

To Mate or to Steal Food? A Male Spider's Dilemma

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Abstract: We report a sequence of unusual male behaviors observed in *Nephila pilipes* (Fabricius, 1793) (Araneae: Nephilidae Simon, 1894), a sexually size dimorphic tropical spider species in Singapore. We documented a male suitor using his mouth parts (chelicerae) rather than his copulatory organs (pedipalps) to repeatedly probe female genitals. The behaviors may have served as a strategy to assess the female's mating status, functioned as a courtship strategy, or, most plausibly, represented an attempt to remove a genital plug. The documented chrono-sequence culminated in the male's attempted commensalism, followed by an aggressive attack by the female, resulting in near-fatal injury to the male. Notably, the attack did not escalate into cannibalism, suggesting that the extreme size difference in *Nephila* may render small males unappealing as prey.

Keywords: sexual size dimorphism; eSSD mating syndrome; genital plugging; sexual cannibalism; *Nephila pilipes*; Nephilidae



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1. Introduction

Extreme female-biased sexual size dimorphism (eSSD) has evolved in multiple animal lineages, notably in spiders, leading to gigantic females and tiny males [1]. The evolutionary mechanisms driving this phenomenon are complex [2] and are shaped by opposing and reinforcing pressures of natural selection, sexual selection, and ecological factors [1]. In the giant golden orb weaver spider genus *Nephila* Leach, 1815, eSSD is extremely pronounced, with females being, on average, eleven times the size of their male counterparts [3].

Spider eSSD is often associated with a suite of extreme reproductive traits, collectively termed eSSD mating syndrome, including sexual cannibalism, genital damage, genital plugging, genital severance, and mate binding [1]. In *Nephila* and the related *Trichonephila*, mating strategies diverge significantly from the mating rituals of the majority of spider species that are less sexually size dimorphic, fostering fierce male–male competition due to the shorter maturation time of males relative to female giants [1]. This disparity results in a surplus of sexually mature males, intensifying both direct male–male competition and sperm competition [4].

In effect, several males often compete for access to the same female, a condition that may be energetically costly to females. To counter relentless male pressure, female *Nephila* exert strong control over their mating encounters through sheer aggression, often

culminating in the forceful removal or even killing of male suitors [5]. In addition, females seal off access to their genitals with a hardened amorphous plug made during oviposition that physically prevents further episodes of superfluous mating [6]. These adaptations may be interpreted as female resistance mechanisms within a sexual arms race [6].

Male *Nephila* and *Trichonephila* exhibit a range of behavioral strategies aimed at maximizing their paternity while simultaneously mitigating sexual conflict. For example, male–male competition is severe, whereby males compete for access to a single resident female [7]. In *T. plumipes* (Latreille, 1804), the most contested females are freshly molted, virgin ones [8]. Being polyandrous, *Nephila* females store sperm from several males, but males also use alternative tactics such as breaking parts of their copulatory organs (emboli) inside the female copulatory organs, physically blocking entry by other males and securing their own paternity. Such genital plugging in *N. pilipes* is, however, not entirely effective [9]. Males, therefore, resort to additional strategies. Males also engage in mate-binding, a courtship behavior where *Nephila* males deposit fine silks over the female’s body to chemically and physically stimulate her, which has been shown to reduce female aggression, suggesting this behavior to be the male’s counter-strategy to avoid sexual cannibalism and reduce sexual conflict [10].

Whether *Nephila* males attempt to mate with females that have sealed their genitals with amorphous plugs, and, if so, how they manage to do so, remains largely unexplored. Given the pressure on males to evolve male persistence mechanisms, it is plausible that they have evolved the ability to remove such plugs. However, this behavior has not been documented. Below, we describe a rare one-time observation of a *Nephila* male exhibiting behavior that may represent an attempt at amorphous plug removal.

2. Materials and Methods

Nephila pilipes (Fabricius, 1793) is a conspicuous eSSD spider species inhabiting tropical forests across South Asia, Southeast Asia, and Australasia [11]. In Singapore, it is commonly encountered in the Southern Ridges, a belt of rainforest patches stretching from west to east. While surveying *N. pilipes* webs at the Kent Ridge campus of the National University of Singapore on 12 January 2024 (at N1.295018, E103.777822), we documented a suite of intriguing behaviors related to mating, foraging, and sexual conflict (see Figure 1).

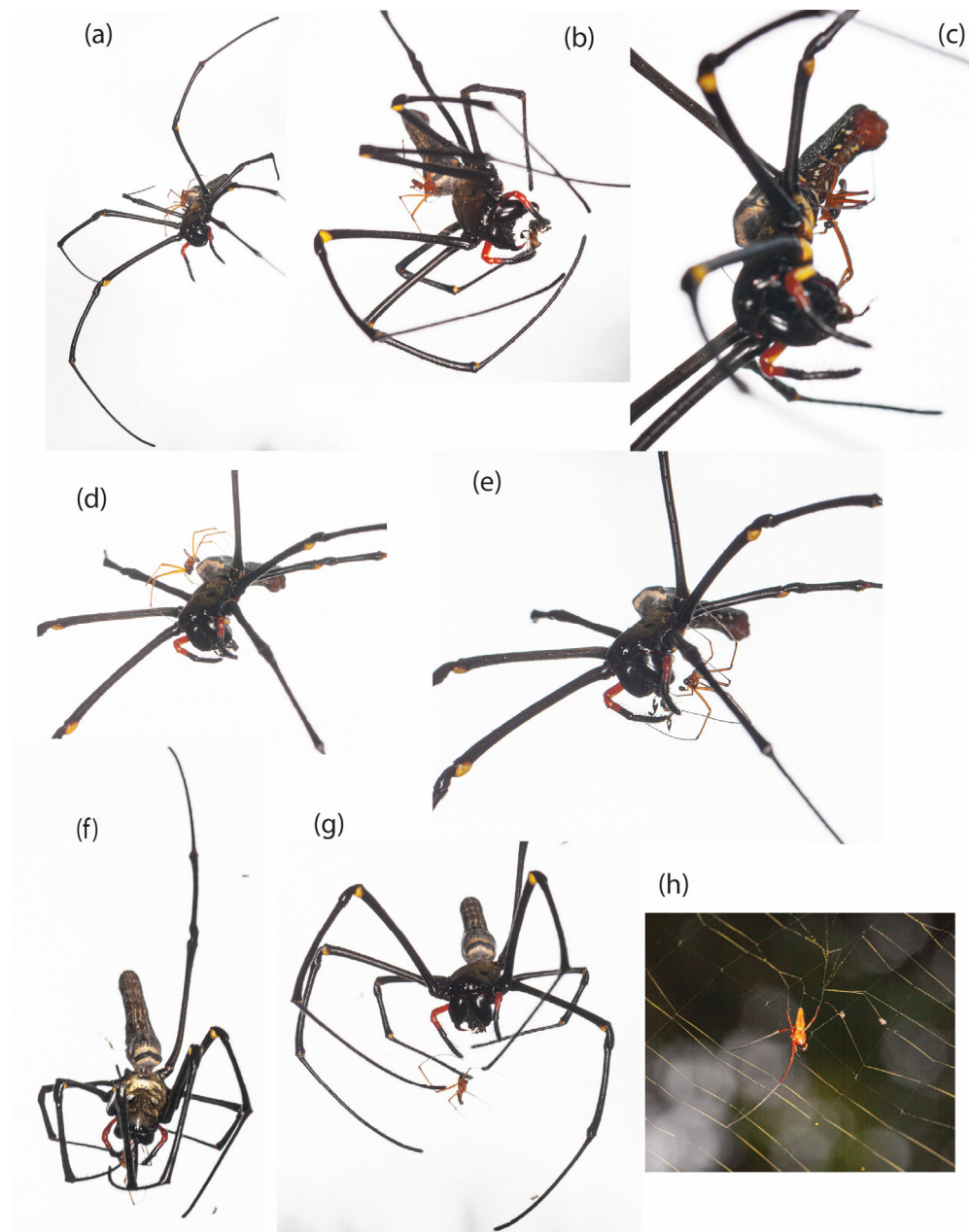


Figure 1. A chronological sequence of events leading to the female *Nephila pilipes* attacking, but not consuming, her male suitor. A female *N. pilipes* was in the hub of her web, carrying a male suitor on her dorsal side (a). A bee was captured in the web below the hub, and the female seized the prey, all the while carrying the male (b). While she fed on the bee, the male continued to shift from the female dorsum to the venter, seemingly seeking copulation, but rather than using his pedipalps to mate, he employed his chelicerae, presumably in an attempt to remove the genital plug over the female's genitals (c). While feeding on the captured prey, the female still showed no aggression towards the male (d). However, as soon as the male decided to try to partake in the feeding and approached the female mouthparts (e), the female attacked the male by aggressively seizing his legs (f) and then discarding him off the hub (g). The injured male survivor was glued to sticky spirals in the lower part of the female web (h), but with four lost legs, his fate was sealed. Matjaž Kuntner took these photos at Kent Ridge, Singapore, on 12 January 2024.

3. Results

A female *N. pilipes* was observed at the hub of her web with a single male suitor present on her dorsal side (Figure 1a). Notably, no rival males were present, allowing

the observed male unrestricted movement between the female's dorsal and ventral sides without aggression from either the female or competing males. During the observation, a bee became entangled in the sticky spirals of the web, prompting the female to swiftly seize it with her chelicerae for consumption. Meanwhile, the male remained positioned on her body (Figure 1b). As the female fed, the male continued to shift from her dorsum to her venter, seemingly exploiting the “safer sex with feeding females” strategy, a common opportunistic mating tactic [12]. However, rather than using his paired sperm transferring organs (pedipalps) to inseminate the female in typical spider copulation, the male repeatedly probed the female genitalia (epigyne) with his mouthparts, the chelicerae (Figure 1c). This behavior may have been a strategy to assess the female's mating status, a courtship strategy, or, most plausibly, an attempt to remove a genital plug to facilitate copulation.

Although *Nephila pilipes* females can sometimes show aggression towards males [9], remarkably, the observed female remained calm and continued feeding during this phase (Figure 1d). Eventually, the male gave up his genital probing and instead attempted to partake in the female's prey by approaching the female mouthparts while she was feeding (Figure 1e). This action immediately provoked an aggressive response from the female, who grabbed several of his legs (Figure 1f) and forcibly discarded him from the hub (Figure 1g). The injured male, having lost three legs on one side and one on the other, became ensnared in the sticky spirals of the lower web (Figure 1h), rendering his chances of further mating success bleak.

We refrained from interfering with the observed interactions and did not collect the specimens. Our prior taxonomic and behavioral expertise on *N. pilipes* allowed us to confidently identify the species and interpret the context of the mating behaviors. We infer that the female likely possessed an amorphous genital plug [6] for several reasons: (i) The female's body size exceeded 30 mm, indicating that she had been an adult for weeks, if not months. *Nephila pilipes* undergo one or several additional post-maturation molts [13], during which they retain sperm in their spermathecae, which are not molted/replaced. (ii) The female's abdomen appeared shrunken, suggesting recent oviposition. *Nephila pilipes* females produce amorphous plugs during egg-laying [6]. (iii) The male did not attempt copulation using his palps as is the norm in spiders [14], but instead used his chelicerae (Figure 1c).

4. Discussion

Nonconceptive sexual acts, i.e., those with no opportunity to result in the union of sperm and egg [15], may be widespread in vertebrates but are rarely reported in invertebrates. Oral sexual contacts may be such acts, but they are virtually unknown in spiders, with a notable exception of Darwin's bark spider (Araneidae: *Caerostris darwini* Kuntner & Agnarsson, 2010) from Madagascar [16]. To our knowledge, no prior studies have documented male chelicerae application to female genitals in *Nephila*. This one-time observation detected differences to the behavior described in Darwin's bark spider, where males invariably use both chelicerae and saliva directly on female copulatory organs [16]. We do not consider the observed behavior in *N. pilipes* as a nonconceptive sexual act but rather interpret it to represent an attempt to remove an amorphous genital plug to enable subsequent mating.

Alternative explanations to attempted amorphous plug removal are less plausible. For example, while it is possible that the male might have been attempting to eliminate emboli from a prior male, emboli in this species are too thin and deeply embedded in the spermathecae for chelicerae to effectively remove them. Another alternative explanation, that the male was merely assessing the female's receptivity, is likewise less plausible as, for this purpose, he would likely have used his pedipalps rather than his chelicerae. Thus,

the most reasonable interpretation is that the male attempted amorphous plug removal to access the female's copulatory opening. Genital plug removal, albeit not by means of using mouthparts, has been documented in several distantly related spider groups [17–19].

Our observation raises new questions and suggests testable hypotheses. Prior laboratory studies on *Nephila* have not documented successful mating with females that had produced an amorphous plug during oviposition [6]. However, we hypothesize that some males may have evolved mechanisms to remove existing plugs using their chelicerae, as we observed in this case, albeit seemingly unsuccessfully.

This challenges the assumption that amorphous plugs in *N. pilipes* function solely as an impenetrable mating barrier. Instead, they may serve as a test of male quality, potentially acting as a selective mechanism favoring males capable of overcoming this obstacle. If females can mate at a relatively advanced age and still produce viable offspring, this could have significant implications for the reproductive strategies of *N. pilipes*. Such a prolonged mating system may contribute to the species' high abundance and broad geographical range, spanning from Pakistan to the Solomon Islands and from China to Australia [11]. Future studies should explore whether males can successfully remove amorphous plugs and whether this ability confers a selective advantage in sperm competition.

Our observation adds a new layer to the understanding of sexual cannibalism in *Nephila*. A key question arises: Why did the female not consume the “kleptoparasitic” male as a potential food source but instead discarded his body after attacking him? We propose that the extreme size difference in this species may render small males nutritionally insignificant, potentially leading to poor nutrient extraction from male bodies [20]. Consequently, *Nephila* males may not face the same high likelihood of cannibalism observed in certain other spiders [21–24]. This aligns well with the results from a comparative study that found *N. pilipes* females to be aggressive, but not cannibalistic towards males, compared to the higher rates of cannibalism in other sexually size dimorphic orbweavers [25].

5. Conclusions

Nephila pilipes males, particularly those courting females that had produced amorphous plugs, face a critical dilemma. They must decide whether to continue with mating attempts that are unlikely to succeed or conserve energy for potential future opportunities with other females. At the same time, feeding commensally along with giant females seems to be a risky strategy that exposes them to aggression and potential injury. This predicament encapsulates the challenges faced by small male spider suitors navigating a cannibalistic mating landscape.

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Abbreviations

The following abbreviation is used in this manuscript:

eSSD Extreme female-biased sexual size dimorphism

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