

Article

Male opportunistic mating increases with intensity of female sexual cannibalism in 3 web-building spiders

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Abstract

Sexual conflict is common in animals, and female sexual cannibalism represents an extreme form of sexual conflict. Males in many species have evolved a variety of strategies to circumvent or decrease the risk of female sexual cannibalism. Opportunistic mating, by which a male mates with a female when she is disturbed or when she is feeding or undertaking moulting, is one of such kinds of strategies, and widely occurs in many animals, especially in spiders. However, whether the occurrence of male opportunistic mating depends on the intensity of female sexual cannibalism remains largely unexplored. We predicted a positive correlation between them. In this study, we tested this prediction by performing a series of mating trials in the laboratory using 3 species of web-building spiders with different intensities of female sexual cannibalism: *Nephila pilipes*, *Nephilengys malabarensis*, and *Parasteatoda tepidariorum*. We found that the occurrence of male opportunistic mating was positively, though not statistically significantly, correlated with the intensity of female sexual cannibalism, thus supporting our hypothesis. All together, we provide evidence that male opportunistic mating may have evolved to respond to the selection pressure posed by female sexual cannibalism.

Key words: opportunistic mating, sexual cannibalism, web-building spider.

Sexual conflict arises when the reproductive interests of the 2 sexes diverge and is ubiquitous in sexually reproducing animals (Arnqvist and Rowe 2005; Chapman 2018). The reproductive success of a male largely depends on the number of receptive females it can succeed in mating, whereas the reproductive success of a female may depend on a male's quality. Sexual cannibalism, by which a female devours a male before, during, or after mating (Robinson and Robinson 1980), is often viewed as an extreme form of sexual conflict (Wilder et al. 2009). It is widespread in animals, especially in arthropods, such as mantis (Kynaston et al. 1994; Barry et al. 2009), crickets (Eggert and Sakaluk 1994; Johnson et al. 1999), and spiders

(Elgar 1992; Lawrence 1992; Schneider 2014). From a female's perspective, sexual cannibalism toward males can serve as general screening of male quality, which can pose a great selection pressure on males (Schneider 2014).

To counter against female sexual cannibalism, males in cannibalistic species have evolved a variety of behavioral and morphological traits (Elgar 1992; Linda et al. 2019). In spiders, for example, these traits include nuptial gifts presentation during courtship (Toft and Albo 2016), remote copulation (i.e., genital mutilation and plugging; Li et al. 2012), abdominal constriction (Andrade et al. 2005), mate binding (Zhang et al. 2011), induction of catalepsy (Singer

et al. 2000), mate with immature females (Biaggio et al. 2016; Waner et al. 2018; SentenskÅ et al. 2020), playing death (Bilde et al. 2006), sacrifice their legs to feed females (Neumann and Schneider 2020), and opportunistic mating (Robinson and Robinson 1980; Fromhage and Schneider 2005). Opportunistic mating refers to a male that mates with a female while she is foraging (i.e., hunting or feeding) or moulting (Robinson and Robinson 1980; Foellmer and Fairbairn 2003). Opportunistic mating can exclusively occur while the female is hunting or feeding in a variety of species such as *Trichonephila plumipes*, *Trichonephila inaurata*, and *Metellina segmentata* (Prenter et al. 1994a, 1994b; Elgar and Fahey 1996; Schneider and Elgar 2005). In *T. plumipes*, for example, males copulate with the female during the process of prey capture. As soon as the prey is motionless and the female starts wrapping it, copulation ends (Schneider and Elgar 2002). Opportunistic mating can also occur while female is moulting in many spiders, during which the female is completely defenseless and cannot resist the male's mating attempt, such as in *Argiope aurantia* (Foellmer and Fairbairn 2003), *Nephila pilipes* (Robinson and Robinson 1973), and *Parasteatoda wau* (Theridiidae) (Lubin 1986). Males in some species highly rely on opportunistic mating. For example, in *A. aurantia*, the majority of copulations occur when females are moulting (Foellmer and Fairbairn 2005).

Opportunistic mating in males has evolved to reduce their risk of cannibalism (Prenter et al. 1994a, 1994b). For example, in *T. fenestrata*, males can mate a female with and without prey. Males that mated without prey had injuries and were cannibalized more often than males that mated opportunistically when females were feeding (Fromhage and Schneider 2005). Sexual cannibalism prevented males from mate guarding so that a second mate could gain an average of 50% paternity as opposed to roughly 25% if the first male survived (Fromhage and Schneider 2005). Elgar and Schneider (2004) suggested that the strategic choice of opportunistic mating may be confined only to sexually cannibalistic species. However, the relationship between the dependency of opportunistic mating of males and the intensity of female sexual cannibalism in these sexually cannibalistic species is still unknown. Here, we predicted a positive correlation between them: the higher the intensity of female sexual cannibalism after male's first insertion, the higher the dependency of a male on opportunistic mating.

To test our hypothesis, we performed mating trials in the laboratory using 3 species of web-building spiders: the orb-web spiders *N. pilipes* (Araneae: Araneidae) and *Nephilengys malabarensis* (Araneae: Araneidae), and the cobweb spider *Parasteatoda tepidariorum* (Araneae: Theridiidae) (Figure 1). We observed female sexual cannibalism in all these 3 species in the field, and we hypothesized that males in these species may take certain strategies to counteract female sexual cannibalism. In *N. pilipes*, males are known to mate opportunistically when the females are moulting and the female bodies are still soft (Robinson and Robinson 1980). In *N. malabarensis*, females are very aggressive toward courting males, and males often quickly break a large part (i.e., genitalia) of its sexual organ (i.e., palp) after successfully mounting the females and inserting palps into female epigynum. The detached genitalia still can transfer sperm to the female. This genital mutilation behavior may decrease the risk of being cannibalized by females because it gives time for males to escape (Li et al. 2012). In *P. tepidariorum*, we observed that in the field, the males always stay on the fringe of a female's 3D web, either guarding the female from other males, or waiting for mating chances. Therefore, these 3 species are good candidates for testing our hypothesis.

Materials and Methods

Spiders and maintenance

Spiders used in the experiments were collected from 2 study sites. We collected *N. pilipes* and *N. malabarensis* in Pulau Ubin in Singapore (1°24'30" N, 103°57'40" E) in February 2019, and *P. tepidariorum* in Lushan Scenic Area, Jiangxi Province (29°25'18" N, 115°52' 38" E) in China in May 2019 and May 2020. We collected all females as subadults (i.e., penultimate instar stage) and reared them until adulthood in the laboratory. We collected *N. malabarensis* and *P. tepidariorum* males as subadults, and *N. pilipes* males as adults from the webs of subadult females. In *N. pilipes*, males are usually actively searching females once they have matured, and then guarding in a subadult female's web, and waiting for the female to mature (Robinson and Robinson 1980). We thus assumed that these males collected were virgin, and we checked their palps during collection to ensure their 2 palps were intact (Zhang et al. 2011). Only males with intact palps (i.e., without any damage, see Kuntner et al. 2009) were used in the experiments.

Males were kept individually in foam-covered plastic vials (0.25 L). All males and females were housed in the laboratory with controlled environmental conditions (temperature: $25 \pm 10^\circ\text{C}$; relative humidity: $80 \pm 10\%$; photoperiod: 12L: 12D with lights between 800 and 2,000 h), and experiments were also conducted under the same conditions. We sprayed spiders with water daily and fed males daily with 10 fruitflies *Drosophila melanogaster*, and females daily with 1 mealworm *Tenebrio molitor* (~3 cm in length), which is nutritionally enough for *N. pilipes* (mean \pm standard error: 34.79 ± 0.39 mm in body length, $N=20$) (Cheng et al. 2017), and would be also enough for relatively smaller sized *N. malabarensis* (mean \pm SE: 13.40 ± 0.23 mm in body length, $N=19$) and *P. tepidariorum* (mean \pm SE: 6.46 ± 0.11 mm in body length, $N=40$). We also checked and recorded their developmental status (especially the maturity date) daily.

Mating trials

We conducted mating trials in the laboratory. We first kept females individually in plastic frames ($35 \times 35 \times 35$ cm for *N. malabarensis* and *P. tepidariorum*, and $50 \times 50 \times 10$ cm for *N. pilipes*) with bamboo sticks attached to the inner sides to allow them to build webs on which all mating trials were conducted. To examine the importance of opportunistic mating to the males, we performed mating trials under web disturbed and undisturbed (i.e., control) conditions. Because opportunistic mating was mostly referred to mating with the female during her feeding (Robinson and Robinson 1980; Neumann and Schneider 2020), in order to set a disturbed condition, we put a living mealworm (~2 cm in body length) on the fringe of the female's web. The struggling of the mealworm would cause vibration to the web. For the undisturbed condition, we kept a female's web clean. For each species, to ensure no significant differences in size sexual dimorphism in a mating pair between 2 treatment groups, we measured body length and body weight of the male and the female in each mating pair 1 h before the mating trial, and recorded their post-maturation age (days after maturity). We estimated sexual dimorphism of spider body for each mating pair using the ratio of female body length to male body length and also the ratio of female body weight to male body weight.

Under both conditions, we introduced the male gently to the female's web about 5 cm away from the female. Upon the introduction of the male, we started to record the dynamics of the spider pair for 1 h, mainly the courtship behaviors of the male and response of

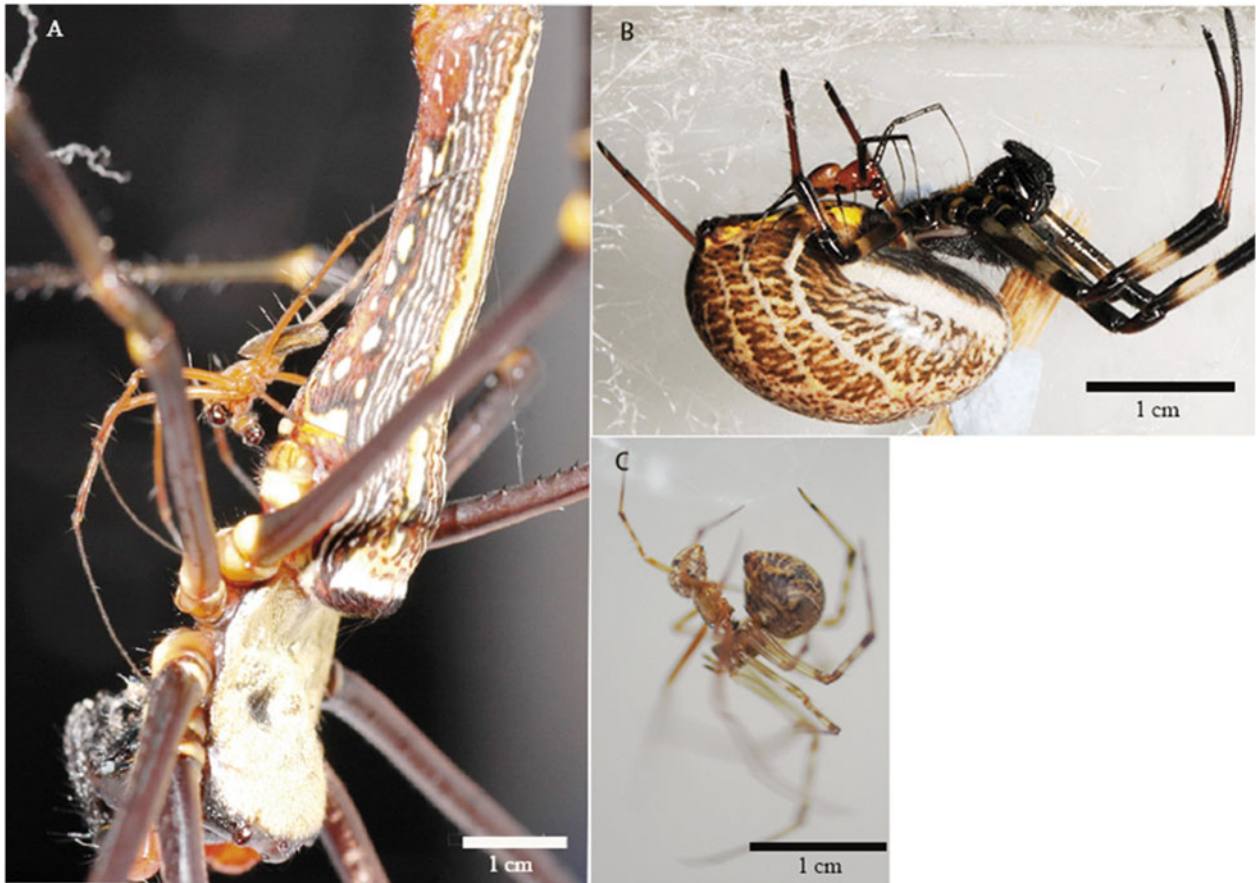


Figure 1. Mating pair of the 3 species of web-building spiders used in this study: (A) *N. pilipes*; (B) *N. malabrensis*; and (C) *P. tepidariorum*.

the female. We recorded 5 measures: 1) the male's courtship duration before its first insertion (i.e., the time in seconds from the male started jerking the web silk and approached toward the female to the male mounted the female); 2) whether the male successfully mated; 3) if so, mating duration (i.e., total insertion duration); 4) insertion times; and 5) whether the male was cannibalized by the female. Mated spiders were not used more than once.

Statistical analysis

For each spider species, we checked the normality of all the data with Shapiro–Wilk tests and performed unpaired Wilcoxon rank-sum tests to compare size sexual dimorphism between 2 treatment groups before the analyses. There were no significant differences between the 2 treatments in sexual dimorphism in body length (Wilcoxon rank-sum tests, *N. malabrensis*: $W=209$, $N_1=19$, $N_2=23$, $P=0.820$; *N. pilipes*: $W=217$, $N_1=20$, $N_2=22$, $P=0.950$; *P. tepidariorum*: $W=941$, $N_1=N_2=40$, $P=0.176$) and body weight (Wilcoxon rank-sum tests, *N. malabrensis*: $W=186$, $N_1=19$, $N_2=23$, $P=0.419$; *N. pilipes*: $W=204$, $N_1=20$, $N_2=22$, $P=0.696$; *P. tepidariorum*: $W=923$, $N_1=N_2=40$, $P=0.239$). In addition, there were no significant differences between 2 treatments in post-maturity age of females in *N. pilipes* ($W=243.5$, $N_1=20$, $N_2=22$, $P=0.542$) and in *P. tepidariorum* ($W=908$, $N_1=N_2=40$, $P=0.295$), but there was a significant difference in *N. malabrensis* ($W=303$, $N_1=19$, $N_2=23$, $P=0.029$). The post-maturity age of males was not significantly different in both *N. malabrensis* ($W=259.5$, $N_1=19$, $N_2=23$, $P=0.303$) and *P. tepidariorum* ($W=750.5$, $N_1=N_2=40$, $P=0.635$).

For each species, we then used Fisher's exact test (if sample size <5) or chi-squared test for goodness of fit to compare rate of male mating success and rate of female sexual cannibalism between disturbed and undisturbed situations. We used unpaired Wilcoxon rank-sum tests to compare courtship duration and mating durations between the 2 treatments.

To examine the relationship between the intensity of female sexual cannibalism and the dependency of opportunistic mating of male, we used the rate of sexual cannibalism of male after first insertion under undisturbed condition as the intensity of female sexual cannibalism for each species. We used the value calculated by using the rate of male mating success in “disturbed” situation minus that in “undisturbed” situation as the occurrence of male opportunistic mating. We then performed Spearman correlation to test the relationship between the intensity of female sexual cannibalism and the occurrence of male opportunistic mating. All data analyses were performed using R version 4.1.0 (R Core Team 2021).

Results

The rate of male mating success was significantly higher in disturbed group than that in undisturbed group in *N. malabrensis* (Fisher's exact test, $P<0.001$), but significantly lower in disturbed group than that in undisturbed group in *P. tepidariorum* (chi-square test, $\chi^2_1=20.01$, $N=40$, $P<0.001$). However, there was no significant difference in the rate of male mating success between disturbed and undisturbed groups in *N. pilipes* (Fisher's exact test, $P=0.22$) (Figure 2A). This result demonstrates that disturbing female webs

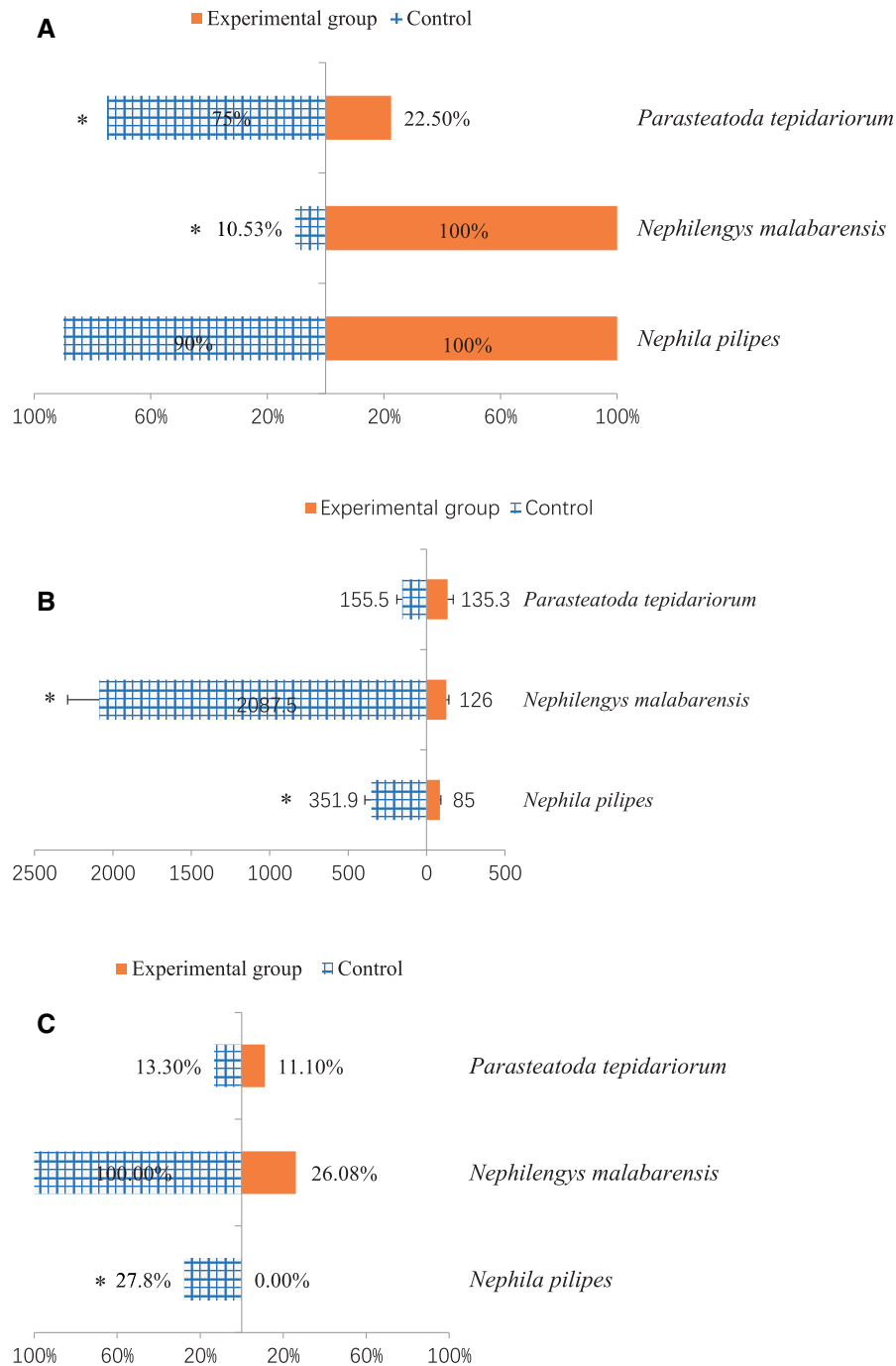


Figure 2. (A) Rate of male mating success; (B) courtship duration(s) of males before their first insertions; and (C) rate of female sexual cannibalism during/after male first insertion under the condition of with disturbance (experimental group) and without disturbance (control) in the 3 spider species. Asterisk denotes significant differences.

significantly affects the mating success in *N. malabarensis* and *P. tepidariorum*, but not in *N. pilipes*.

In addition, males of *N. malabarensis* (Wilcoxon rank-sum test, $W=46$, $N_1=19$, $N_2=23$, $P=0.007$) and *N. pilipes* ($W=377$, $N_1=20$, $N_2=22$, $P<0.0001$) courted females significantly longer on undisturbed webs than they did on disturbed webs, but males of *P. tepidariorum* courted females in disturbed webs as long as they did on undisturbed webs ($W=131$, $N=40$, $P=0.799$) (Figure 2B). In *N. malabarensis*, we found that most of males in undisturbed groups kept still on female webs in the 1 h period of experiment time

after attempting courting for several bouts because the females were too aggressive, and finally only 10.53% (2 out of 19) of them were successfully mated (Figure 2A). However, in *P. tepidariorum* we observed that some females actively cooperated with males during mating (6.25%, 5 out of 80) by presenting her epigynum to the courting male.

Males of *N. malabarensis* ($W=0.5$, $N_1=19$, $N_2=23$, $P=0.026$) and *N. pilipes* ($W=46.5$, $N_1=20$, $N_2=22$, $P<0.0001$) mated significantly longer on undisturbed webs than they did on disturbed webs, but there was no significant difference in mating

duration between the 2 groups in *P. tepidariorum* ($W = 124$, $N = 40$, $P = 0.731$). These results suggested that dependency of opportunistic mating varied in the 3 species, in which *N. malabarensis* is highly dependent on opportunistic mating, but *P. tepidariorum* is negatively affected by the disturbance (Figure 2A). Therefore, the degree of dependency of opportunistic mating in the 3 species is ranked from low to high as: *P. tepidariorum* < *N. pilipes* < *N. malabarensis*.

The rate of female sexual cannibalism during/after male first insertion in *N. pilipes* was significantly decreased on disturbed webs compared with that on undisturbed webs (Fisher's exact test, $P < 0.001$), but no significant difference was observed in *P. tepidariorum* (Fisher's exact test, $P = 1$) and in *N. malabarensis* (Fisher's exact test, $P = 0.22$) though the rate of female sexual cannibalism in the control group was greater than that in the experimental group in this species (Figure 2C). On undisturbed webs, female sexual cannibalism occurred 100% in *N. malabarensis*, but 27.8% in *N. pilipes*. The intensity of female sexual cannibalism in the 3 species can be thus ranked from low to high as: *P. tepidariorum* < *N. pilipes* < *N. malabarensis*.

We observed that in *P. tepidariorum*, the male almost exposed to the mouthpart of the female due to proximity during mating (Figure 1C), so it would be dangerous if the female was aggressive. In addition, we did not observe any mating during female feeding. Females stopped feeding once they sensed the males' movement on their web and approached the males. Males usually retreated because the vibration signals caused by the struggling of the mealworm scared males (Zhang's personal observation).

There was a trend that the intensity of a female's sexual cannibalism was positively correlated with a male's dependency of opportunistic mating during mating in the 3 web-building spider species though the correlation was not statistically significant (Spearman's rank correlation, $r_s = 1$, $df = 5$, $P = 0.167$; Figure 3).

Discussion

Opportunistic mating is a well-known strategy to counter female sexual cannibalism in many animals (Foellmer and Fairbairn 2003; Neumann and Schneider 2020), but how frequently this strategy is used in species with its intensity of female sexual cannibalism remains unclear. In this study, we investigated this relationship in 3 species of web-building spiders with varying intensities of female sexual cannibalism. Our results show a positive trend between them, supporting our hypothesis.

Opportunistic mating has been found almost in all cannibalistic spider species (Schneider 2014). It is the male's strategy to circumvent the attack of the female during mating process. Our study has shown that by performing opportunistic mating, a male's risk of being cannibalized could be significantly reduced in both *N. malabarensis* and *N. pilipes* (Figure 2C). As predicted, however, in *P. tepidariorum* in which the intensity of female sexual cannibalism is low, whether the webs are disturbed does not really make any difference in the risk of female sexual cannibalism. This suggests that *P. tepidariorum* males may not rely on or evolve opportunistic mating. Thus, for species with an intensive female sexual cannibalism, mating opportunistically probably is the better and/or only effective strategy, such as in *N. malabarensis* in our study. On undisturbed webs, only 10.5% (2 out of 19) males succeeded in mating, which were killed by females after mating, whereas the rest of males (17 out of 19) even did not approach females at all at a very close distance (e.g., ~2 cm) because females were too aggressive to courting

males. Therefore, opportunistic mating is highly dependent on how intensive female sexual cannibalism is.

Many factors can affect the intensity of female sexual cannibalism (Schneider 2014). For example, the frequency and occurrence of sexual cannibalism is positively correlated with hunger level (Roggenbuck et al. 2011). A hungrier female is more likely to kill a male than a less hungry female (Herberstein et al. 2002; Wilder and Rypstra 2008). Thus, in some species, such as the black widow spider *Latrodectus hesperus* (Theridiidae), males have evolved to differentiate cannibalism risk from chemical cues of female silk, which indicate a female's hungry level (Johnson et al. 2011). In our study, all spiders have been well-fed, decreasing female's motivation to cannibalize males for food purpose. Thus, female hungry level may not explain the difference in occurrence of sexual cannibalism in our test species.

The intensity of sexual cannibalism is also affected by sexual size dimorphism (Persons and Uetz 2005; Wilder and Rypstra 2008; Wilder et al. 2009). In general, if the intensity of sexual size dimorphism is higher, the smaller sized one would be more vulnerable (Johnson 2005; Persons and Uetz 2005), even in sexual role reversed species (Sentenská and Pekár 2013). This is consistent with the situation between predator and prey in a wide range of species, in which size differences can affect the outcome of predatory interactions (Brose et al. 2006). However, our study shows that the size of both males and females had no significant effect on female sexual cannibalism, and the correlation between intensity of sexual cannibalism and sexual size dimorphism may be not strictly positive. Although *N. pilipes* is probably the greatest sexual size dimorphic animals in terrestrial habitats (Kuntner et al. 2012a, 2012b), the intensity of female sexual cannibalism in *N. pilipes* is relatively lower compared with *N. malabarensis*. It is probably because *N. pilipes* males have evolved an effective strategy (i.e., mate binding) to decrease the risk of female sexual cannibalism during mating (Zhang et al. 2011). In addition, there was no significant difference in the rate of male mating success in *N. pilipes* between disturbed and undisturbed groups (Figure 2A). We also observed in the field that up to 8 males were waiting on a web of a subadult female for a mating chance (Zhang et al. 2011). These suggest that moulting females may be more attractive to males than females that are distracted by food.

In addition, male age may also affect the intensity of sexual cannibalism (Nessler et al. 2009b; Gavón-Centol et al. 2016). Old males are more likely to be attacked by females (Morse and Hu 2004; Nessler et al. 2009b), and young adult females are more aggressive (Gavón-Centol et al. 2016). In our study, we did not find that post-maturity spider age plays a role in determining female aggression, because the ages of males in *N. malabarensis* and *P. tepidariorum* were not significantly different varied between disturbed group and undisturbed group, in which the rates of female sexual cannibalism also did not show a significant difference. Though females of *N. malabarensis* in disturbed group were significantly older than those in undisturbed group, the rate of female sexual cannibalism in disturbed group was not significantly higher than those in undisturbed group. Future study may investigate the impact of spider ages to female aggressiveness during mating using more spider species with significantly different spider ages.

Under the strong selection pressure of sexual cannibalism, certain behaviors of males have evolved to be plastic, such as genital emasculation (Kuntner et al. 2015). Nessler et al. (2009a) reported that there was a strong relationship between sexual cannibalism and genital damage: genital damage was most frequent in species with a higher intensity of female sexual cannibalism. The self-sacrifice may be of a low cost but high benefit if the male

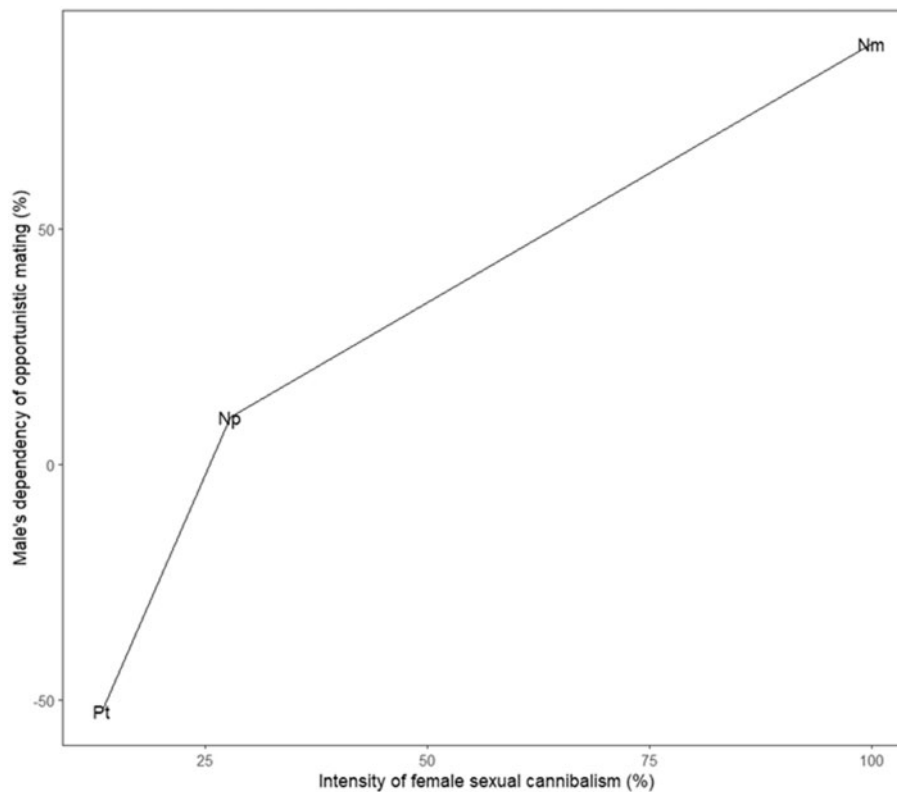


Figure 3. Relationship between intensity of female sexual cannibalism with male's dependency of opportunistic mating in the 3 web-building spider species. Male's dependency of opportunity mating (%) = rate of male mating success on disturbed webs—rate of male mating success on undisturbed webs. Intensity of female sexual cannibalism (%) = the rate of female sexual cannibalism after male's first insertion under undisturbed webs. Pt: *P. tepidariorum*; Np: *N. pilipes*; Nm: *N. malabarensis*.

has blocked the female's copulatory opening, because it can reduce the risk of sperm competition. In *Argiope lobata*, successful obstruction of the female copulatory opening reduced the share of paternity of subsequent males (Nessler et al. 2009a). This phenomenon has been observed in a variety of spider species, especially those who break their palps and used as "mating plugs" to block the copulatory openings of females (Uhl et al. 2010; Kuntner et al. 2015). This phenomenon also occurred in our study. We found that the ratio of palp damage rate is 0, 14.3, and 100% in *P. tepidariorum*, *N. pilipes*, and *N. malabarensis*, respectively. This is consistent with our evaluation of the rank of the intensity of female sexual cannibalism in these 3 species.

In summary, by studying 3 species of web-building spiders with different intensity of female sexual cannibalism, we showed a trend toward the positive correlation between a male's use of the strategy of opportunistic mating and the intensity of female sexual cannibalism. This behavioral plasticity may have evolved to respond to the predation and mate choice pressure of females.

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Author's Contributions

S.Z. and D.L. conceived and designed the study. S.Z., Y.M., A.M., and Z.H. collected the spider in the field, S.Z., Y.M., A.M., and Z.H. conducted experiments and collected data, S.Z. and D.L. analyzed the data and wrote the manuscript. All authors gave final approval for publication.

Conflict of Interest Statement

The authors declared that they had no competing interests related to this work.

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