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ORIGINAL PAPER

Sexual cannibalism facilitates genital damage in *Argiope lobata* (Araneae: Araneidae)

Stefan H. Nessler · Gabriele Uhl · Jutta M. Schneider

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Abstract Sperm competition is a potent driving force in evolution leading to a remarkable variety of male adaptations that prevent or reduce fertilization by rivals. An extraordinary defensive strategy against sperm competition has evolved in a number of web spiders where males break off parts of their paired genitalia in order to obstruct the copulatory openings of females (mating plug). A recent comparative analysis on the family level reports that genital damage is most frequent in species with sexual cannibalism although, as yet, a functional association between sexual cannibalism and genital damage has not been found. Using the moderately sexually cannibalistic orb-web spider *Argiope lobata*, we show for the first time that males cannibalized during their first copulation damaged their pedipalps with significantly higher probability (74%) than males that escaped (15%). Of all males that damaged their genitalia, 44% were able to place a genital fragment inside the copulatory opening of the female, resulting in a relatively low total plugging rate of 14%. Successful obstruction of the female copulatory opening reduced the share of paternity of subsequent males (P_2=0.06%), thus, indicating that genital damage may have evolved as a response to sperm competition in this species as well. However, the low incidence of successful plugging and the strong relationship between sexual cannibalism and genital damage suggest that apart from paternity protection, the nature of genital damage in *A. lobata* is further shaped by sexual conflict or cryptic female choice.

Keywords Sexual conflict · Sexual cannibalism · Genital damage · Mating plug · Cryptic female choice

Introduction

Sexual cannibalism describes the killing and consumption of a potential or actual mating partner which usually is the male. Sexual cannibalism is known from several taxa and is relatively common among orb-web spiders (Elgar 1992). The costs and benefits of sexual cannibalism critically depend on the timing of the aggressive interaction. A deadly attack before sperm can be transferred is obviously not beneficial for the male, while the female gains an extra meal. Sexual cannibalism during or after insemination, however, can be part of a male mating strategy as long as the male successfully transferred sperm (Elgar and Schneider 2004). Males of the black widow, *Latrodectus hasselti*, even invite sexual cannibalism through a characteristic somersault onto the chelicerae of the female mating partner and, thereby, benefit from prolonged copulation and reduced female attractiveness (Andrade 1996). Self-sacrifice likely evolved in concert with a monogynous male mating strategy where the male invests maximally in protecting his paternity with a single female (Andrade and Banta 2002). In theory, such terminal investment can evolve under a male-biased effective sex ratio with a high risk of sperm competition (Fromhage et al. 2005). However, while males may benefit from monopolizing their mating partner, females might bear costs if they benefit from

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S. H. Nessler (✉) · J. M. Schneider
Biozentrum Grindel, University of Hamburg,
Martin-Luther-King-Platz 3,
20146 Hamburg, Germany
e-mail: stefan.nessler@uni-hamburg.de

G. Uhl
Department of Neuroethology, Institute of Zoology,
University of Bonn,
Bonn, Germany

mating with more than one male, resulting in a sexual conflict which may lead to an antagonistic coevolution (Arnqvist and Rowe 2005).

Most spiders belong to the entelegynes that have paired genitalia in both sexes. Males possess two secondary copulatory organs, the pedipalps that consist of several sclerites, one of which is the embolus, the sperm transferring device. Female genitalia are equally paired with two independent copulatory openings, each connected with a spermatheca via an insemination duct (Foelix 1996). Interestingly, several studies (Wiehle 1967; Levi 1968, 1983; Andrade and Banta 2002; Fromhage and Schneider 2006; Kuntner 2007) describe a peculiar male trait that seems to be widespread in cannibalistic spider species (Elgar and Schneider 2004; Miller 2007): males variably damage their genitalia during copulation, and broken off parts often remain lodged inside the insemination duct or copulatory opening of the female. However, across taxa, the adaptive function of male genital damage varies: for example, Schneider et al. (2001) suggested it might be a result of sexual conflict over copulation duration in *Nephila plumipes*. The authors proposed that the tip of the male sperm-transferring device may act as a hold-on, preventing females from easily detaching the male from her genitalia. Forceful removal of the male eventually ends in genital breakage of the tip. Quite different is the nature of genital damage in the congener *Nephila fenestrata* where broken off genital parts act as a mating plug by preventing copulations of rival males (Fromhage and Schneider 2006). Similar results were found for the black widow *L. hasselti* where broken off genital parts can physically block the entrance to the spermatheca. However, in this species, plugs do not prevent remating, and subsequent males can circumvent the mating plug when it is not placed correctly by the former male (Snow et al. 2006). In the congeners *Latrodectus geometricus* (Segoli et al. 2008) and *Latrodectus mactans* (Breene and Sweet 1985), the adaptive value of genital damage is unclear.

The costs of genital damage for males seem very high because the damaged pedipalp may render the male functionally sterile (Breene and Sweet 1985; Foelix 1996; Berendonck and Greven 2002; Fromhage and Schneider 2005; Herberstein et al. 2005; Snow et al. 2006), limiting males to one copulation per pedipalp. However, Snow et al. (2006) argue that males usually do not have more than two matings in their lifetime and that costs of genital damage are, therefore, low. The link between sexual cannibalism and genital mutilation creates an interesting evolutionary twist: the costs of damage to copulatory organs are low if male mating rates are already severely limited through sexual cannibalism; yet, the reverse argument that self-sacrifice may be of low cost if the genitalia are no longer functional may also be true. To date, the direction of this twist and whether there is a causal relationship at all between both traits have not been resolved. The few studies that exist were done on highly cannibalistic species, which show little variation within traits (Snow et al. 2006, Nessler et al. 2007). Species with moderate rates of cannibalism are needed to elucidate a possible causal connection between cannibalism and genital damage since they allow comparing the probability of genital damage between cannibalized and surviving males.

In the cannibalistic and polyandrous spider genus *Argiope*, genital damage is reported from several species (Levi 1968, 1975; Levi and Coddington 1983). Only recently, it was shown for the highly aggressive *Argiope bruennichi* (about 80% of all males die during their first copulation) that a successful plug reduces the copulation duration of rival males and, thus, results in higher shares of paternity, implying a function under sperm competition (Schneider et al. 2006; Nessler et al. 2007). Here, we study the orb-web spider *Argiope lobata*, in which preliminary investigations showed that females are polyandrous and moderately sexually cannibalistic (40% of all males survive their first copulation; S. H. Nessler 2006, personal observation). We investigate the factors that determine genital damage and the consequences for rival males that mate into a previously used copulatory opening.

Material and methods

Study animals

The orb-web spider *A. lobata* used for this study were F_1 offspring derived from eight females collected in March 2005 in Spain, near the national park of Cabo de Gata. Hatched spiderlings were reared for 4 weeks in plastic boxes (15×12×7 cm) and then separated into individual 250-ml plastic cups. They were watered five times per week and fed with *Drosophila melanogaster* and *Calliphora* sp. twice a week. Adult or sub-adult females were transferred into Perspex frames (36×36×6 cm) where they build their typical orb-webs. Adult males remained in their plastic cups until matings took place.

Experimental design and mating procedure

We conducted double-mating trials where both males copulated successively into the same copulatory opening of the female. In this species, males have a fixed ipsilateral mating scheme, i.e. left pedipalps can only be inserted into the left and right pedipalps into the right genital opening of the female. This allowed us to predetermine the insertion side by selectively amputating one pedipalp of each male before the mating trials were conducted. Pedipalps were removed by gently squeezing the femur with tweezers until the male autotomized the appendage without losing hemolymph. Males were not noticeably affected by this procedure as was shown for two other spider species previously (Rovner 1967; Nessler et al. 2007).

All males used for this experiment had no prior mating experience. Mating trials were conducted by carefully placing males in the lower right corner of the Perspex frames where adult females had previously built their webs. Females sit in the centre of the web, the hub, and males usually approach the female while tugging on the web. When males reach the hub, they briefly contact the female, before they proceed to the upper edge of the web. After an average of 23.18±2.89 min (n=50) males re-approached and began courtship. Courtship is here defined as the first contact of the first pair of legs and the pedipalps of a male with the abdomen of the female. In 97% (56 out of 58) of all mating trials, courtship was followed by a copulation that always ended with the females' attack with or without the result of cannibalism. Since males were removed after each mating trial from the female for investigation of the genitalia, cannibalism is here defined as the capture but not the consumption of the male. While mating occurred in all trials involving virgin females (first males), second males were sometimes reluctant to court or copulate with the previously mated female. These males were replaced after 1 h, and we used a maximum of two replacement males. If three males did not mate with a female, we scored this trial as "remating not possible." In total, we achieved 27 double-matings and two single-matings, i.e., females mated with only one male.

We recorded copulation duration, defined as the time period between insertion and removal of the pedipalp from the female genitalia, and the occurrence of genital damage. Additionally, we recorded whether broken-off genital parts remained lodged in the copulatory opening or insemination duct of the female (see below). In cases where males had broken off the whole embolus, females were inspected for lodged emboli immediately after the copulation. After a successful double-mating trial, females were transferred into 400-ml plastic cups in order to produce egg sacs, and they were handled as described above.

All males were killed by hypothermia and fixed in 70% ethanol immediately after the end of the trial and investigated under a stereomicroscope. When females died, their genitalia were macerated with NaOH to become translucent, which allowed us to detect embolus tips inside the insemination ducts.

We were interested in whether males that plug a copulatory opening with broken off embolus parts are able to bias paternity in their favor. Therefore, we determined relative paternity (P_2) of second males that either used a plugged or unplugged copulatory opening of a previously mated female. If genital damage functions as a paternity protection mechanism, P_2 should be reduced in those trials where the first male succeeded in obstructing the copulatory opening. We used the sterile male technique (Parker 1970), in which doubly mated females copulated either with a normal (N) or an irradiated (I) male in variable order. The I males were irradiated with a dosage of 40 Gy (0.8 Gy/min) from a gamma radiation source (Gulmay XStrahl RS225, Universtätsklinikum Eppendorf, Hamburg, Germany). Sperm of irradiated males is still competitive (but see Jones and Elgar 2008) and fertilizes eggs; however, irradiation causes DNA damage which interferes early with the development of the embryo such that eggs fertilized by irradiated males do not develop and can easily be distinguished from eggs with a normal development. Thus, we could assign hatched eggs to normal males and undeveloped eggs to irradiated males. Twenty-seven females were randomly mated with either an irradiated (I) or normal (N) male first ($N_{\mathrm{NI\ matings}}$=14, $N_{\mathrm{IN\ matings}}$=13). However, several females were parasitized by a parasitic fly (*Megaselia scalaris*) that laid eggs in their copulatory opening or the egg sacs, resulting in only 12 females that produced viable egg sacs. Therefore, we analyzed paternity of 12 second males that either copulated in plugged (n=5) or unplugged (n=7) copulatory openings. Irradiated males were used as first males in half of the double-mating trials. We were not able to determine a correction factor for hatching success in natural clutches of females that had mated with two non-irradiated males; thus, we could not determine sperm-precedence patterns of first and second males. However, such controls are not necessary to determine the relative paternity success of second males only since the reciprocal treatment effectively corrects for a systematic bias due to the sterilization method.

Irradiated and normal males did not differ in weight (I males=15.16±0.58 mg, n=25; N males=16.27±0.52 mg, n=25; t test$_{50}$=−1.43, P=0.16) and size (measured as tibia-patella length of the first leg: I males=3.81±0.06 mm, n=18; N males=3.69±0.06 mm, n=20; t test$_{38}$=1.45, P=0.16). In order to control effectiveness of sterilization, we mated females with two irradiated males (n=7), and none of the egg sacs from these females hatched.

Data analyses were carried out with JMP IN 5.1.2. All statistical tests are two-tailed (α=0.05). Nonparametric tests were used where the requirements of parametric statistics could not be achieved through transformation. Sample sizes may differ between analyses because not all data were available for each mating trial. Descriptive statistics are given as mean ± SE and are shown as untransformed data unless noted otherwise.

Results

Cannibalism and genital damage

In total, 41% (23 out of 56) of all males were cannibalized. The probability of cannibalism did not differ between first (13 out of 29) and second males (ten out of 27; G test$_{2,56}$=0.35, P=0.55). Males that were cannibalized damaged their genitalia with significantly higher probability than males that escaped, independently of whether they mated with a virgin (first males; G test$_{2,29}$=9.81, $N_{\text{cannibalized}}$=10/13, N_{escaped}=3/16, P=0.002; Fig. 1A) or a previously mated female (second males: G test$_{2,27}$=9.61, $N_{\text{cannibalized}}$=7/10, N_{escaped}=2/17, P=0.002; Fig. 1A). Within both groups, we found no influence of female and male size and weight and female age on genital damage (Table 1).

However, first males that were cannibalized copulated significantly longer than first males that escaped (Fig. 1B; Table 2); thus, genital damage could have potentially been influenced by copulation duration. Therefore, we performed a multiple logistic regression with copulation duration as covariate and found that genital damage was predicted by cannibalism (χ^2=5.26, P=0.022) but not copulation duration (χ^2=0.58, P=0.45; whole model: χ^2=11.57, R^2=0.29, P=0.0031). Whether the second male was cannibalized or escaped had no significant effect on the duration of copulation (Fig. 1B; Table 2). This may be due to the relatively low sample size and high variation in copula duration within cannibalized males. Cannibalized or escaped males that mated with either a virgin (first males) or an already mated female (second male) did not differ in weight and size (Table 2).

Genital damage and plugging probability

Genital damage occurred in 39% (22 out of 56) of all staged matings (first and second males combined). We found no difference in the probability of genital damage between first (45%, 13 out of 29) and second males (33%, nine out of 27; G test$_{2,56}$=0.77, P=0.38).

Males damaged their pedipalps at one of two distinct points: either the whole embolus (68%, 15 out of 22; Fig. 2A, B) or the tip of the embolus (32%, seven out of 22; Fig. 2C, D) that broke off during copulation. First and second males did not differ in the proportions of breakage of the larger (first males: 36%, nine out of 25; second males: 25%, six out of 24; G test$_{2,49}$=0.70, P=0.40) or the smaller fragment of the embolus (first male: 20%, four out of 20; second males: 14%, three out of 21; G test$_{2,41}$=0.24, P=0.63).

Six (46%) of the 13 first males that damaged their pedipalp could place a genital fragment inside the copulatory opening (five whole emboli and one embolus tip). Of the nine second males, only two males (22%) placed a whole embolus, while none of the three broken-off embolus tips remained stuck.

Stuck pedipalp parts of first males could potentially function as mating plugs by decreasing copulation duration or impairing sperm transfer of second males. Therefore, we compared copulation duration and paternity success (P_2) of second males that copulated in a copulatory opening that contained a genital part or did not. Since one of the six females that had a plugged copulatory opening did not remate, five males remained for the statistical analysis. The copulation duration of second males that used a plugged side (11.84±6.10 s, n=5) did not significantly differ from the copula duration of males that used an unplugged

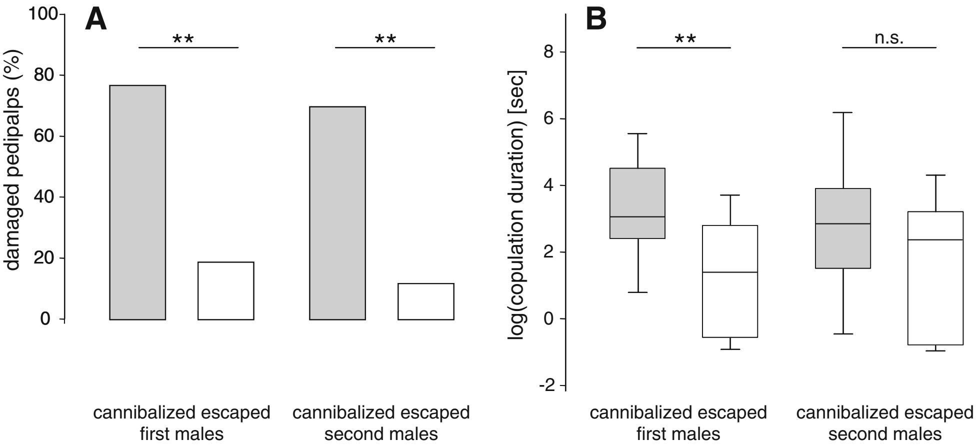

Fig. 1 Frequency of genital damage (**A**) and copulation duration (**B**) of males that copulated either with a virgin (*first males*) or a previously mated female (*second males*). **A** Cannibalized males damaged their genitalia with higher probability than males that escaped. **B** When males copulated with a virgin female, cannibalized males copulated significantly longer than males that escaped. This effect could not be found for second males. Not log-transformed data are given in Table 2. **P≤10.01, *n.s.* not significant

Table 1 Comparison of female and male size (mm), weight (mg) and age (days) between males that damaged their genitalia (broken) and males that left their genitalia intact (not broken)

Parameters	First males				Second males			
	Broken	Not broken	Test statistics	*P*	Broken	Not broken	Test statistics	*P*
Female size	9.79±0.23 (10)	9.47±0.26 (13)	$t=-0.96$	0.35	9.39±0.30 (8)	9.73±0.19 (15)	$Z=-1.26$	0.21
Female weight	416.86±28.01 (13)	472.26±55.36 (16)	$t=0.42^{a}$	0.68	399.84±41.73 (9)	459.29±47.21 (18)	$Z=0.13$	0.90
Female age	12.00±2.2 (11)	15.06±2.23 (16)	$t=1.15^{a}$	0.26	8.89±1.60 (9)	15.72±2.23 (18)	$t=1.71^{a}$	0.10
Male size	3.84±0.09 (11)	3.74±0.08 (11)	$t=-0.79$	0.44	3.81±0.12 (4)	3.69±0.08 (13)	$Z=0.74$	0.46
Male weight	16.25±0.78 (12)	16.27±0.59 (14)	$t=0.02$	0.98	16.09±1.29 (7)	14.72±0.72 (17)	$t=-0.98$	0.34

Data are given as mean±SE (*N*). The comparison is subdivided in males that mated with virgin females (first males) and males that mated with mated females (second males). Sample sizes are given in *brackets*

t t test, *Z* Mann–Whitney *U* test

[a] Statistics were performed on log-transformed data

copulatory opening ($N_{\text{unplugged}}=21$, 55.39±26.16 s, $n=21$; t test on log-transformed data: $t_{26}=1.04$, $P=0.34$). The means are very different in the expected direction, and with increased sample sizes, the difference may become statistically significant. Second males that used a plugged copulatory opening fertilized nearly no eggs (0.06±0.04%, $n=5$), while males that used unplugged copulatory openings were able to fertilize more than half of all eggs (0.61±0.17%, $n=7$; t test on arcsine transformed data: $t_{12}=3.00$, $P=0.02$).

Of the five first males that were successful in plugging the female, two escaped the attack, while the other three were cannibalized.

Discussion

Males of *A. lobata* survived their first copulation with a probability of 57% which lies in between the congeners *A. bruennichi* (about 20%, Schneider et al. 2006) and *Argiope aurantia* (71%, Foellmer 2008) but is similar to *Argiope keyserlingi* (about 55%, Elgar et al. 2000; Gaskett et al. 2004; Herberstein et al. 2005) and *Argiope aemula* (62%, Sasaki and Iwahashi 1995). While almost every male damages his genitalia in *A. bruennichi* (85%, Nessler et al. 2007) and in the congener *A. aurantia* (93%, Foellmer 2008), genital damage in *A. lobata* was rare in survivors (15%) but occurred with a probability of 74% in males that were cannibalized. In less than half (44%) of all mutilated males did the broken-off genital fragment remain stuck inside the genial opening of the female. Hence, 21% of the males that mated with a virgin female were able to deposit a genital fragment inside the female copulatory opening.

In several spider species, broken-off parts of genitalia function as mating plugs (*L. hasselti*: Snow et al. 2006; *N. fenestrata*: Fromhage and Schneider 2006), including the congeners *A. bruennichi* (Nessler et al. 2007) and *A. aurantia* (Foellmer 2008). In *A. bruennichi*, broken-off genital fragments that remain inside the female's insemination duct significantly reduce the copulation duration of rival males which results in reduced sperm transfer and paternity success (Schneider et al. 2006; Nessler et al. 2007). The low incidence of plugging in *A. lobata* does not permit an interpretation of the effects of genital fragments on copula duration with our dataset. Despite a reduced mean duration of copulations into plugged ducts, there was

Table 2 Comparison of copulation duration (sec), male size (mm) and weight (mg) between males that were cannibalized or escaped

	First males				Second males			
Parameters	Cannibalized	Escaped	Test statistics	P	Cannibalized	Escaped	Test statistics	P
Copulation duration	73.21±37.07 (13)	11.13±3.84 (16)	$t=3.30$	0.003	85.26±53.41 (10)	22.28±7.53 (17)	$t=-1.25$	0.23
Male size	3.37±0.09 (9)	3.80±0.08 (12)	$t=0.60$	0.56	3.76±0.09 (7)	3.69±0.10 (10)	$t=-0.50$	0.62
Male weight	16.99±0.63 (11)	15.73±0.65 (15)	$t=-1.40$	0.18	16–59±0.91^{a} (9)	14.24±0.78 (15)	$t=-1.96^{a}$	0.07

Data are given as mean ± SE (*N*). The comparison is subdivided in males that mated with either virgin (first male) or mated females (second males). Sample sizes are given in brackets

t t test

[a] Statistics were performed on log-transformed data

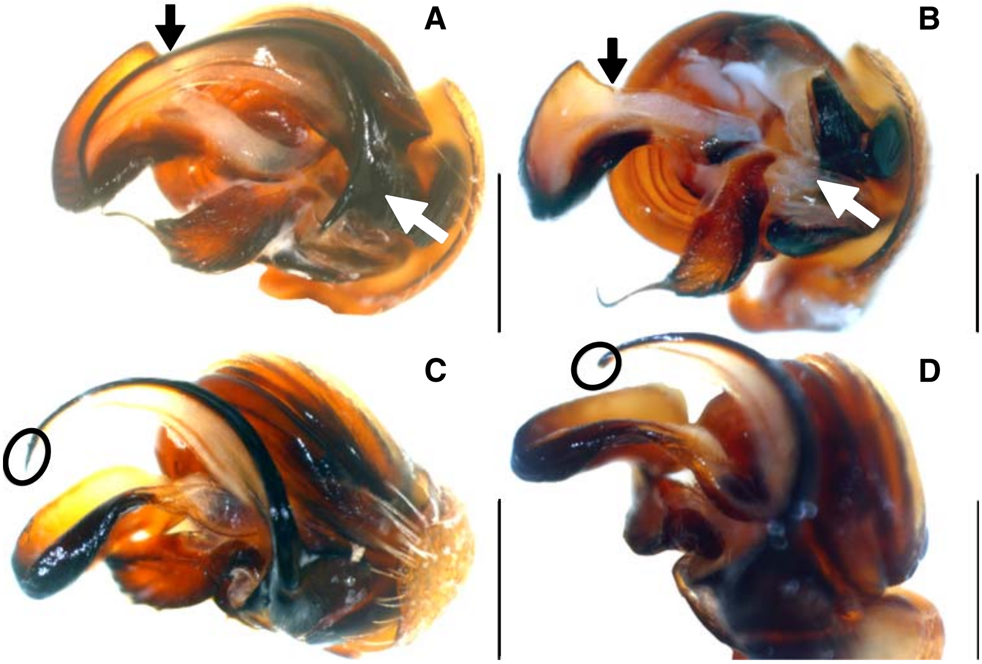

Fig. 2 Pedipalps of *A. lobata*. (**A** and **B**): right pedipalp with and without embolus (*black and white arrows* indicate margins of embolus). (**C** and **D**): right pedipalp with and without embolus tip (*circle*). *Scale bar*= 500 µm

no statistically significant difference to the copulation duration of males that mated in used but unplugged ducts. However, despite the same low sample size, the relative paternity of second males that had mated into plugged or unplugged insemination ducts was statistically different. The low variance in the P_2 values within the two male groups and the large effect size were responsible for this result. Males that mated into a plugged side basically had no paternity, suggesting that genital parts likely constitute efficient mating plugs in *A. lobata*.

A comparative study by Miller (2007) showed that genital damage and sexual cannibalism often co-occur in the same taxa. However, both traits are also found in isolation from each other suggesting that they may be independent adaptations to a low male mating rate (Miller 2007). The present study provides first evidence that this may not be the case but that indeed sexual cannibalism facilitates genital damage or alternatively that genital damage results in sexual cannibalism.

Previous investigations on other *Argiope* species suggest that males use each of their paired pedipalps only once. While they usually attempt to survive their first insertion, they always die during their second copulation either due to spontaneous death or cannibalism (Sasaki and Iwahashi 1995; Foellmer and Fairbairn 2003; Herberstein et al. 2005; Schneider et al. 2006). In the present study, all males were used only once and had no prior mating experience so that these data are not available, but it is a parsimonious assumption that *A. lobata* does not behave differently from all other examined congeners. As a consequence of such a mating pattern, emptying both of their pedipalps equals the maximal mating success a male can achieve. Males can use both pedipalps either with the same or two different females and should, therefore, have a high motivation to escape the attack of the female after his first copulation. This interpretation is supported by the observation that males of *A. lobata* did not show any obvious complicity in sexual cannibalism but actively struggled with the female, possibly in order to escape the attack. The physical force that the female puts on a male while she is trying to dislodge him from her copulatory opening may help the male to break off the tip of his embolus. Alternatively, a male that actively plugs a female copulatory opening may put himself into an increased risk of being successfully captured by the female. Whether this might be mediated by copulation time cannot be inferred with our limited dataset. Further experiments are needed to clarify this although it would be challenging to experimentally vary cannibalism or genital damage.

Sexual cannibalism during a male's first mating in *A. lobata* is mediated by the female and acts against the interest of the male who struggles to escape. Monopolizing a spermatheca of a female by placing a genital fragment inside the insemination duct would be beneficial for a male if it maximizes his paternity success by excluding sperm competition. If the female suffers costs as a result of being monopolized by a male, a sexual conflict results where females resist genital plugging or at least manipulate the probability that a male also fills and plugs her second spermatheca by cannibalizing him.

Alternatively, the variation in plugging success could be mediated by cryptic female choice (Eberhard 1985). Since females control the onset of cannibalism, they can potentially decide which male to attack and which not and, thereby, which male to allow application of a plug.

However, females seem to stereotypically attack every copulating male. We found no difference between males that were cannibalized or escaped in the traits we measured irrespective of whether they mated with a virgin or a mated female. In addition, if females had control over plugging success through selective cannibalism following damage of the genitalia, one may expect that the plugging success of cannibalized males would be higher than the observed 43%. Further experiments are needed to distinguish between these hypotheses.

Interestingly, males of *A. lobata* damaged their genitalia at two predetermined breaking points as was described only once before in the congener *A. bruennichi* (Uhl et al., 2007). In the latter species, both fragment sizes function as plugs (Nessler, unpublished data) although this cannot yet be concluded for *A. lobata*. Due to the low incidence of plugging in *A. lobata*, we are currently unable to further analyze this polymorphism. The adaptive function of such heterogeneity is very interesting, and further experiments may elucidate whether the size of the broken-off parts might influence plug removal by rivals or by females, remating of the female, or male sterility.

Recently, the evolution of genital damage in spiders has gained much attention (Eberhard 2004; Elgar and Schneider 2004; Fromhage et al. 2005; Miller 2007). In theory, the evolution of genital damage as an ultimate means to prevent sperm competition may be favored under a male-biased sex ratio where it is beneficial for a male to monopolize the probably only female he mates with (Fromhage et al. 2005). Here, we present novel data that reveal a previously undetected relationship between genital damage and sexual cannibalism. This relationship in concert with a relatively low plugging probability suggests an active part of the female in controlling a male's accomplishment in avoiding sperm competition. Whether antagonistic co-evolution or cryptic female choice ultimately drives these processes cannot be discerned with the currently available data. However, a comparative approach within the genus *Argiope* might help us to distinguish between the current hypotheses and will contribute to the ongoing debate of the rapid and divergent evolution of male genitalia (Eberhard 1985; Arnqvist and Rowe 2005; Fromhage et al. 2005).

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