Inside the trap: Biology and behavior of the pitcher-dwelling crab spider, *Misumenops nepenthicola*

1 | INTRODUCTION

Symbioses—the close association of two species living permanently together—capture human imagination like few other aspects of biology. As do carnivorous plants, which Charles Darwin (1875) described as the "most wonderful plants in the world." The idea that a plant should turn the tables on animals was fiercely disputed by early naturalists like Carl Linnaeus who deemed it "against the order of nature as willed by God" in a letter to his American colleague John Ellis in 1869. Today, over 800 species of carnivorous plants are known (Ellison & Adamec, 2018) with a vast number of scientific publications dedicated to all aspects of their biology. Yet, the fascination for these strange plants persists, as evidenced by their frequent coverage in the media and their ever-growing popularity with hobbyists and plant collectors.

While most school children are familiar with carnivorous plants, even among adults few will be aware that carnivorous plants may also provide a living space for animals. However, the idea is not new and the first descriptions of the diverse communities inhabiting pitcher plant traps (Figure 1a) date back to the 18th century (Catesby, 1754; Rumphius, 1750). The pools of digestive liquid inside the pitcher traps provide an aquatic habitat for a surprisingly diverse range of specialist species from microbes to insect larvae and even tadpoles (Adlassnig, Peroutka, & Lendl, 2011; Weaver, 1983). Symbiotic associations between (predominantly) terrestrial animals and pitcher plants are much less common. Among the better known is the association of *Colobopsis schmitzi* ants with the myrmecophyte (*ant plant*) *Nepenthes bicalcarata*, where the plant provides food and shelter for the ants (Clarke & Kitching, 1995) which, in turn, defend the plant against herbivores (Merbach et al., 2007) and keep the trapping surfaces clean and slippery (Thornham, Smith, Grafe, & Federle, 2012). Remarkably, the ants are able to safely navigate the slippery surfaces and even swim and dive in the digestive liquid to forage for freshly captured prey (Bohn, Thornham, & Federle, 2012). Other terrestrial pitcher inhabitants include the pitcher-roosting Hardwicke’s Woolly bat *Kerivoula hardwickii* (Grafe, Schöner, Kerth, Junaidi, & Schöner, 2011) and the much less studied pitcher-dwelling red crab spider *Misumenops nepenthicola* (Pocock, 1898; alternative name *Henriksenia labuanica* suggested by Striffler & Rembold, 2009; see Figure 1b). Here we review the latter association and supplement the sparse information from scientific literature with observations and experiments from two natural sites in Brunei, Northern Borneo, during 8 weeks of field work in spring 2007.

2 | CRAB SPIDERS AND PITCHER PLANTS

Spiders are often considered to be terrestrial, although most arachnid families include species that live in close association with water...
Crab spiders (Thomisidae) are specialized ambush predators named after their peculiar sideways gait. They are easily identified by their elongated first two leg pairs that are equipped with strong claws to grab prey (Comstock, 1948). While most of the over 2,000 species (Platnik, 2007) are—often exquisitely camouflaged—sit-and-wait predators on flowers, a few species in the genera Misumenops, Thomisus, and Synema have evolved close associations with carnivorous Nepenthes pitcher plants (Beaver, 1983; Rembold, Fischer, Striffler, & Barthlott, 2012). The best known of these is the red crab spider, M. nepenthicola, first described by Pocock (1898) as living inside Nepenthes traps in northern Borneo. Pocock also noted that the spiders responded to disturbance by dropping into the digestive liquid and hiding among the debris in the bottom of the pitcher (Figure 1c,d; see also Movie S1). Despite this unusual behavior and choice of abode, an entire century was to pass before pitcher-dwelling crab spiders received significant further scientific interest, and their natural history remains largely a mystery to date.

3 | ADAPTATIONS FOR LIFE INSIDE A CARNIVOROUS PLANT

Nepenthes pitchers (Figure 1a) are highly specialized organs that evolved to trap, kill, and digest arthropods (Juniper, Robins, & Joel, 1989). The pitcher rim and inner walls are lined with extremely slippery surfaces (Bohn & Federle, 2004; Knoll, 1914), and the fluid contains a range of digestive enzymes (Amagase, 1972) and can be strongly acidic (Bauer, Willmes, & Federle, 2009; Morissey, 1955). Some species also have highly viscoelastic pitcher fluids that aid the retention of captured prey and make aquatic locomotion a challenging task (Gaume & Forterre, 2007). How can crab spiders thrive in such a hostile environment? Pocock (1898) and Dover, Fage, Hirst, Tams, and Ghosh (1928) noted that the spiders cover the pitcher interior with a fine mesh of silk that presumably helps them to negotiate the extremely slippery surfaces (Figure 1e,f; Movie S1). In order to test whether spiders rely on silk when colonizing a pristine pitcher without such a “safety scaffold” in place, we performed running trials with eight individual spiders (10 trials each) on the cleaned rim of a Nepenthes rafflesiana pitcher in the field, under dry (i.e. safe) and experimentally wetted (i.e. very slippery) conditions (cf. Bohn & Federle, 2004). The rim was chosen as the test surface because it is the first trapping surface an approaching spider encounters, and because of its unique “switchable” slipperiness which provides a baseline measure for performance under non-slippery (dry) conditions. In a second set of identical dry versus wet trials, we then covered the spinnerets of our test spiders with a small droplet of superglue to test the importance of ad hoc silk attachment for safe locomotion. Unsurprisingly, spiders performed better with functional spinnerets and on dry surfaces: only two individuals slipped, once each. Both wetting and spinneret manipulation significantly decreased the performance of the spiders (Wilcoxon Matched-Pairs tests, n = 8, 10; dry versus wet (intact): p = 0.02; intact versus manipulated (dry): p = 0.04); however, under wet conditions, spinneret manipulation did not lead to a further significant loss of performance (intact versus manipulated (wet): p = 0.30; Figure 1g).

The reasons for these findings are not entirely clear. Spider silk has been shown to absorb water and therefore attach well even under humid conditions (Singla, Amarpuri, Dhopatkar, Blackledge, & Dhinoojwala, 2018); however, the continuous water film on the wet pitcher rim might be too wet even for the most sophisticated adhesive. It is also worth noting that we thoroughly cleaned the rim surface prior to our trials, thereby removing any “safety scaffolds” that the spiders had previously built (Figure 1e,f). Previous studies also noted that M. nepenthicola spiders rarely leave the pitchers; therefore, they might simply wait for non-slippery dry conditions before moving into a new pitcher with a pristine, clean rim. On the other hand, we found that the spiders in our field site generally moved between pitchers overnight and thus during times when the traps are definitely wet (Bauer, Bohn, & Federle, 2008). Silk use aside, electron micrographs show that the tarsi of M. nepenthicola are well equipped with adhesive hairs (setae) and claws (Figure 1h).

4 | NOT ALL PITCHERS ARE EQUAL: OBSERVATIONS ON PITCHER CHOICE AND PHILOPATRY

In line with previous reports (Dover et al., 1928; Mogi & Chan, 1997; Pocock, 1898; Reiskind, 1978), we found spiders exclusively in N. rafflesiana and Nepenthes gracilis, but not in any of the other five common species of lowland Nepenthes in our field sites. In both species, spiders preferred ground pitchers over aerial pitchers (chi-square test, n = 44, p = 0.001). Adult spiders were generally solitary. Only newly hatched spiderlings were occasionally found in small groups inhabiting the same pitcher. Occupied pitchers were characterized by an intermediate fluid level. Pitchers that were flooded after heavy rain as well as pitchers with naturally or experimentally reduced fluid levels were promptly abandoned. We only found spiders in pitchers that had caught prey and regularly observed spiders feeding on freshly captured insects that were still floating at the fluid surface (Figure 2a; see also Movie S1).

Mating attempts are risky for the male that may easily become a meal for the female instead (Figure 2b). We were unable to observe mating events directly, but occasionally found mating pairs residing in the same pitcher for several days at a time. Female aggression was common, and the males generally kept a safe distance. After mating, the females spun one or two cocoons attached to the inner pitcher wall and laid clutches of beige eggs inside (Figure 2c). Females showed a strong preference for N. gracilis pitchers for breeding: only two out of 12 observed nests were found in N. rafflesiana pitchers, and one of those was unsuccessful and prematurely abandoned by the female. We observed a range of quite remarkable brood care behaviors in M. nepenthicola. The female aggressively guarded the eggs against intruders (Figure 2d). Once the spiderlings had hatched, she provided them with pre-digested food (Figure 2e) and assisted them...
to leave the cocoon. As the juveniles grew and became more independent, the female eventually abandoned the pitcher and moved on.

5 | CONCLUDING REMARKS

Many mysteries around the secret life of crab spiders in pitcher plant traps still remain to be unraveled. How do they manage to move in and out of the— in the case of N. rafflesiana—highly viscoelastic—pitcher fluid with such ease? Why are they found only in certain species of pitcher plant? How often do spiders move between pitchers, and why? One particularly interesting question is whether spider and plant benefit from each other or not. Early naturalists often assumed that the spiders are competitors or even kleptoparasites of the pitchers (Reiskind, 1978). This is in line with our observations that spiders routinely retrieved freshly captured prey from the pitcher fluid. Chua and Lim (2012) suggested that spiders feed primarily on aquatic infauna organisms; however, we rarely observed spiders hunting for live prey such as mosquito larvae in the pitcher fluid. Recent studies point toward a neutral or even mutualistic relationship because they observed spiders amnestically feeding her immature offspring with pre-digested food.

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AUTHORS’ CONTRIBUTIONS

IK conducted the experiments and observations. UB designed the study, analyzed data, and wrote the paper. Both authors took photographs.

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