$, $k = 3$ repeated measures). The video analysis revealed that the first insertion is always terminated by the male, not by the female (see Results). Therefore, in addition to the morphological traits, we included the duration of the first insertion as a male behavioural trait in the analyses.

In the field, males infrequently cohabit with mature females, and rarely is more than one male associated with a mature female. In a population in an old field in Quebec in 2000, 89.9% (187/208) of sampled webs with mature females had no male present during the mating season, 7.7% (16/208) had one male present and 2.4% (5/208) had more than one male present (M.W. Foellmer, unpublished data). A mature female is therefore unlikely to be courted by more than one male at any given time. Furthermore, while several males may mate with a newly moulted female (opportunistic mating), mature mated females do not frequently re-mate (M.W. Foellmer, unpublished data). We therefore estimated selection on males using a simple experimental design in which we introduced one virgin adult male into a cage with one virgin adult female.

The pool of individuals available for mating on any given day consisted of females that had built at least one new catching web after the maturation moult (age in days after final moult = 5.5 ± 1.7 days; mean \pm standard deviation) and males that were at least 8 days after the maturation moult, because this species is protandrous [age = 18.1 ± 2.4 days; male age had no effect on fitness (results not shown)]. Males and females were chosen randomly from the available pool, and each male and female was used only once. Each mating trial began when we placed a male carefully into one of the upper corners of a screen cage containing a female without touching the female's web. Males that started walking around usually found web support threads quickly and approached the female on her web. Mating trials lasted until males had achieved two insertions or were killed, or until all mating interactions had ceased for at least 30 min. We did not allow females to consume any males. All interactions ($n = 99$) were videotaped for later analysis. We weighed females immediately after the experiment to obtain an estimate of female condition (calculated as the residuals of the regression of female mass on prosoma width) on the day of the trial. We kept females until their natural death and stored any egg sacs in high humidity at 25°C for 1 month. The egg sacs were then preserved in alcohol and any spiderlings and sterile eggs were later counted under a dissecting microscope.

Analyses

For our analyses, we distinguished five selection episodes during courtship and mating and scored male fitness for each episode as successful or unsuccessful (the criterion of success is given in parentheses): (1) crossing the web (male reaches hub); (2) first courtship (leads to insertion); (3) first insertion (male survives); (4) second approach (male reaches hub again); and (5) second courtship (leads to second insertion). For each stage, we recorded whether the male was attacked (yes/no) and whether the male survived the attack (yes/no).

Principal components (PC) analysis of male morphological traits extracted only one component (PC1) explaining 93% of the total variance. We analysed male fitness as a function of the general size of males using PC1 as the independent variable in univariate regressions. To examine selection on leg length independent of body size, we performed

multiple regression analyses with the average patella–tibia length of the first pair of legs and prosoma width as predictors. While representing only a single linear dimension, prosoma width is a reasonable indicator of body size in spiders (Foelix, 1996). In multivariate regression models, the partial regression coefficients estimate the effect of one trait while holding the effect of other traits constant (Kleinbaum *et al.*, 1998). We included only the first pair of legs to preserve power, since all leg measurements were highly correlated (Pearson $r > 0.97$). The first pair of legs is especially important during male–female interactions, because it is used along with the second pair in the male’s tactile courtship to stimulate the female. It is also the longest pair of legs, thus possibly offering the female a good target to catch the male. We used logistic regression to test models with dichotomous response variables (Kleinbaum *et al.*, 1998). Predictors were either normally distributed or successfully normalized through appropriate transformation. All variables were standardized to a mean of zero and a standard deviation of one to facilitate comparisons and to calculate selection gradients for overall selection on males during the mating interactions (using non-standardized data did not change the statistical conclusions).

Our main aim in this study was to determine whether male morphology and the duration of the first insertion are under selection due to sexual cannibalism. However, the likelihood of a male being attacked might also depend on other factors, for example characteristics of the female. To evaluate this effect, we conducted exploratory analyses of the following additional variables: female age, size, condition and courtship duration.

RESULTS

Females attacked males during all episodes of the mating interaction except during the re-approach of the males. The frequency of attacks was especially high during the first and second insertions, when about 80% of males present during the respective episode were attacked (Fig. 2). However, only during episode three (first insertion) were a substantial

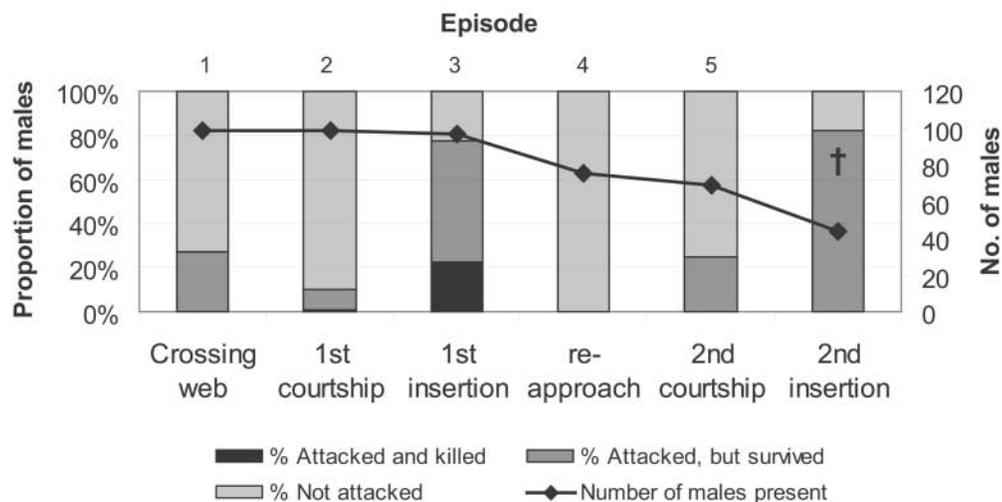


Fig. 2. Relative frequencies of attacked and killed males per episode and the number of males present per episode (on the secondary y-axis). †All males die spontaneously during the second insertion (see text).

number of males (22/97 or 23%) caught and killed. Only one male was killed during the first courtship and none during the other episodes. Almost all males (97/99 or 98%) achieved the first insertion. Most males that survived the first insertion (69/75 or 92%) courted the female again. Sixty-four percent (44/69) of these males achieved a second insertion (44% of all males). All males died spontaneously during the second insertion and were eventually pulled out by the female.

Episode 1: crossing the web

All males approached the female slowly and with frequent hesitation, occasionally plucking at silk strands as they moved towards the female. Almost a third of all males (27/99 or 27.3%) were attacked by the female, but this was independent of male morphology (Table 1). All males reached the hub.

Episode 2: first courtship

All females reacted to the courting male by assuming the acceptance posture. Ten percent (10/99) of males were attacked during courtship and one was killed. Male morphology did not predict the probability of an attack during the first courtship (Table 1). Due to the low variance in male fitness (98% achieved the first insertion), we did not test for an effect of male morphological traits on fitness.

Table 1. Regression coefficients with the associated standard errors and Wald statistics for logistic regression of female attack as a function of male morphology during each selection episode (episode 4 is omitted, because no male was attacked)

Episode	Variable	<i>b</i>	Standard error	Wald	d.f.	<i>P</i>
1. Crossing the web (<i>n</i> = 99)	General male size (PC1)	0.420	0.235	3.19	1	<0.1
	Prosoma width	-0.206	0.694	0.09	1	>0.7
	Patella-tibia length	0.620	0.694	0.80	1	>0.3
2. First courtship (<i>n</i> = 99)	General male size (PC1)	-0.006	0.335	0.00	1	>0.9
	Prosoma width	1.094	0.967	1.28	1	>0.2
	Patella-tibia length	-1.096	0.977	1.26	1	>0.2
3. First insertion (<i>n</i> = 97)	General male size (PC1)	0.523	0.263	3.94	1	<0.05
	Prosoma width	-1.095	0.758	2.09	1	>0.1
	Patella-tibia length	1.641	0.793	4.28	1	<0.05
5. Second courtship (<i>n</i> = 69)	General male size (PC1)	0.361	0.297	1.48	1	>0.2
	Prosoma width	0.980	0.877	1.25	1	>0.2
	Patella-tibia length	-0.585	0.865	0.46	1	>0.4

Note: The effect of general male size (PC1) was evaluated in univariate regressions. For prosoma width and patella-tibia length, the partial regression coefficients are given from the bivariate model containing both traits.

Episode 3: first insertion

The attack

Seventy-seven percent (75/97) of males were attacked during the first insertion (Fig. 2). An attack commenced when the female collapsed over the male, flipping about 180°. The female then started to throw silk over the male while he was still inserted. Larger males were attacked more frequently (Table 1). Multiple regression analysis indicated that this effect was due to males that were attacked having relatively longer legs. However, neither effect was significant after correcting for multiple tests. The likelihood of being attacked was independent of the insertion duration ($n = 96$, $b \pm$ standard error = -0.071 ± 0.247 , Wald = 0.08, d.f. = 1, $P > 0.7$). Males always tried to escape from the female by jumping off her body (median insertion duration = 3.5 s, range = 1–27 s, $n = 97$). Some males whose first jump was blocked by the female's silk threads still managed to escape by what appeared to be slipping through the layers of silk with extended legs. Males that got entangled in the female's threads were inevitably caught.

Twenty-two (29%) of the attacked males were caught and killed, while 53 (71%) males escaped and survived. The timing of the female's attack (seconds after palp insertion; Fig. 3) did not differ between males that survived and those that did not ($U = 566$, $P > 0.8$). However, males that were killed had stayed inserted for a longer time after the onset of the female's attack than males that survived ($U = 358$, $P < 0.01$). Thus, the longer a male

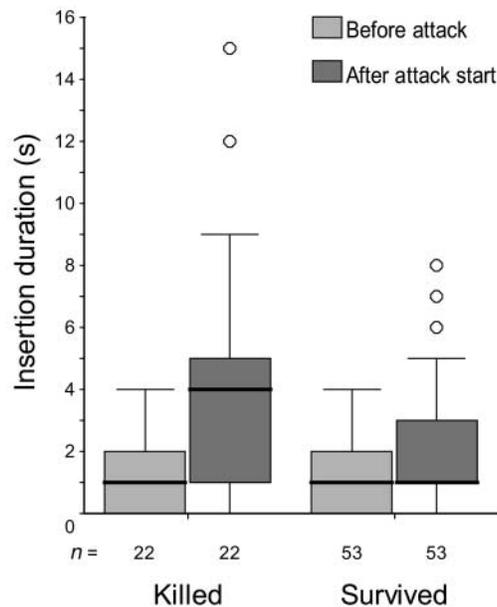


Fig. 3. Timing of the female's attack during the first insertion. Before attack: time (seconds) males had inserted their palp when the female attacked. After attack: time males stayed inserted after onset of the female's attack. Box plots show medians (centre horizontal line), 25th and 75th percentile (upper and lower box border), highest and lowest values (whiskers) and outliers (outside 1.5 box lengths; open circles).

inserted his palp, the more likely he was to be caught. The likelihood of a male being killed once attacked was independent of general male size (PC1: $n = 75$, $b \pm$ standard error = 0.243 ± 0.255 , Wald = 0.90, d.f. = 1, $P > 0.3$). Similarly, neither male prosoma width nor patella–tibia length independently influenced the ability to escape (prosoma width: $n = 75$, $b \pm$ standard error = 0.127 ± 0.851 , Wald = 0.02, d.f. = 1, $P > 0.8$; patella–tibia length: $n = 75$, $b \pm$ standard error = 0.133 ± 0.854 , Wald = 0.02, d.f. = 1, $P > 0.8$; multiple logistic regression model: $\chi^2 = 1.03$, $P > 0.5$).

Leg loss

Fifty-seven percent (30/53) of surviving males lost at least one leg, whereas only 14% (3/22) of males that were not attacked lost one leg during the first insertion ($\chi^2 = 11.65$, d.f. = 1, $P < 0.001$). This suggests that males often autotomize legs to increase their chance of escaping the attacking female. Note that a comparison of males that survived the attack and those that were caught was not possible, because we could not determine with confidence which legs males had autotomized before they were definitely caught by the female. Surviving males were most likely to autotomize a leg of the first pair of walking legs. Of the 30 males that lost at least one leg, 23 lost at least one leg of the first pair, but none of the three pairs of hind legs. Two males lost one leg of the first pair and another leg, and five males lost one leg of the hind three pairs. We tested whether males with longer legs were more likely to autotomize legs in an attack, thereby possibly compensating for a greater risk of being caught. Absolute patella–tibia length did not predict leg autotomy (univariate logistic regression: $n = 53$, $b \pm$ standard error = -0.072 ± 0.291 , Wald = 0.06, d.f. = 1, $P > 0.8$). Multiple logistic regression of leg loss on prosoma width and patella–tibia length indicated a non-significant trend for small males with long legs to be more likely to lose at least one leg of the first pair in the attack (patella–tibia length: $n = 53$, $b \pm$ standard error = 2.032 ± 1.091 , Wald = 3.47, d.f. = 1, $P < 0.1$; prosoma width: $n = 53$, $b \pm$ standard error = -2.301 ± 1.165 , Wald = 3.90, d.f. = 1, $P < 0.05$; model: $\chi^2 = 4.56$, $P > 0.1$).

Selection during the first insertion

To determine whether the cannibalistic behaviour of females resulted in selection on insertion duration during this episode, we included all males present during the episode in the analysis – that is, males that were not attacked as well as those that were. Insertion duration was a significant predictor of survival during the first insertion ($n = 96$, $b \pm$ standard error = -0.600 ± 0.262 , Wald = 5.24, d.f. = 1, $P < 0.025$). Overall, larger males with relatively longer legs were more likely to be attacked and several males were killed. This could lead to differential survival during the first insertion, even though the likelihood of being killed was independent of male morphology. However, there was no selection on general male size (PC1: $n = 75$, $b \pm$ standard error = 0.081 ± 0.244 , Wald = 0.11, d.f. = 1, $P > 0.7$) and no direct selection on male prosoma width and patella–tibia length during this episode (prosoma width: $n = 75$, $b \pm$ standard error = 0.418 ± 0.748 , Wald = 0.31, d.f. = 1, $P > 0.5$; patella–tibia length: $n = 75$, $b \pm$ standard error = -0.321 ± 0.750 , Wald = 0.18, d.f. = 1, $P > 0.6$; multiple logistic regression model: $\chi^2 = 0.416$, $P > 0.8$). This suggests that the effect that male morphology had on the likelihood of being attacked was too weak and/or too few males were killed to result in statistically detectable selection on male size or leg length during this episode.

Episode 4: re-approach

Of the 75 males that survived the first insertion, only six (8%) did not re-approach the female. These six males had not lost more legs than the males that re-approached (Fisher's exact test: $P > 0.6$). Re-approaching males typically quickly climbed up the security thread which they had fastened on the female's web before copulation. None was attacked by the female.

Episode 5: second courtship

All females reacted to the courting male by assuming the acceptance posture. Twenty-five percent (17/69) of males were nevertheless attacked during courtship, but none were killed. Male morphology did not predict the probability of an attack during the second courtship (Table 1). Only 44 (64%) of the courting males achieved the second insertion, although all females assumed the acceptance posture and no male was killed. Males that did not manage to insert their second palp tried several times to insert, but jumped off without inserting. The probability of achieving a second insertion was not influenced by general male size ($n = 69$, $b \pm$ standard error = 0.085 ± 0.261 , Wald = 0.11, d.f. = 1, $P > 0.7$), prosoma width or patella-tibia length (prosoma width: $n = 69$, $b \pm$ standard error = 0.737 ± 0.796 , Wald = 0.86, d.f. = 1, $P > 0.3$; patella-tibia length: $n = 69$, $b \pm$ standard error = -0.614 ± 0.796 , Wald = 0.60, d.f. = 1, $P > 0.4$; multiple logistic regression model: $\chi^2 = 0.987$, $P > 0.6$). Furthermore, males that had lost at least one leg during the first insertion did not achieve the second insertion less frequently than males that had not lost a leg (60 vs 76%; $\chi^2 = 1.28$, d.f. = 1, $P > 0.2$). Males that did not achieve the second insertion courted the female longer ($n = 69$, $b \pm$ standard error = -1.154 ± 0.356 , Wald = 10.52, d.f. = 1, $P < 0.005$). However, it is impossible to distinguish whether a long courtship was the cause or consequence of males being unable to insert.

Female impact on male survival

During the first episode, older females were slightly more likely to attack web-crossing males than younger ones ($n = 99$, $b \pm$ standard error = 0.28 ± 0.14 , Wald = 3.91, d.f. = 1, $P < 0.05$), but this was without consequence for the males, because none was killed. During the third episode, we found a non-significant trend for a decreasing likelihood of male survival with increasing female size. To test for an effect of female size, we performed a multiple logistic regression analysis, where the full model included insertion duration, PC1 (general male size), female prosoma width and all resulting interaction terms (Table 2). None of the interaction terms were significant. When we dropped these from the model, insertion duration remained the sole significant predictor of male survival during the first insertion. Finally, during the fifth episode, the likelihood of inserting the second palp decreased with increasing female age ($n = 69$, $b \pm$ standard error = -0.40 ± 0.18 , Wald = 5.08, d.f. = 1, $P < 0.05$). In summary, female characteristics had no effect on male survival, but female age was negatively correlated with the probability of inserting the second palp. Note, however, that none of these trends were significant after Bonferroni correction for multiple tests within episodes.

Table 2. Multiple logistic regression analysis of the outcome of an attack during the first insertion as a function of insertion duration, general male size (PC1) and female prosoma width

Variable	<i>b</i>	Standard error	Wald	d.f.	<i>P</i>
Insertion duration	-1.086	0.382	8.08	1	<0.005
General male size (PC1)	0.449	0.290	2.40	1	>0.1
Female prosoma width	-0.549	0.293	3.52	1	<0.1
Insertion duration × female prosoma width	-0.407	0.448	0.83	1	>0.3
Insertion duration × male prosoma width	0.116	0.446	0.07	1	>0.7
Male prosoma width × female prosoma width	0.056	0.389	0.02	1	>0.8
Insertion duration × male prosoma width × female prosoma width	-0.621	0.644	0.93	1	>0.3

Note: The effect of the three main predictors was tested in a model only containing the main predictors. The contribution of the interaction terms was tested in the full model. The full model was significant ($\chi^2 = 16.21$, d.f. = 7, $P < 0.025$).

Fertilization success and total selection on males

Ninety-two females constructed egg sacs (number of egg sacs = 4.25 ± 1.65 , mean \pm standard deviation; range = 1–7). Of these females, only 13 built sacs that were completely empty, and another 48 females built at least one sac that was completely empty. The number of empty sacs was independent of the number of palpal insertions received ($\chi^2 = 12.8$, d.f. = 10, $P > 0.2$). Therefore, empty egg sacs were excluded from the following analyses, since they do not convey any information about fertilization success.

We used the total number of fertilized eggs for all egg sacs combined as a measure of male fertilization success. However, since females probably construct fewer sacs in the wild than in the laboratory (Tolbert, 1976; M.W. Foellmer, unpublished data) due to a higher mortality rate, we also analysed fertilization success for only the first egg sac. We report these results where different from the analysis of all sacs.

Males that achieved two insertions fertilized more eggs than males that achieved one insertion, and this was highly significant for the first egg sac (Table 3). In contrast, the total number of eggs laid by females did not differ between females that received one or two insertions.

Since the probability of male survival during the first insertion decreased with increasing insertion duration, males may face a trade-off during the first insertion, if the insertion duration is positively related to fertilization success. We tested this hypothesis by regressing the number of fertilized eggs on the duration of the first insertion for males that achieved only one insertion. The duration of the first insertion was not a significant predictor of fertilization success ($\beta \pm$ standard error = -0.064 ± 0.075 , d.f. = 40, $t = -0.86$, $P > 0.3$). Thus we could not detect any trade-off between fertilization success and survival during the first insertion. Similarly, the total insertion duration (insertion 1 and 2 combined) was unrelated to the total number of eggs fertilized, when the number of insertions was controlled for (Table 4). Note that the duration of the second insertion (median = 8 s, range = 1–55 s) includes time that males were already dead (Foellmer and Fairbairn, 2003).

To estimate overall selection on male morphology, we included all males in the analyses – that is, also those that did not achieve any insertion. We performed univariate and

Table 3. Means and standard errors for total number of eggs, number of fertilized eggs and proportion of fertilized eggs laid by females that received one or two insertions

		One insertion		Two insertions		<i>U</i>	<i>P</i>
		Mean	Standard error	Mean	Standard error		
First egg sac (<i>n</i> = 74)	Total number of eggs	338.3	13.5	366.4	22.0	560.0	>0.2
	Number of fertilized eggs	247.6	17.9	347.0	26.8	342.5	<0.001
All egg sacs (<i>n</i> = 78)	Total number of eggs	1108.5	62.5	983.3	99.0	586.0	>0.1
	Number of fertilized eggs	596.0	45.8	783.5	79.4	573.0	<0.1

Note: Values are given for first egg sacs and all egg sacs that contained eggs combined. Unequal sample sizes are due to empty egg sacs (excluded from analysis, see text).

Table 4. Results of analysis of covariance of the effect of total insertion duration controlled for number of insertions on the total number of fertilized eggs

Source	d.f.	Mean square	<i>F</i>	<i>P</i>
Total insertion duration	1	81 422.1	0.53	>0.4
Number of insertions	1	574 106.3	3.71	<0.1
Error	73	154 632.6		

Note: The residuals of the model were normally distributed. The model is not significant ($F = 2.15$, d.f. = 2, $P > 0.1$, adjusted $R^2 = 0.03$).

Multivariate regression analyses in the same way as earlier, but we employed two different estimates of male fitness. First, we used the number of fertilized eggs converted to relative fitness (absolute fitness divided by the mean absolute fitness) to calculate selection gradients (Lande and Arnold, 1983). Second, we used the probability of achieving two insertions, because the sample size in the analyses of fertilization success was reduced due to females failing to lay any eggs. We did not detect overall selection on general male size or direct selection on male prosoma width and patella–tibia length during the mating interactions with either method (Table 5).

DISCUSSION

In this study, we examined in detail the consequences of the cannibalistic behaviour of females on male size, male leg length and copulation duration in *Argiope aurantia*. Females attacked males during all episodes of the mating interactions except episode 4, when males climb back up to the female on their security thread, but most frequently during the first and second insertion.

Our results suggest that pre-copulatory cannibalism may be rare in this species. Instead, cannibalism occurred almost exclusively during the first insertion (23% of males were

Table 5. Estimates of overall selection on male morphology during the mating interactions

(a) Variable	β	Standard error	t	P	
General male size (PC1)	0.033	0.068	0.48	>0.6	
Prosoma width	-0.169	0.207	-0.82	>0.4	
Patella-tibia length	0.191	0.207	0.92	>0.3	
Model: $F = 0.44$, $P > 0.6$					
(b) Variable	b	Standard error	Wald	d.f.	P
General male size (PC1)	0.131	0.204	0.41	1	>0.5
Prosoma width	0.555	0.615	0.81	1	>0.3
Patella-tibia length	-0.407	0.612	0.44	1	>0.5
Model: $\chi^2 = 1.14$, $P > 0.5$					

Note: (a) Selection gradients with standard error and t -statistic obtained from a univariate LS regression (PC1) and a multivariate LS regression (prosoma width and patella-tibia length) with total number of fertilized eggs as the response ($n = 78$). (b) Logistic regression coefficients with standard error and Wald statistic obtained from a univariate logistic regression (PC1) and a multivariate logistic regression (prosoma width and patella-tibia length) with the probability of achieving the second insertion as the response ($n = 99$).

killed), when males were apparently most vulnerable. This pattern is very similar to that observed in other highly dimorphic orb-weaving spider species in which the male has to cross the web to reach the female (Elgar and Fahey, 1996; Uhl and Vollrath, 1998; Elgar *et al.*, 2000; Schneider *et al.*, 2000; Schneider and Elgar, 2001). The crossing of the female's capturing device therefore seems generally unlikely to put males at an increased risk. Nevertheless, Elgar and Fahey (1996) noted that larger male *Nephila plumipes* elicited more aggressive movements by females during the web crossing and inferred selection against large male size during this phase. In *A. aurantia*, there was a trend for males of larger general size to be attacked more frequently during the first insertion, which appeared to be due to attacked males having longer legs for their size measured as prosoma width. In all other cases, larger males were not more likely to be attacked than smaller ones. An absence of an effect of male size on attack frequencies was also found in *N. edulis* (Schneider *et al.*, 2000), but most studies do not distinguish between attacking and catching a male.

In *A. aurantia*, male size or leg length had no effect on the probability of surviving an attack. Furthermore, although larger males tended to be attacked more frequently, this did not translate into larger males being overall less likely to survive the first insertion. The effect of male morphology on the likelihood of being attacked was probably too weak and/or too few males were killed to result in statistically detectable selection on male morphology during this episode. Consequently, male size was neutral with respect to male survival during the mating interactions. In addition, the size of the male was unrelated to fertilization success, suggesting that larger males do not successfully transfer more sperm to the female. In the congener *A. keyserlingi*, there was a non-significant trend for small males to be cannibalized more frequently (Elgar *et al.*, 2000). In *Nephila* spp., male size had on average no effect on the likelihood of being cannibalized (Uhl and Vollrath, 1998; Schneider *et al.*, 2000; Schneider and Elgar, 2001). In *N. edulis*, small males achieved greater fertilization success than large males, but this was unrelated to cannibalism (Schneider *et al.*, 2000). Instead, small males employed a more efficient mating tactic (Schneider *et al.*,

2000). Hence, there is no evidence to date that male size is under selection due to sexual cannibalism in highly dimorphic orb-weaving spiders.

Male size appears to be more relevant in less dimorphic species. In the orb-weaver *Araneus diadematus*, larger males achieved more pedipalp insertions with a given female, because they were better at escaping the attacking female (Elgar and Nash, 1988). In fishing spiders of the genus *Dolomedes*, large males were also better at escaping the female, although large males may not gain more palp insertions with a given female (Arnqvist and Henriksson, 1997; Johnson, 2001). Nevertheless, an escaped male will have the opportunity to search for another mate. This suggests that, in less dimorphic species, sexual cannibalism may often select for larger male size, at least in spiders.

Males that survived the attack autotomized legs of the first and longest pair of legs most frequently, but the absolute length of the first pair of legs did not predict leg autotomy. Only small males with long legs for their size tended to lose legs more often. This could mean that males of this particular proportion might be at a disadvantage, but our results do not allow a firm conclusion at this point. In any case, a male's ability to achieve a second insertion was not affected by leg loss they incurred. Lost legs may thus only become important if the male does not achieve a second insertion with the same female and has to move on to search for another female. Since no other study has yet examined selection on leg length independent of body size in the context of sexual cannibalism, comparisons are not possible.

The results of the present study, together with those of others (see above), suggest that extremely small male size relative to female size does not increase male survival during mating in cannibalistic species. Rather, male size appears to be neutral during cannibalistic interactions in species with pronounced sexual size dimorphism, whereas larger males may be favoured in less dimorphic species. Phylogenetic reconstruction of the evolution of extreme sexual size dimorphism in orb-weavers suggests that sexual size dimorphism has evolved several times in the Araneoidea, and that in general females increased in size over evolutionary time whereas males stayed small (Hormiga *et al.*, 2000). Thus, as the sexes diverged, there was probably first selection for larger male size in cannibalistic species, since this seems to be the case in less dimorphic ones. In addition, male–male competition likely selects in several species for larger size, even in highly dimorphic species (Christenson and Goist, 1979; Elgar and Fahey, 1996; M.W. Foellmer, unpublished data). This means that, during the course of their evolution, there must have been strong selection against an increase in male size, for example during mate search or the juvenile stage (e.g. Ghiselin, 1974; Vollrath and Parker, 1992), to counteract selection for large male size and the increase in size due to the genetic correlation with females (Lande, 1980; Reeve and Fairbairn, 2001). Schneider *et al.* (2000) have shown a small male size advantage during mating in the orb-weaver *Nephila edulis*, but this to date is the only direct evidence of this kind. Further demonstrations of selective factors that might have given rise to and/or are maintaining extreme sexual size dimorphism in spiders will be necessary to resolve the controversy concerning its evolution and adaptive significance (see Coddington *et al.*, 1997; Vollrath, 1998).

The copulation duration during the first insertion is under male control in *A. aurantia*, and selection appears to favour short copulation duration during the first insertion. Males that had their first pedipalp inserted longer after the onset of the female's attack were more likely to be caught. The first insertion lasts a median duration of 3.5 s and we could not detect any correlation between insertion duration and fertilization success. This suggests that sperm is transferred rapidly and in an all-or-nothing fashion, as has been found, for

example, in *Gasteracantha cancriformis* (Bukowski *et al.*, 2001). Males that achieve only one pedipalp insertion fertilize fewer eggs than those that insert both palps, a pattern found also in other spiders (e.g. Arnqvist and Henricksson, 1997). In addition to this immediate cost of sexual cannibalism, males leave one of the female's paired sperm receptacles uninseminated. Another male transferring sperm into the empty receptacle would almost inevitably greatly reduce the first male's fertilization success, since sperm from both spermathecae are likely to be used by the female to fertilize the eggs (see, for example, Schneider *et al.*, 2000; Schneider and Elgar, 2001). Sexual cannibalism is perhaps not the only selective process favouring short insertion duration in this species. During opportunistic mating, males that have a palp inserted are frequently attacked by other males (Foellmer and Fairbairn, 2003). Thus rapid sperm transfer is likely to be advantageous in this situation too.

Although our study was not designed to test hypotheses about female attack motivation, the fact that larger males were more frequently attacked could point to a mechanism of overt female choice. However, females did not receive more pedipalp insertions from smaller males. Thus mate choice is unlikely to account for cannibalistic attacks in *A. aurantia*. Moreover, females risk being sperm-limited by killing their mate. Cannibalism has been hypothesized to be maladaptive in the fishing spider *Dolomedes fimbriatus*, where females may similarly risk staying only partially inseminated (Arnqvist and Henricksson, 1997). According to this hypothesis, females are selected to be non-discriminate aggressive foragers as juveniles, and are genetically constrained to behave aggressively towards mates. This model thus assumes that populations are not at genetic equilibrium with regards to female behaviour, and it would be of great interest to test this hypothesis in *A. aurantia*.

Other female characteristics besides the cannibalistic behaviour had no significant effect on male survival in our study. However, our exploratory analyses suggested that males may tend to be less successful in inserting the second palp into older females. Perhaps this is related to the gradual hardening of the female's cuticle. For example, in *Nephila clavipes*, males achieve greater fertilization success when mating within a few hours after the female's final moult while her cuticle is still soft (see Eberhard, 1996, and references therein). Perhaps it is more difficult for male *A. aurantia* to insert a palp into a 'hard' female. However, this does not explain why all males that tried to insert their first palp were successful, regardless of female age.

We estimated selection on male traits imposed by sexual cannibalism using only virgin females. Does this reflect sufficiently the risk of males being cannibalized in the field where they may encounter both virgin and mated females? Mated females do not behave more aggressively towards an approaching or courting male than virgin females (M.W. Foellmer, unpublished data), and we have not yet observed any male being killed by a female during the approach. Females that are unreceptive to courting males often signal this unresponsiveness by web-shaking or brushing-off the male, rather than with overt aggression (M.W. Foellmer, unpublished data). Thus encountering a non-virgin female does not put the male at increased risk of being killed by the female.

In conclusion, male body size does not appear to be under selection due to sexual cannibalism in *A. aurantia*. Hence sexual cannibalism is unlikely to be an important contributor to the maintenance of the extreme sexual size dimorphism in this species, and this is in line with findings in other highly dimorphic orb-weavers. Our study is the first to examine selection on male leg length in a spider. We did not find significant net or direct selection on leg length in the context of sexual cannibalism. Sexual cannibalism does select

for very short copulation duration during the first insertion. This supports the hypothesis that sexual cannibalism is a major factor driving the evolution of male copulatory behaviour in spiders.

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