Safer sex with feeding females: sexual conflict in a cannibalistic spider

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Mating strategies are to a large degree shaped by conflicts between the sexes, causing a rapid antagonistic coevolution of traits involved in reproduction. The view that sexual cannibalism represents a form of sexual conflict leads to the prediction of male traits that facilitate escape from cannibalistic females. A variety of traits have been suggested to serve this function in spiders, where sexual cannibalism is comparatively common. Empirical evidence, however, is virtually absent. Here we show experimentally that opportunistic mating with feeding females, which has been reported from several species of orb-weaving spiders, greatly reduces the risk of cannibalism and injury for males in the spider *Nephila fenestrata*. This has direct consequences for a male's fertilization success because surviving males can reduce the female's remating probability by guarding her against rivals. Although copulation with previously mated females sometimes appears to be mechanically impossible, second males that do copulate can expect to fertilize on average 64% of a female's eggs. Our results support the view that opportunistic mating may have evolved as a male tactic in a context of sexual conflict over sexual cannibalism. *Key words:* Araneidae, mate guarding, *Nephila fenestrata*, opportunistic mating, paternity, sexual cannibalism. *[Behav Ecol 16:377–382 (2005)]*

Sexual encounters offer a high potential for conflicts of interests between males and females, impacting on the evolution of physiological, morphological, and behavioral traits (Parker, 1979; Partridge and Hurst, 1998; Rice, 2000). To understand the evolutionary consequences of sexual conflict, it may be helpful to identify extreme sources of conflict that have led to variable evolutionary outcomes in different species. Sexual cannibalism, where a female devours a male in the context of mating, has received attention in this context as a favorable target of study (Elgar, 1992). Sexual cannibalism is likely to affect male and female fitness in radically different ways and offers considerable variation between and within taxa. However, the exact nature of its fitness consequences are often less obvious than one might naively expect. For example, a cannibalistic female may benefit in several ways. First, she obtains a meal (Birkhead, 1988; Elgar and Nash, 1988). Second, she can exert mate choice by varying her attack behavior according to characteristics of the male (Elgar et al., 2000). Third, in spiders where males cohabit on a female's web, females may avoid the costs of cohabitation through cannibalism once fertilization is ensured (Herberstein et al., 2002).

The fitness cost to the cannibalized male is most apparent if he is consumed before he could copulate because in this case he will obviously fail to reproduce. If cannibalism occurs during or after mating, his loss of reproductive future may be at least partly outweighed by associated benefits. Such benefits can include increased female fecundity (Birkhead, 1988; Elgar and Nash, 1988), an advantage in sperm competition due to prolonged copulation duration (Andrade, 1996; Elgar et al., 2000; Schneider et al., 2000), or reduced female receptivity (Andrade, 1996).

Moreover, under certain circumstances sexual cannibalism need not inflict a cost on the male at all: in several spider species, the male's copulatory organs, the pedipalps, regularly become damaged (Andrade and Banta, 2002; Knoflach and van Harten, 2000; Levi, 1975) or depleted of sperm (Christenson, 1989) as a result of copulation. If this causes functional sterility of the male, he has no reproductive future regardless of whether or not he is cannibalized (Andrade and Banta, 2002).

Theory predicts that sexual conflict will lead to an antagonistic coevolution in which adaptations in each sex select for counteradaptations in the other (Dawkins and Krebs, 1979; Parker, 1979). Hence, if sexual cannibalism represents a sexual conflict, we can expect to find male traits that reduce and female traits that increase the risk of cannibalism. Indeed, a wide variety of behavioral and morphological male traits in sexually cannibalistic species have been suggested to reduce the risk of cannibalism (Schneider and Lubin, 1998). For example, Darwin (1871) speculated that male spiders may often be small compared to females because sexual cannibalism selects for small male size. In the praying mantids, the insect group most notorious for sexual cannibalism, males have been suggested to reduce the females' aggression by courtship displays and "cautious behavior" (reviewed in Lawrence, 1992). Other suggested mechanisms to prevent cannibalism in spiders include transfer of nuptial gifts, interlocking of mouthparts during copulation, immobilization of the female by silk threads (Bristowe, 1958; Elgar, 1992), and "opportunistic mating" while the female is molting or feeding (Robinson and Robinson, 1980).

The dramatic appearance of sexual cannibalism may easily mislead us into overestimating its impact on a species' biology. For example, in contrast to earlier suggestions (Bristowe, 1958; Foelix, 1996), Stalhandske's (2001) experimental study on the spider *Pisaura mirabilis* revealed that the donation of nuptial gifts in this species is maintained by sexual selection independent of sexual cannibalism. On the other hand, if a trait is under strong selection through sexual cannibalism, this may reduce variation in the trait to a degree that makes empirical analysis difficult. For example, both Elgar and

Fahey (1996) and Prenter et al. (1994) provide suggestive evidence that male spiders are less likely to be cannibalized if they initiate mating in response to female prey capture. However, due to lack of variation in this behavior, they were unable to measure the effect on cannibalism directly. In summary, male traits with a bearing on sexual cannibalism are of fundamental importance for our understanding of sexual cannibalism in a context of sexual selection and sexual conflict. Nevertheless, to date there has been no demonstration that a putative mechanism of cannibalism avoidance actually provides an adaptive advantage.

In the present study, we use the golden orb spider *Nephila fenestrata* to investigate the relation between opportunistic mating and cannibalism directly. The species is ideal for this purpose because it allows experimental manipulation of its mating behavior: we are able to manipulate whether mating occurs with a feeding female and measure the effect on male injury and sexual cannibalism. To clarify how this translates into male fitness, we supply each female with a second male, while surviving first males have the opportunity to guard their mate against the rival. In cases where the female remates, we determine the relative fertilization success of each male. We focus on the effect of mate guarding here because males usually damage their genitalia during mating and are therefore unlikely to mate again in the future.

METHODS

Spiders were F1 offspring derived from 74 individuals collected in March 2003 near Ashburton, KwaZulu-Natal, South Africa. Subadult and adult females were housed in separate Perspex frames (60 × 60 × 12 cm), where they built typical orb webs. They were watered on 6 days per week, fed 5–8 *Calliphora* sp. flies 2–3 times per week, and weighed after their final molt. After mating, they were transferred to individual plastic cups (400 ml), where they were checked for egg sacs on 6 days per week. Egg sacs were stored in individual plastic vials and preserved in alcohol after 45–48 days of incubation at 25°C. After death of a female, we used calipers to take the tibia-patella length of a foreleg as a measure of its fixed body size. Males were maintained in individual cups (150 ml) on a diet of *Drosophila*. On the day after the final molt, each male was weighed and the tibia-patella length of a foreleg was measured while he was anesthetized with CO_2. Sexual size dimorphism is extreme in *N. fenestrata*. Males used in the present study weighed roughly 5% of females (9.74 ± 0.24 mg as opposed to 243.04 ± 11.74 mg).

Virgin males and females were randomly assigned to one of two mating treatments: in the "fly" treatment ($n = 39$), a *Calliphora* fly was introduced into the female's web shortly after a male was placed in an upper corner of her web. The female always captured and consumed the fly, so that the male had the opportunity to mate with a feeding female. Subsequent flies were introduced if the female had finished her meal before mating was over. In the "no-fly" treatment ($n = 40$), mating took place in the absence of prey.

In typical matings, males used both of their paired mating organs, the pedipalps, for one copulatory insertion each, without getting off the female. If a male dismounted the female after his first insertion, he was given 1 h to resume mating with his second pedipalp. After this time or after both pedipalps had been used, the male was given up to 1 h to assume the typical "mate-guarding position," about 3–10 cm above the hub. At this stage, a second, virgin, male was introduced into an upper corner of the web. Both males were then monitored for a period of 8 h while they could interact with each other and with the female. After 1 h and again after 6 h during this period of "mate guarding," the female was fed

a *Calliphora* fly, which often induced an increase in activity of the males. All interactions were recorded. Because of the long overall observation period, it was sometimes necessary to interrupt a trial during the phase of mate guarding and continue it on the following day. Such interruptions did not result in noticeable changes in the spiders' behavior. Trials were terminated by removing both males.

Before copulation, males frequently performed "pseudo-copulations" in which they briefly poked the female's genital openings with their pedipalps. In contrast to these pseudo-copulations, true copulations lasted much longer and were associated with rhythmical movements of the male in the initial phase. The classification of pseudocopulations as such was later confirmed by the fact that they did not result in measurable paternity gains.

To detect potential genital damage arising due to mating, the males' pedipalps were visually inspected before and after the experiment, using a 40× stereomicroscope. The conductor is a sclerotized, hooklike process of the pedipalp that is anchored to the female's genitals during copulation. The embolus is a flexible tube through which sperm transfer is accomplished.

Animals did not differ between mating treatments in any of the following: mass, age, and fixed body size of females; age and fixed body size of first and second males; and mass of first males. However, there was an unintended marginal difference in body mass of second males, which was smaller on average in the "no-fly" treatment (ANOVA: $F_{1,77} = 0.16$, $p = .045$). This difference was controlled for statistically by using mass of second males as a covariate when examining the effect of mating treatment.

Paternity was determined using standard double-mating trials (following Parker, 1970). Mature males were randomly assigned to either normal (N) or sterilized (S) treatments; males in the latter were irradiated with a 60-Gy dosage of γ-rays. The proportion of developed eggs was then used to calculate P_2, the proportion of eggs fertilized by the second male. Females were randomly assigned to one of four different treatments, which varied the order and composition of the two kinds of male mating partners. Thus, each female was provided with either of the following: (1) a normal male and then a sterilized male (NS), (2) a sterilized male and then a normal male (SN), (3) two normal males (NN), which control for the proportion of unhatched eggs in a normal clutch, or (4) two sterilized males (SS), which control for the success of the sterilization procedure. Treatments 1–4 were each distributed over the "fly" and "no-fly" mating treatments.

Following the standard method of calculating P_2, the proportion of eggs hatched in the two treatments was corrected for the proportion of eggs hatched in the NN control (0.32) and the SS control (0 eggs hatched). Mating sequence (SN or NS) had no significant effect on P_2 (ANOVA: $F_{1,14} = 0.55$, $p = .47$). We obtained 0–2 clutches per female. Successive clutches were evaluated jointly to estimate paternity with respect to a female's total progeny.

Statistical analyses were carried out with JMP 5.0. Both parametric and nonparametric tests were used as appropriate. Where possible, data were transformed to fit a normal distribution. Sample sizes can differ between analyses because not all data were available for all trials. Means are given ± SE.

RESULTS

Effects of mating treatment

First males mounted the female more quickly in the "fly" treatment, without significant effects on copulation duration or the number of copulatory insertions performed (Table 1).

Table 1

Effects of mating treatment on performance of first males

Dependent variable	"No fly"	"Fly"	Test
% Males cannibalized	33% (40)	0% (39)	$G_1 = 20.2$, $p < .0001$
% Males injured	89% (27)	36% (39)	$G_1 = 20.2$, $p < .0001$
Legs lost per survivor	2.22 ± 0.22	0.62 ± 0.15	$Z = 5.01$, $N_1 = 27$, $N_2 = 39$, $p < .0001$
Mounting latency [a] (min)	99.05 ± 21.97	44.92 ± 9.53	$F_{1,75} = 4.20$, $p = .044$
Total copulation duration (min)	123.33 ± 20.66	91.51 ± 14.04	$Z = -1.44$, $N_1 = 39$, $N_2 = 40$, $p = .15$
Number of insertions	1.63 ± 0.09	1.80 ± 0.07	$Z = 1.47$, $N_1 = 39$, $N_2 = 40$, $p = .14$
% Second males reached the female	75% (40)	44% (39)	$G_1 = 8.24$, $p = .004$
% Second males copulated	63% (40)	30% (37)	$G_1 = 6.83$, $p = .004$
% Second males copulated (among those that reached the female)?	83% (30)	65% (17)	$G_1 = 2.04$, $p = .15$
P_2	0.73 ± 0.29	0.58 ± 0.25	$F_{1,14} = 0.18$, $p = .68$

[a] Test performed on log-transformed data.

Test statistics indicate use of the following tests: $G = G$ test, $Z =$ Mann-Whitney U test, $F =$ ANOVA. Male injury refers to surviving males that lost one or more legs during mating.

Sexual cannibalism occurred only in the "no-fly" treatment (Table 1): males were captured before copulation (one case), during copulation (six cases), or immediately after copulation (four cases) while attempting to dismount the female. In two cases it was unclear whether the male was captured during or immediately after copulation.

In the "no-fly" treatment, surviving first males were more frequently injured and lost more legs, and there was an increased probability that the female remated (Table 1). Using female remating as the dependent variable, a logistic fit including mating treatment as the factor and mass of the second male as a covariate yielded significant partial effects of both mating treatment (effect likelihood ratio test: $\chi^2 = 5.36$, $p = .021$) and mass of the second male ($\chi^2 = 9.45$, $p = .002$). The interaction was non-significant and removed from the model. Second males of small mass were at an advantage because they were more likely than heavier males to reach the female while a guarding male was present (Figure 1; logistic fit: $\chi^2 = 7.32$, $p = .007$).

Correlates of cannibalism and male injury

The occurrence of cannibalism of first males within the "no-fly" treatment did not correlate with their mass, fixed body size, or age or with the corresponding parameters of the female (all $p > .1$).

Across mating treatments, first males that were cannibalized achieved a higher total copulation duration, but no higher number of copulatory insertions, than those that survived copulation (Table 2). Female fecundity was not significantly affected by male consumption (Table 2). If the first male was cannibalized and thus could not guard the female, the second male always reached the female and was significantly more likely to mate (Table 2). If the first male survived, the number of legs he lost during mating was a significant predictor of whether or not the second male reached the female (female reached: 1.65 ± 0.25 legs lost; female not reached: 0.98 ± 0.17 legs lost; Mann-Whitney U test: $Z = -2.25$, $N_1 = 32$, $N_2 = 34$, $p = .03$).

Copulation success and pedipalp damage

Across treatments, 11 out of 46 second males (23%) that mounted the female achieved no copulatory insertion but performed what might have been unsuccessful copulation attempts. The number of insertions performed by the first male negatively predicted the number of insertions performed by the second male (ranging from 0 to 2 insertions each; Spearman correlation: $r_s = -.34$, $p = .018$). In two cases, the second male inserted each pedipalp several times, with a total of five and nine insertions per male. This was exceptional because no other male used a pedipalp more than once. Because neither of these two males received any paternity success, it seems likely that what looked like insertions here were in fact unsuccessful insertion attempts without sperm transfer. We therefore excluded these two cases from analyses regarding copulation and paternity success.

Pedipalps were in most cases visibly damaged after use (95% in first males, 79% in second males) such that the tip of the conductor was missing and/or the embolus was missing or oddly protruding.

Determinants of paternity

Paternity was determined for offspring of females that received at least one copulatory insertion from each of two males. P_2 did not significantly differ between mating treatments (Table 1) or between cannibalized and noncannibalized males across mating treatments (Table 2).

Across mating treatments, mean P_2 (0.64 ± 0.17) did not significantly differ from 0.5 (t test: $t_{15} = 0.81$, $p = .43$). Neither relative copulation duration (linear regression: $F_{1,16} = 0.93$, $p = .35$) nor absolute copulation duration of the first (linear
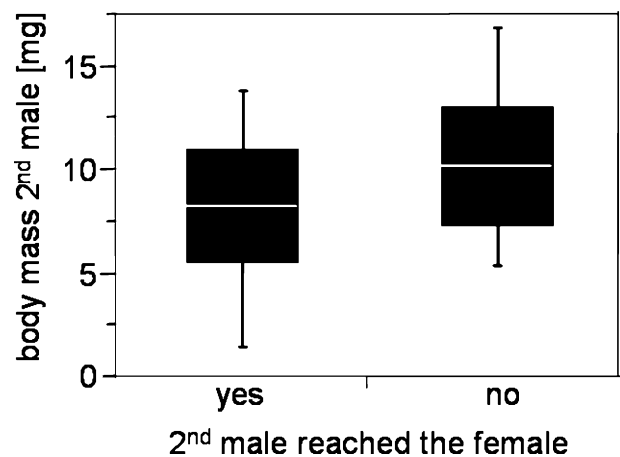

Figure 1
Body mass of second males that did ($n = 34$) or did not ($n = 32$) reach the position of the female while a surviving first male was present. Mean, SD, and range are given.

Table 2

Effects of sexual cannibalism on mating performance and reproductive success of first males

Dependent variable	Cannibalized	Not cannibalized	Test
Total copulation duration (min)	206.62 ± 55.53	88.12 ± 8.96	$Z = 2.89$, $N_1 = 13$, $N_2 = 66$, $p = .004$
Number of copulatory insertions	1.54 ± 0.13	1.74 ± 0.6	$Z = -1.06$, $N_1 = 13$, $N_2 = 66$, $p = .29$
Number of eggs per female	477 ± 56	470 ± 37	$F_{1,53} = 0.40$, $p = .53$
% Second males reached the female	100% (13)	52% (66)	$G_1 = 15.22$, $p < .0001$
% Second males copulated	85% (13)	39% (64)	$G_1 = 9.62$, $p = .002$
% Second males copulated (among those that reached the female)	85% (13)	74% (34)	$G_1 = 0.69$, $p = .41$
P_2	0.42 ± 0.28	0.77 ± 0.22	$F_{1,14} = 0.99$, $p = .34$

Data are pooled across mating treatments. Test statistics indicate use of the following tests: $G = G$ test, $Z =$ Mann-Whitney U test, $F =$ ANOVA.

regression on log-transformed data: $F_{1,14} = 0.027$, $p = .87$) or second males (linear regression on log-transformed data: $F_{1,14} = 0.62$, $p = .45$) had a significant effect on P_2. However, P_2 was significantly predicted by the number of copulatory insertions performed by the second male (ranging from 1 to 2), relative to the total number of insertions received by the female (ranging from 2 to 4; Spearman correlation: $r_s = .66$, $p = .005$).

DISCUSSION

Sexual cannibalism in *N. fenestrata* was detrimental to male fitness because it eliminated the possibility of mate guarding. Mate guarding reduced the likelihood of female remating by approximately 50%, being most successful against rivals of large size. Mating opportunistically while the female was feeding removed the risk of cannibalism, thus providing an advantage in a context of sexual conflict over cannibalism.

To clarify the evolutionary significance of a male trait in a context of sexual cannibalism, the function of the trait in question needs to be established and the fitness consequences arising from sexual cannibalism must be known. One trait that has repeatedly been suggested to reduce the risk of cannibalism in spiders is the initiation of mating after female prey capture. Such behavior is widespread in *Nephila* (Elgar and Fahey, 1996; Miyashita, 1993; Robinson and Robinson, 1973, 1980) and also occurs in other spider genera (Prenter et al., 1994; Segev et al., 2003). Here we demonstrate that mating with a feeding female indeed greatly reduces the risk of sexual cannibalism in *N. fenestrata* (Table 1).

Mating with feeding females also occurs in various species of insects where females receive food gifts from the male prior to or during mating (reviewed in Vahed, 1998). A widespread function of nuptial feeding is the prolongation of copulation (Stalhandske, 2001; Vahed, 1998), which would also seem to be a plausible function of opportunistic mating in spiders. However, such a function is not supported by our data because mating with feeding females in *N. fenestrata* did not result in prolonged copulations (Table 1).

Regarding the costs of cannibalism, it is important to note that *N. fenestrata* males appear to be functionally sterile after their second pedipalp insertion, which precludes the possibility of mating with additional females. We conclude this from the high incidence of pedipalp damage after use (79–95%), along with the fact that *N. fenestrata* males never reuse a previously used pedipalp (Fromhage L and Schneider JM, unpublished data). Interestingly, a high incidence of pedipalp damage after mating has also been found in other highly sexually cannibalistic species (Foellmer and Fairbairn, 2003; Knoflach and van Harten, 2001; Schneider et al., 2001), including the redback spider, *Latrodectus hasselti*, where pedipalp damage has been demonstrated to lead to postmating male sterility (Andrade and Banta, 2002).

It is tempting to speculate that pedipalp damage and sexual cannibalism might be causally linked in that pedipalp damage rules out the possibility of future matings, which in turn eliminates selection to avoid cannibalism (but see Andrade, 2003). This interpretation is consistent with the fact that males in several spiders do not attempt to escape from cannibalism at least after their second pedipalp insertion. Examples include active male complicity (Forster, 1992; Grasshoff, 1964) as well as passive permission of cannibalism (Foellmer and Fairbairn, 2003; Sasaki and Iwahashi, 1995). The case of *N. fenestrata*, however, shows that this argument is at least not universally true.

Our results demonstrate that surviving males can enhance their reproductive success regardless of functional sterility by guarding their mate against rival males. In contrast, cannibalized males face an increased risk of losing paternity due to female remating. At the same time, we found no indications that the fitness cost of sexual cannibalism might be balanced by associated benefits. First, there was no detectable effect of male consumption on female fecundity, which indicates that sexual cannibalism in this species does not represent a form of paternal investment sensu Simmons and Parker (1989). This result is in accordance with findings from other spiders with strong sexual size dimorphism (Andrade, 1996; Elgar et al., 2000; Fromhage et al., 2003). Second, although cannibalistic matings lasted longer than noncannibalistic ones, this had no measurable effect on relative paternity. In this respect *N. fenestrata* differs from other sexually cannibalistic spiders where copulation duration is an important predictor of paternity (Andrade, 1996; Elgar et al., 2000; Schneider et al., 2000). This difference may relate to how copulation duration is determined: in contrast to all other cannibalistic spiders studied to date, copulation duration in *N. fenestrata* appears to be largely under male control. Although females frequently attempt to capture the male during copulation, these attempts are rarely successful while he remains in his characteristic mating position. In this position, the male presses his tiny body against the female with his posterior legs encircling her abdomen, thus presenting a minimum profile to her fangs. Given that the relationship between copulation duration and paternity shown in other species appears to be largely mediated by female behavior (Andrade, 1996; Elgar et al., 2000; Schneider et al., 2000), it is perhaps not surprising that this relationship is less pronounced or absent in a species where females have little control over copulation duration. In contrast, paternity in *N. fenestrata* was predicted by the number of copulatory insertions performed by a male (one or two), which was independent of mating treatment and cannibalism.

Observations indicate that mate guarding is not the only mechanism of paternity protection in *N. fenestrata* but there may also be additional protection through mating plugs: the broken embolus of a damaged pedipalp sometimes protrudes

from the female's epigyne after mating (Fromhage L and Schneider JM, personal observation), although no quantitative data on this are presently available. Given that the number of pedipalp insertions of the second male was negatively predicted by the number of insertions performed by his predecessor, it seems possible that the females' genital openings were sometimes obstructed by broken pedipalp parts. Consistent with this explanation, some of the second males appeared unable to insert their pedipalps. Alternatively, these males may have been reluctant rather than unable to mate. This interpretation would imply that males assess female status (e.g., Suter, 1990), modifying their mating decisions according to female mating history.

Contrary to a study on *Nephila plumipes* (Elgar and Fahey, 1996) but in accordance with results from *Nephila edulis* and *Nephila clavipes* (Uhl and Vollrath, 1998), our data give no indication that sexual cannibalism represents an important selection pressure on male size. Nevertheless, second males of lower body mass were significantly more likely to reach the female (Figure 1) and achieve a copulation while a guarding male was present. A likely explanation for this is that males of lower mass may produce less conspicuous vibrations as they move across the web (Elgar and Fahey, 1996) and are therefore less easily detectable for guarding males.

Given the significant fitness benefits to be gained through opportunistic mating, it seems surprising that *N. fenestrata* males mate nonopportunistically at all. However, because males who are less hesitant to initiate courtship presumably have better chances of being the first to mate in nature, this behavior may be explained by an advantage of mating with a virgin female. Even in the nonopportunistic mating treatment, 38% of females did not remate, while the average paternity share of second males in the remaining cases was not significantly different from 0.5. This indicates that there is an overall advantage for first males. A recent study on *N. plumipes* revealed that mating with virgin females may also be important if females mate more than twice: in a triple-mating experiment, Elgar et al. (2003) demonstrated that paternity of second but not first males was diminished if female *N. plumipes* mated with a third male. It is known that males in several spider species can discriminate between virgin and mated females using olfactory cues (Herberstein et al., 2002; Schulz and Toft, 1993). Hence, it seems possible that males trade-off the advantages of opportunistic mating for the advantages of being first to mate when facing a virgin female. The latter interpretation fits well with field observations from two congeners, *N. clavipes* (Christenson et al., 1985) and *N. clavata* (Miyashita, 1993), where nonopportunistic matings were observed only with females that were no older than 2 days, whereas matings with older (presumably nonvirgin) females were always opportunistic.

The present study is the first to demonstrate the adaptive value of a male trait that reduces the risk of sexual cannibalism. Because males in *N. fenestrata* suffer a fitness cost from being unable to guard their mate, sexual cannibalism in this species can be safely classified as a case of sexual conflict. Nonopportunistic matings occur despite being risky for the male, presumably because the risk is outweighed by an advantage of being the first to mate. In conclusion, our results are consistent with the view that opportunistic mating has evolved as a male counterstrategy in a context of sexual cannibalism.

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