Male sexual cannibalism in a sand-dwelling wolf spider with sex role reversal

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Sexual cannibalism usually involves females attacking and consuming males before, during or after copulation. Sex role reversed systems may provide insight into the debate about whether it arises as mistaken identity, a spillover in female aggressiveness, foraging decisions, and/or extreme mate choice. In such systems, males may be selective and voracious to compensate for their higher reproductive costs, and thus males may be the sexually cannibalistic sex. *Allocosa brasiliensis* shows a reversal in sex roles and male-biased sexual size dimorphism (the opposite of the common pattern in spiders). The present study aimed to test whether males cannibalize or mate according to female reproductive status or body characteristics. Each of 20 adult males was consecutively exposed to one virgin and one mated female, alternating the order of exposure. Males preferred to mate with virgin females in good body condition and heavier-mated females. Males attacked 15% of virgins and 40% of mated females and cannibalized 10% and 25% of the total trials, respectively. The astonishing male cannibalistic behaviour best agrees with extreme mate choice hypotheses because attacks were more frequent on mated females of low body condition. This is the first report of male sexual cannibalism in a sex role reversed system. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 68–75.

ADDITIONAL KEYWORDS: adaptive foraging hypothesis – extreme mate choice – reversed – selective males – selection.

INTRODUCTION

Sexual cannibalism is infrequent in relation to other types of cannibalism and mainly restricted to some taxa of insects and arachnids (Elgar, 1992; Schneider & Elgar, 2005; Prenter, MacNeil & Elwood, 2006). In general, it refers to cases when the male is attacked and consumed by the female at some stage during courtship and/or mating (Elgar, 1992). This behaviour could rely on the fact that vulnerable and small sized males need to approach and mate with large predacious females (Wilder & Rypstra, 2008; Wilder, Rypstra & Elgar, 2009). Sexual cannibalism is considered an extreme case of sexual conflict (Chapman & Partridge, 1996; Schneider & Lubin, 1998; Schneider & Lubin, 2005) and many non-exclusive hypotheses have been proposed to explain the evolution of this behaviour. Gould (1984) proposed that most reports of sexual cannibalism could be explained in terms of mistaken identity between sexual partners. Elgar & Nash (1988) interpreted the phenomenon as an extreme case of female mate choice. According to this hypothesis, females would estimate male quality during pre-inseminatory phases and cannibalize mates of lesser qualities. Newman & Elgar (1991) postulated that mating or cannibalism could be performed according to nutritional requirements of the strongest sex (i.e. adaptive foraging or economic hypothesis). Finally, Arnqvist & Henriksson (1997) proposed that aggressiveness, which is adaptive in juvenile phases, could be out of control in adults and maintained at non-adaptive levels (i.e. aggressive-spillover hypothesis), making females dangerous for potential sexual partners.

These hypotheses have been applied to cases of reversed sexual cannibalism (i.e. when the female is

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attacked and eaten by her sexual partner) (Prenter *et al.*, 2006). Reversed sexual cannibalism is very infrequent but has been reported in amphipods (Dick, 1995), isopods (Tsai & Dai, 2003), crabs (Haddon, 1995), and spiders (Schütz & Taborsky, 2005; Aisenberg *et al.*, 2009). In the amphipods *Gammarus pulex* and *Gammarus duebeni* females cannibalize males, although males can also kill and consume small recently moulted females, when other foraging opportunities decrease (Dick, 1995). These observations would be in agreement with the economic model of sexual cannibalism (Newman & Elgar, 1991). In the isopod *Ichthyoxenus fushanensis*, pairs of parasitic males and females inhabit cavities excavated in the body of a small fish. Tsai & Dai (2003) observed female-on-male cannibalism early in the breeding season, whereas males attacked females towards the end of this period. Males satisfy their foraging needs when female reproductive value is low and refuges are scarce, so these data would also agree with Newman & Elgar (1991) hypothesis. In the crab *Ovalipes catharus*, females with soft carapaces are occasionally eaten by males during or after mating (Haddon, 1995). In *Argyroneta aquatica*, the unique sub-aquatic spider and one of the few spider species where males are larger than females, Schütz & Taborsky (2005) reported a single case of reversed sexual cannibalism in 40 trials, although sexual cannibalism was more frequent when they increased the number of competing males. Thus, all these examples of reversed sexual cannibalism occur in aquatic animals and seem to be related to male foraging opportunism and vulnerability of the victim, as was stressed by Prenter *et al.* (2006).

When males have a high reproductive investment, sex roles can reverse from typical patterns, turning males into the choosy sex, whereas females initiate courtship and compete for mate access (Gwynne, 1991; Andersson, 1994). Examples of this kind may also lead to a reversal in sexual cannibalism because males could be selective to compensate their higher reproductive costs (Bonduriansky, 2001). Moreover, in sex role reversed species with male-biased size dimorphism, reversed sexual cannibalism would be favoured. However, there are no clear examples of male mate choice via reversed sexual cannibalism (Prenter *et al.*, 2006).

The sand-dwelling wolf spider *Allocosa brasiliensis* (Petrunkevitch 1910) shows sex role reversal and males are larger than females (Aisenberg, Viera & Costa, 2007; Aisenberg & Costa, 2008). Adult males of *A. brasiliensis* dig deep burrows in the sand dunes where they remain sedentary for long periods (Costa, 1995; Costa, Simó & Aisenberg, 2006; Aisenberg *et al.*, 2007). By contrast, females are the mobile sex that searches for males and initiates courtship. Males can respond by courting the females and both sexes exchange positions inside the male burrow (the male goes to the top and the female to the bottom) (Aisenberg *et al.*, 2007; Aisenberg & Costa, 2008). The male mounts the female's back and facing opposite to her, in the typical mating position of wolf spiders. After mating, the male exits the burrow and seals the entrance (Aisenberg *et al.*, 2007; Aisenberg & Costa, 2008). The female will lay the egg-sac inside the burrow and exit approximately 1 month later for spiderling dispersal (Costa *et al.*, 2006; Postiglioni, González & Aisenberg, 2008). The first egg-sac contains the most eggs (approximately 180), although females can lay up to four consecutive egg-sacs under laboratory conditions (between 70 and 100 eggs) (Aisenberg, 2006; Postiglioni *et al.*, 2008; A. Aisenberg, F. G. Costa & M. González, unpubl. data). Females must remate to obtain a new burrow for each egg-sac and so their reproductive success is limited by access to the burrows constructed by males. On the other hand, males need to construct a new deep burrow to generate new opportunities for mating.

We had previously observed *A. brasiliensis* adult males eating females in the wild (Aisenberg *et al.*, 2009) and, in the laboratory, one of these males cannibalized a courting mated female but mated a virgin female under the same conditions (A. Aisenberg, pers. commun.). This was consistent with our hypothesis that *A. brasiliensis* would show reversed sexual cannibalism because of its sex role reversal. In addition, it suggests that males may use cannibalism as a mechanism of mate choice, perhaps to avoid the cost of losing a burrow to a low-quality female. The present study aimed to test whether males of *A. brasiliensis* exert extreme mate choice and mate or cannibalize according to female reproductive status, weight, or body condition. Virgin females remain buried after copulation and until spiderling emergence (Costa *et al.*, 2006; A. Aisenberg, unpublished data), so males would enhance exclusive paternity in the first egg-sac that is the most successful. It is predicted that males will preferentially cannibalize already mated females and those in poor body condition. This study would be the first report of reversed sexual cannibalism in a system with sex role reversal.

MATERIAL AND METHODS

COLLECTING AND HOUSING

We collected adult and sub-adult individuals of *A. brasiliensis* in the coastal sand beaches of Marindia, Canelones, Uruguay (34°46′49.9″S, 55°49′34.1″W), from November 2007 to March 2008, and from November 2008 to March 2009. Spiders were cap-

tured by sifting the sand during daylight or during the night, by using head-lamps to locate them walking or leaning out from the burrow entrances. We captured 45 adult males, 84 adult females (15 with an egg-sac, 11 carrying spiderlings on the dorsum of the carapace) and 66 sub-adults. Adult and sub-adult spiders were individually housed in Petri dishes (diameter 9.5 cm, height 1.5 cm), with sand as substrate and cotton wool embedded in water. All the individuals were fed three times a week with mealworm larvae *Tenebrio* sp. (Coleoptera; Tenebrionidae) and small cockroaches *Blaptica dubia* (Blattaria, Blaberidae). We monitored individuals daily and recorded moulting occurrence in sub-adults, aiming to determine the exact date of reaching adulthood.

EXPERIMENTAL DESIGN

Virgin females were obtained by individually raising subadult individuals until reaching adulthood. Females used in the experimental trials as mated females had been captured in the wild during the sand-sifting with their egg-sac on their spinnerets, or walking with spiderlings on their dorsum. In those cases, we removed the egg-sac or spiderlings, and waited 10 days before using the individuals. Females of both mating status (virgin and mated) were raised under similar conditions and with the same food regime. For the trials we used virgin females of at least 10 days of adult age (median ± quartile: 15.5 ± 10.0 days). Males and mated females were used 7 days after their capture at the field. We did not reuse individuals. The experiments were carried out along two consecutive reproductive seasons ($N = 10$ males for each period), between 30 November 2007 and 2 April 2008, and between 1 January and 3 March 2009. All the animals were fed for the last time 48 h before the trial. The trials began at dusk, coinciding with the period of activity described for the species (Costa, 1995). Experimental trials were carried in glass cages (length 30 cm, width 16 cm, height 20 cm), with a layer of 15 cm of sand as substrate and water supply. Each male was placed in the arena 48 h before the trial to allow burrow construction. Individuals usually construct their burrows against the glass walls, allowing the observation of their behaviours when they are inside the burrows (Aisenberg *et al.*, 2007).

Each of 20 males of *A. brasiliensis* was randomly selected and consecutively exposed to one virgin and one mated female. One half of the males were exposed first to the virgin females and then to the mated females, and the other half was exposed in the inverse order. We only considered trials in which the female detected the male's burrow within one hour. We moni-

tored the occurrence of male attacks on females that resulted on injuries, leg loss and/or cannibalism. We considered female courtship to comprise the female entering the male's burrow and waving alternately her forelegs (Aisenberg *et al.*, 2007; Aisenberg & Costa, 2008). Each of these sequences of leg waving was considered as one shaking bout. The male sometimes responded by shaking the body and forelegs rhythmically. If female courtship did not take place, the trial ended 30 min after the female detected the male's burrow. If female courtship occurred but copulation did not occur, the trial ended 1 h after placing the female in the arena. Forty-eight hours after their first trial, males were exposed to a second female. All the trials were recorded in darkness, with a Sony DCR-SR85 digital video-camera equipped with nightshot. The video recordings were analyzed with JWATCHER software (Blumstein, Evans & Daniel, 2000).

We measured carapace width, a measurement considered representative of body size in spiders (Marshall & Gittleman, 1994; Eberhard *et al.*, 1998), abdominal width, and weighed each individual immediately before the trials. The index abdominal width/carapace width was considered as representative of body condition, as described by Moya-Laraño, Pascual & Wise (2003) for *Lycosa tarantula*. Virgin and mated females did not show differences in their body indices when they were used in the trails (virgin: 1.11 ± 0.99; mated female: 1.11 ± 0.96; $U = 183$, $N_1 = N_2 = 20$, $P = 0.66$). During the experimental trials, mean ± SD temperature was 24.63 ± 1.27 °C (range 21–26 °C). Voucher specimens were deposited in the arachnological collection of Sección Entomología, Facultad de Ciencias, Montevideo, Uruguay.

STATISTICAL ANALYSIS

Copulation and cannibalism occurrences were compared in trials of virgin and mated females. For analyses related to weight and body condition preferences, we performed comparisons with virgin females, mated females, and all the females together (without considering their reproductive status). We analyzed the results using PAST PALAEONTOLOGICAL STATISTICS, version 1.18 (Hammer, Harper & Ryan, 2003) and WINPEPI, version 1.6 (Abramson, 2004). Variables were checked for normal distribution (Shapiro–Wilk test) and homogeneity of variances (Levene's test). When variables did not follow parametric conditions, we used the nonparametric Mann–Whitney *U*-test or Wilcoxon paired test. We compared frequencies with chi-square tests for independent samples and Fisher's exact probability tests.

Table 1. Female and male body measures (median ± quartile) distinguishing when mating occurred or did not occur

	Females		Males	
	Body condition index	Weight (g)	Body condition index	Weight (g)
Virgin				
Mated ($N = 8$)	1.23 ± 0.22	0.35 ± 0.04	0.87 ± 0.21	0.37 ± 0.18
Did not mate ($N = 11$)	1.05 ± 0.13	0.30 ± 0.08	0.88 ± 0.10	0.43 ± 0.23
Statistics	$U = 18, P = 0.03$	$U = 22, P = 0.08$	$U = 36.5, P = 0.79$	$U = 33, P = 0.39$
Mated				
Mated ($N = 3$)	1.12 ± 0.03	0.36 ± 0.03	0.89 ± 0.31	0.43 ± 0.17
Did not mate ($N = 16$)	1.05 ± 0.26	0.27 ± 0.19	0.87 ± 0.16	0.39 ± 0.04
Statistics	$U = 19, P = 0.61$	$U = 3, P = 0.02$	$U = 13, P = 0.24$	$U = 21, P = 0.78$
Virgin plus mated				
Mated ($N = 8$)	1.20 ± 0.19	0.36 ± 0.03	0.88 ± 0.21	0.37 ± 0.13
Did not mate ($N = 11$)	1.07 ± 0.17	0.30 ± 0.07	0.87 ± 0.10	0.41 ± 0.26
Statistics	$U = 84.5, P = 0.04$	$U = 41, P = 0.01$	$U = 111.5, P = 0.24$	$U = 121, P = 0.38$

We used the nonparametric Mann–Whitney U-test for comparisons in trials with virgin, mated, and virgin plus mated females. Measures of a male and his two corresponding partners (one virgin and one mated female) were lost as a result of human error.

RESULTS

COURTSHIP AND MATING

Virgin females performed a median plus-minus quartile of 4.0 ± 12.5 courtship bouts per minute and mated females performed 2.0 ± 9.0 bouts per minute. No significant differences were found with respect to courtship by virgin and mated females (Wilcoxon test: $W = 84.5$, $P = 0.39$). All the 20 females of the trials entered into male's burrows and 16 virgins and 18 mated females performed courtship behaviour ($\chi^2 = 0.17$, $P = 0.68$). Males courted all the females, in both groups.

Males of *A. brasiliensis* ($N = 20$) mated with nine virgin females and three mated females (McNemar test: $\chi^2 = 4.29$, $P = 0.03$). Comparisons related to mating occurrences in relation to body condition and weight are shown in Table 1. Copulations occurred more frequently with virgin females showing higher body condition indices and with heavier-mated females. Male characteristics did not show any relationship with copulation occurrence. When virgin and mated females were considered altogether, copulations were more frequent with heavier females and those females showing higher body condition indices.

MALE ATTACKS AND SEXUAL CANNIBALISM

During the trials, males attacked three virgin females and eight mated females, out of 20 for each group (McNemar test: $\chi^2 = 2.29$, $P = 0.13$). In the eight cases of male attacks on mated females and in one case with a virgin, females had performed courtship behaviours before male attacks. Five of the cases of male attacks on mated females and two of the male attacks on virgin females resulted in cannibalism ($\chi^2 = 1.56$, $P = 0.21$). Four females were attacked before the male mount and could escape with injuries. When females were attacked during mount, cannibalism occurred in all cases. Males killed females before insertion, biting them on the carapace dorsum when they were mounting in the typical copulatory position of lycosids. The males closed the burrow entrance before consuming the female. Mated females suffered more attacks and copulated less frequently compared to virgin females (Fisher's exact test: $P = 0.03$).

Comparisons related to the occurrence of male attacks in relation to female and male body condition and weight are shown in Table 2. Body condition and weight were not related with cannibalism occurrence when virgin and mated females were compared separately. However, when both groups were compared together, a higher number of male attacks were registered on those females showing lower weights (Table 2). Male characteristics did not show a significant relationship with the frequencies of attacks.

DISCUSSION

According to the results obtained in the present study, reversed sexual cannibalism appears to be frequent in *A. brasiliensis*. Cannibalism attempts represented 27.5% in total and a 40% of the cases with mated females. Male cannibalism on females is extremely rare and is generally associated with laboratory conditions and species in which males are larger than females (Elgar, 1992; Prenter *et al.*, 2006). Reversed

Table 2. Female and male body measures (median ± quartile) distinguishing when attacks occurred or did not occur

	Females		Males	
	Body condition index	Weight (g)	Body condition index	Weight (g)
Virgin				
Attacked ($N = 3$)	1.09 ± 0.24	0.30 ± 0.05	0.87 ± 0.06	0.37 ± 0.06
Did not attack ($N = 16$)	1.14 ± 0.26	0.33 ± 0.07	0.88 ± 0.23	0.43 ± 0.21
Statistics	$U = 17, P = 0.47$	$U = 8.5, P = 0.09$	$U = 21, P = 0.91$	$U = 15, P = 0.34$
Mated				
Attacked ($N = 7$)	1.02 ± 0.20	0.26 ± 0.08	0.83 ± 0.12	0.40 ± 0.21
Did not attack ($N = 12$)	1.12 ± 0.21	0.28 ± 0.07	0.89 ± 0.22	0.40 ± 0.24
Statistics	$U = 39, P = 0.71$	$U = 27.5, P = 0.23$	$U = 25.5, P = 0.18$	$U = 37, P = 0.70$
Virgin plus mated				
Attacked ($N = 10$)	1.06 ± 0.20	0.27 ± 0.06	0.85 ± 0.08	0.35 ± 0.15
Did not attack ($N = 28$)	1.12 ± 0.26	0.32 ± 0.09	0.88 ± 0.23	0.45 ± 0.17
Statistics	$U = 110, P = 0.49$	$U = 75, P = 0.03$	$U = 108.5, P = 0.31$	$U = 93, P = 0.10$

We used the nonparametric Mann–Whitney U-test for comparisons in trials with virgin, mated, and virgin plus mated females. We distinguished when males attacked or did not attack. Measures of a male and his two corresponding partners (one virgin and one mated female) were lost as a result of human error.

sexual cannibalism in *A. brasiliensis* is not a consequence of laboratory conditions because, as noted above, it was also observed in the wild (Aisenberg *et al.*, 2009). The unexpected finding of male sexual cannibalism in this species leads us to consider the sexual cannibalism hypotheses proposed for females that cannibalize males.

The mistaken identity hypothesis proposed by Gould (1984) would not be in agreement with the results of the present study because, in most cases, both sexes performed courtship behaviours. The results do not appear to agree with the aggressive spillover hypothesis (Arnqvist & Henriksson, 1997) because attacks were not indiscriminate: males attacked more frequently mated females with low reproductive value. In relation to the explanation given by Newman & Elgar (1991), the cannibal sex would attack the potential mate when foraging opportunities are scarce but the possibilities of copulation are high. However, during our trials, all the males were fed regularly and those males with lower weights or poor body condition were not found to attack more frequently.

Finally, the results of the present study best agree with the extreme mate choice hypothesis (Elgar & Nash, 1988). Males of *A. brasiliensis* showed sexual preference towards females with characteristics related to high reproductive success (i.e. virgin and heavier females with higher body condition indices) and attacks were more frequent towards females that showed lower weight values. In spiders, higher weight and body condition index are associated with a higher expected fecundity, reflected, for example, by the number of eggs (Wise & Wagner, 1992). Sexual cannibalism of females towards males based in male body characteristics has been reported for the wolf spider *Schizocosa uetzi* as a mechanism to allow mate choice (Hebets, 2003).

The results lead us to consider the possible advantages of the previously cited atypical sexual strategies for *A. brasiliensis* males and females. Males perform an extreme sexual choice that provides them with mates of high quality or food according to the scenario. Because mated females stay buried after copulation and until spiderling emergence (Costa *et al.*, 2006; A. Aisenberg, unpubl. data), a female that reaches the male burrow has not mated with him, at least recently. Additionally, males are larger than females and, in most cases, are attacked in mating position, mounting with the chelicerae on top of female carapace, minimizing the possibilities of receiving an effective defence or escape from the female. From the female point of view, males are the digging sex that provides the refuge for mating and the nest for the future progeny (Aisenberg *et al.*, 2007; Aisenberg & Costa, 2008). Burrow digging in the sand has been cited as a high-cost activity for spiders in terms of digging and silk deposition (Henschel & Lubin, 1992). For females, it can be more advantageous to take the risk of being attacked to obtain a new, deep, and stable burrow, rather than constructing a new burrow on their own. It is important to emphasize that the first clutch (and most successful one) would be assured of obtaining the first mating and that, although at lower frequencies, males can accept mated females for mating.

Males of *A. brasiliensis* would be selective at the moment of taking mating decisions, preferring virgin to mated females. We also found significant tendencies in male sexual preferences towards females with higher body condition index and/or weight. Male preference towards females with specific body characteristics (size and weight) has been reported in the wolf spider *L. tarantula* (Moya-Laraño *et al.*, 2003). The results of the present study are in agreement with sex role reversal hypotheses that postulate that, as a result of high reproductive investment, males will become choosy when deciding on their sexual partners (Gwynne, 1991; Bonduriansky, 2001). Male preference to virgin females has been reported in other spider species (Herberstein, Schneider & Elgar, 2002; Rypstra *et al.*, 2003; Gaskett *et al.*, 2004; Roberts & Uetz, 2005; Baruffaldi & Costa, 2009; Pruitt & Riechert, 2009) and has been frequently associated with higher possibilities of reproductive success (Huber, 2005). By mating with virgin females, *A. brasiliensis* males would ensure exclusive paternity with the first and most successful egg-sac because, as noted previously, females remain buried after copulation (Aisenberg, 2006; Postiglioni *et al.*, 2008; A. Aisenberg, F. G. Costa & M. González, unpubl. data). On the other hand, differences between virgins and mated females in characteristics such as adult age, period spent under laboratory conditions, or other untested factors, could also affect male mating decisions. These possibilities remain to be tested further.

One mechanism that may underlie these results is that mated females show a different courtship behavioural pattern compared to virgins, which affects copulation occurrence. The reduction in female sexual receptivity after copulation has been reported in other spiders (Helsdingen, 1965; Jackson, 1980; Fernández-Montraveta & Ortega, 1990; Elgar & Bathgate, 1996; Andrade & Banta, 2002; Aisenberg & Costa, 2005; Norton & Uetz, 2005; Schäfer & Uhl, 2005). However, we did not find any differences in the frequencies of approach to male burrows or female courtship performance between females with different reproductive status. Despite that, according to the results obtained in the present study, males are capable of discriminating between virgin and mated females in some way before insemination. Males could be able to detect volatile or contact pheromones belonging to the female or to her previous sexual mate, or detect silk cues released by spiderlings that had hung from the female dorsum; however, additional experiments are required on these topics.

As proposed by Johnson (2001) in *Dolomedes triton*, in the present study, more than one hypothesis could be consistent with the occurrence of sexual cannibalism in *A. brasiliensis*. For example, by testing the variation of male sexual cannibalism occurrences along the reproductive period, changing the operational sex ratio, or manipulating the nutritional status of the individuals, we may gain general insight into the factors underlying the phenomenon of sexual cannibalism in this sex role reversed species.

ACKNOWLEDGEMENTS

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