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Cross-habitat predation in *Nepenthes gracilis*: the red crab spider *Misumenops nepenthicola* influences abundance of pitcher dipteran larvae

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Abstract: Phytotelmata (plant-held waters) are useful ecological models for studying predator–prey interactions. However, the ability of terrestrial predators to influence organism abundance within phytotelmata remains poorly studied. We investigated the predation of two pitcher-dwelling spiders, the red crab spider *Misumenops nepenthicola* and the yellow crab spider *Thomisus nepenthiphilus* (Araneae: Thomisidae) on dipteran larval abundance by manipulating their presence in the pitcher *Nepenthes gracilis*. Lower abundance in the larvae of the mosquito *Tripteriodes* spp. and increased spider mass were recorded after *M. nepenthicola* was introduced into laboratory-maintained pitchers ($n = 10$); *T. nepenthiphilus* did not affect larval abundance and a decrease in spider mass was recorded. Further investigations on two other dipteran larval species, the scuttle fly *Endonepenthia schuitemakeri* and gall midges *Lestodiplosis* spp., reported reduced numbers with the introduction of *M. nepenthicola.* We further tested this predation on dipteran larval abundance by its introduction, removal, and re-introduction to pitchers in the field ($n = 42$) over 1 mo. The spider's absence and presence significantly influenced larval numbers: all four dipteran species reported a significant decrease in numbers after *M. nepenthicola* was introduced. These results are one of the first to demonstrate the influence of a terrestrial phytotelm forager on the abundance of pitcher organisms via direct predation, reiterating the ecological importance of terrestrial phytotelm predators on phytotelm community structure and dynamics.

Key Words: crab spiders, *Culex*, *Endonepenthia schuitemakeri*, *Lestodiplosis*, *Misumenops nepenthicola*, *Nepenthes gracilis*, phytotelmata, predation, *Thomisus nepenthiphilus*, Tripteriodes

INTRODUCTION

Natural microcosms offer opportunities for an array of ecological studies, such as the role of predation in biotic interactions, shaping food webs and altering community structure and ecosystem functions. Phytotelmata (plant-held waters; Kitching 2001) are popular study models of arthropod–plant mutualism food webs and community structure (Armbruster *et al.* 2002, Clarke *et al.* 2009, Kitching 2001, Maguire *et al.* 1968, Moon *et al.* 2010, Peterson *et al.* 2008), focusing on the apex predators that reside within the same aquatic habitat as their prey. However, there has been recent interest in the cross-habitat (i.e. terrestrial to aquatic) predatory effects of terrestrial inhabitants (Romero & Srivastava 2010).

Phytotelm communities have been the focus of numerous studies of community dynamics for the past three decades (Kitching 2000, Maguire *et al.* 1968, Mogi & Chan 1997, Mogi & Yong 1992, Mouquet *et al.* 2008, Naeem 1988, Seifert & Seifert 1976). Amongst these, pitchers are unique as these highly modified leaf structures, holding a digestive fluid, lure, trap and kill any organism that falls into these pitfalls. These vessels possess several key traits that facilitate their heterotrophism: chemical and colour cues that attract prey (Bennett & Ellison 2009, Jurgens *et al.* 2009, Schaefer & Ruxton 2008), slippery inner wall surfaces (Gorb *et al.* 2004, Scholz *et al.* 2010), and a highly viscous (Di Giusto *et al.* 2008), acidic and hypoxic fluid (due to decomposing insects). Collectively, these factors constitute a hostile environment and pose a challenge for any organisms. Rather, numerous organisms have adapted to living, many exclusively, within pitchers as nepenthebionts (i.e. obligate *Nepenthes* pitcher dwellers), holding positions as apex predators, mesopredators and scavengers that regulate top-down and bottom-up forces (Kneitel & Miller 2002). In comparison, little is known about the ecological importance of terrestrial phytotelm organisms (Greeney 2001).

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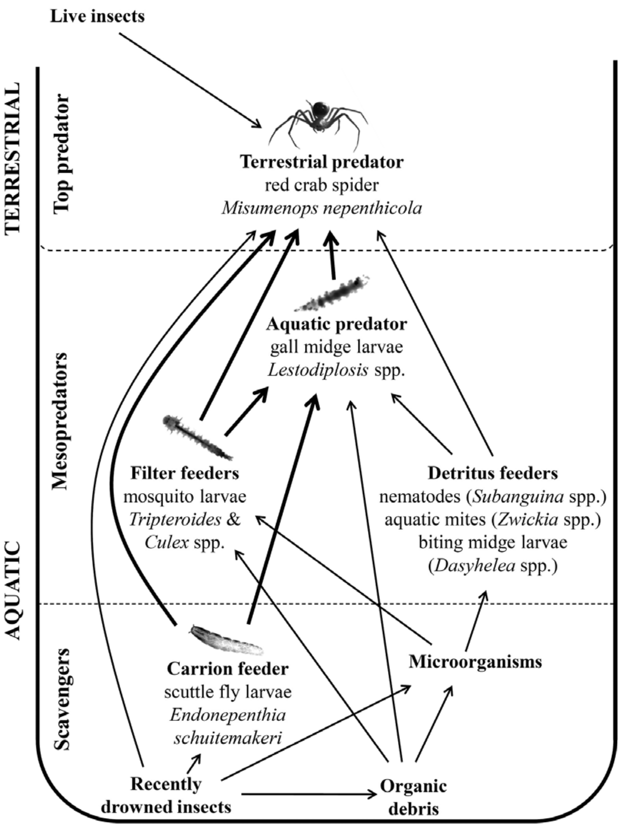

Figure 1. Food web of a *Nepenthes gracilis* pitcher (modified from Clarke & Kitching 1993, Phillipps *et al.* 2008, Tan 1997) organized in trophic levels. Arrows in bold indicate predator–prey interactions involved in this study.

Although many terrestrial phytotelm inhabitants are known (for a review see Greeney 2001), those that forage across terrestrial–aquatic environments are seldom recorded. Clarke & Kitching (1995) probably provided the first empirical evidence of cross-habitat predation in the golden ant *Camponotus schmitzi* and its host plant *Nepenthes bicalcarata*, where the ant significantly influenced the abundance of filter-feeding mosquito larvae. The nepenthebiont crab spiders (Araneae: Thomisidae) are the only other group of organisms documented to forage into *Nepenthes* pitcher fluid (Barthlott *et al.* 2007, Clarke 1997, 2001; Phillipps *et al.* 2008, Pollard 2005; Figure 1) for live dipteran larvae (Clarke 1998, Moran 1993). These larvae are *Nepenthes* obligates and assume key roles within the food web (Figure 1); however, nothing is known about the aquatic foraging ability of the terrestrial crab spiders and their potential to alter dipteran larval abundance.

Here we investigate the nepenthebiont crab spiders' foraging ability to alter the aquatic larval abundance of the tropical pitcher plant *Nepenthes gracilis*. We hypothesize that the crab spiders' presence significantly affects the abundance of nepenthebiont dipteran larvae species in *N. gracilis*. As pitchers provide natural microcosms amenable to both laboratory and field experiments (Srivastava *et al.* 2004), we conducted laboratory-based studies to investigate the aquatic foraging behaviour of the crab spiders by introducing one individual into one pitcher containing any of the three dipteran larvae species; a reduction in larval abundance, coupled with weight increase in the spider will verify this ability. Field experiments then determined the spiders' influence on the abundance of these aquatic dipteran larvae. A significant decrease in larval abundance in the presence of the crab spiders will suggest the ecological importance of these predators, with probable implications for the *Nepenthes* food web, and highlight the importance of the ecological roles of terrestrial animals with aquatic predatory traits within phytotelmata.

METHODS

Study species

Nepenthes gracilis Korth. (Figure 2a) is widespread in Singapore, its pitchers home to a diverse macrofauna dominated by insects (Kitching 2001). Larvae of several dipteran species (mosquitoes *Tripteriodes* spp. and *Culex* spp., scuttle fly *Endonepenthia schuitemakeri* (Schmitz, 1932) and gall midge *Lestodiplosis* spp. (Figure 2d–g)) occupy the various trophic zones within these pitchers (Figure 1). Residing within pitchers and above the fluid are two species of thomsids; the red crab spider *Misumenops nepenthicola* (Pocock, 1898) (Figure 2b) and the yellow crab spider *Thomisus nepenthiphilus* (Fage, 1930) (Figure 2c). Only the foraging of *M. nepenthicola*, but not *Thomisus nepenthiphilus*, has been recorded within *N. gracilis* (Kitching 2000).

Laboratory experiments

We investigated the foraging behaviour of *Misumenops nepenthicola* and *Thomisus nepenthiphilus* on dipteran larvae that dwell within *Nepenthes* pitchers using 10 adult females (*M. nepenthicola*; body length (mean ± SD): 5.4 ± 0.5 mm, *T. nepenthiphilus*; body length: 7.3 ± 0.5 mm) and 200 mosquito larvae (*Tripteriodes* spp.; body length: approximately 4 mm), all collected from Kent Ridge Park, a secondary forest in Singapore. Pitcher fluid (collected from 20 pitchers) was filtered to remove detritus and live organisms. We also purchased *N. gracilis* from a local nursery; these were maintained in clear plastic tanks (39 × 24.5 × 30 cm). Twenty fresh pitchers (mean ± SD: height: 7.30 ± 1.65 cm; width: 1.50 ± 0.28 cm) were selected, each rinsed thoroughly (using distilled water from a squirt bottle) prior to the experiment. Pitcher contents were discarded, and the fluid replaced

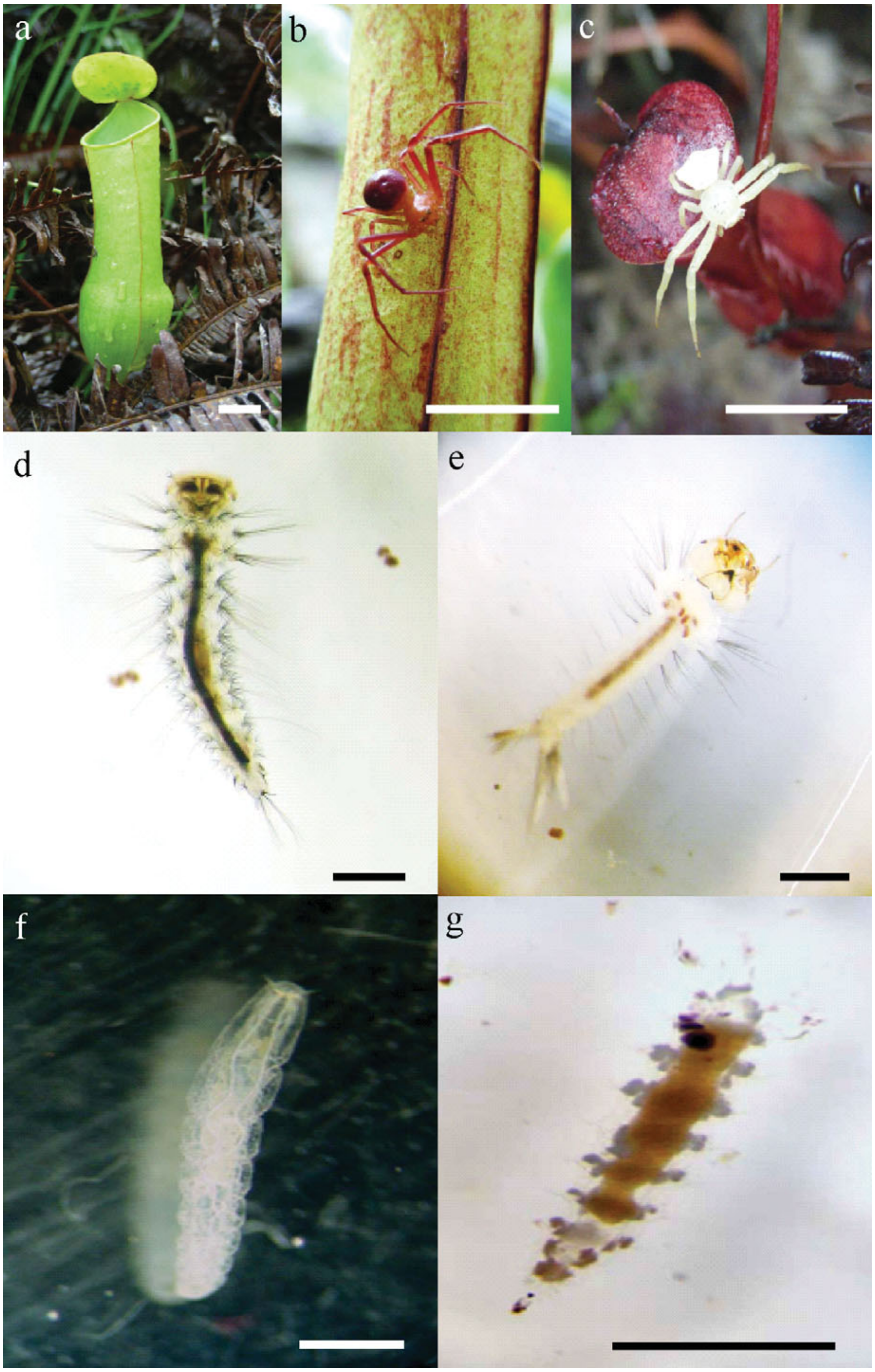

Figure 2. Organisms involved in this study: a freshly opened *Nepenthes gracilis* pitcher (a), red crab spider *Misumenops nepenthicola* (b), yellow crab spider *Thomisus nepenthiphilus* (c), mosquito larvae *Tripteriodes* spp. (d) and *Culex* spp. (e), scuttle fly larva *Endonepenthia schuitemakeri* (f), and gall midge larva *Lestodiplosis* spp. (g). Scale bar represents 1 cm (a, b, c) and 1 mm (d, e, f, g).

by those collected in the field (2 ml of fluid per pitcher) prior to experiment. Two circular plastic containers (4.3 cm diameter × 11.2 cm height) ensured containment of an individual spider in each pitcher. Experiment was limited to 5 d because many *N. gracilis* had withered and most mosquito larvae had moulted into pupae and emerged as adults in earlier trials that lasted 1 wk. We accounted for the number of larvae (10 *Tripteroides* spp.) on days 1 and 3 to check for cannibalism. The mass of each crab spider (to the nearest 0.00001 g) was recorded after collection (i.e. day 1) from Kent Ridge Park, prior to their introduction into the pitchers and maintained on sugar solution ad libitum via dental roll soaked in diluted sugar solution till day 3.

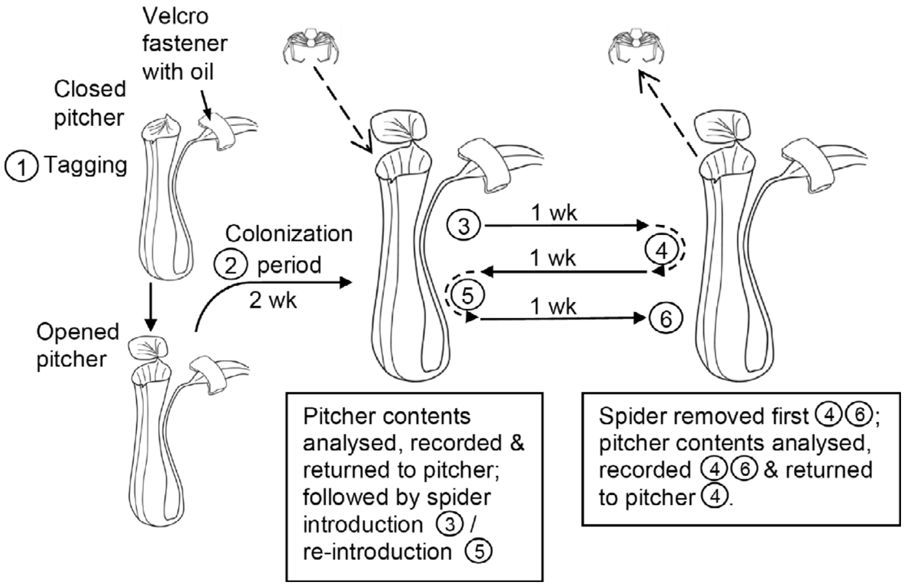

Figure 3. Summary of field-based experiment depicting the periods of colonization, presence and absence of crab spiders, and sequence of data collection and pitcher manipulation (i.e. introduction and removal of spider).

On day 5, we took note of larvae carcases (i.e. dead larvae not eaten by the spider) to ensure that all larvae were accounted for.

We repeated the above procedure but used two dipteran larvae species in separate trials: the carrion-feeding scuttle fly larva *E. schuitemakeri* (length: 0.4 cm) and the predatory gall midge larva *Lestodiplosis* spp. (length: 0.2 cm). Only five individuals of each species were used due to their lower abundance observed in the field (pers. obs.). We excluded *T. nepenthiphilus* from this and further experiments because it did not forage on aquatic mosquito larvae. All experimental animals, plants and units were maintained in a laboratory under controlled environmental conditions (relative humidity 80–85%; temperature 25 °C ± 1 °C; light regime 12:12 h; lights on at 0800 h).

Field experiments

We investigated the relationship between *M. nepenthicola* and the abundance of phytotelm dipteran larvae in natural occurring populations of *N. gracilis* at Kent Ridge Park, Singapore. As *M. nepenthicola* abandoned shorter pitchers (pers. obs.), we only used pitchers more than 6 cm high and unopened at time of selection. From two separate experimental periods (22 October 2009–3 December 2009; 24 December 2009–4 February 2010), we tagged a total of 65 unopened *N. gracilis*. These were surveyed twice a week from the time they opened to the time they withered or until the end of the field experiment, whichever came first. We also introduced a 2-wk colonization period to allow establishment of secondary consumers and scavengers, as freshly opened pitchers harboured neither aquatic dipteran larvae nor crab spiders (pers. obs.).

Field experiments commenced 2 wk after the pitchers had opened (Figure 3); a small number of pitchers that harboured spiders were excluded from our data. Contents of qualified pitchers were emptied into individual collection vials and pitchers rinsed with water via a squirt bottle into a second vial to remove residual contents. Both vials were then transported to a laboratory and the live aquatic dipteran larvae identified (based on morphospecies) and counted under a stereomicroscope. We returned all dipteran larvae and contents to their respective pitchers on the same day, and introduced one female adult *M. nepenthicola* (0.50 ± 0.10 cm) into each pitcher for 1 wk. We repeated the above procedure (i.e. counting of larvae and returning contents to the respective pitcher) two more times; with the resident crab spider first removed and maintained in the laboratory (sugar solution provided ad libitum) and finally reintroduced to the same pitcher (Figure 3). We used 7 d per treatment (i.e. spider absent/present) because laboratory experiments revealed that many *M. nepenthicola* had consumed most of their prey within 2 d. Introduction, removal and subsequent re-introduction of *M. nepenthicola* into pitchers over 4 wk enabled the realistic testing of this spider as a predator along with other concurrent activities (e.g. egg-laying by dipteran adults, newly hatched or moulted aquatic dipteran larvae, newly emerged dipteran adults from pupae, other predation and parasitic activities, and changes to pitcher detritus) that can affect larval abundance.

We inspected all pitchers for spiders every 3–4 d to ensure its status (i.e. spider present or absent). If we found a spider in a pitcher designated as 'spider absent', the pitcher fluid and its contents were first collected before the pitcher was filled with distilled water to the brim so that removal, only if the spider surfaced at the mouth of the pitcher upon depletion of its air supply, was easy. This approach is necessary as, upon disturbance, *M. nepenthicola* never fails to drop into the fluid and stays at the bottom of the pitcher until its air supply (i.e. air bubble entrapped in a small pit on the abdomen ventral side) is depleted after several minutes. Pitcher contents were returned after the spider was removed. We also reintroduced *M. nepenthicola* into pitchers that were supposed to hold a spider but were otherwise absent; a spider usually climbed on and into a pitcher within a few minutes. We assumed that these newly introduced adult female crab spiders, collected from Kent Ridge Park on the same day, have similar satiation levels to other conspecifics in experimental pitchers. We attached a pair of Velcro® fasteners (lightly smeared with Singer® Oil twice a week) on each pitcher's leaf blade to dissuade experimental spiders from leaving their designated pitchers and non-experimental crab spiders from entering experimental pitchers. We also excluded, from data analyses, a small number of pitchers with withered lids and/or contained egg sacs.

Statistical analysis

We compared the larval abundance, in the absence and presence of spiders, of the same pitcher using a related sampling approach, the Friedman test (PASW Statistics, version 18; significance level at 0.05) and a non-parametric pairwise comparison (Siegel & Castellan 1988) for multiple group comparisons of related samples. We only considered pairwise comparisons when the corresponding Friedman test was significant (i.e. absolute difference value exceeds the corresponding critical difference, denoting a significant difference for that respective pair; Siegel & Castellan 1988). We only report relevant pairwise comparisons of interest to our hypotheses.

We adopted a related-sampling approach owing to the limited abundance and occurrences of *M. nepenthicola* within pitchers from only one site in Singapore (i.e. Kent Ridge Park). Each pitcher was used as its own control to minimize any potential confounding variables. We sought to minimize the possibility of temporal effects by (1) repeating the procedure of spider introduction one more time for each pitcher, and (2) carrying out the entire experimental procedure on two separate occasions.

RESULTS

Laboratory experiments

The weight of *M. nepenthicola* increased significantly on day 5 ($\chi^2 = 15.8$, df = 2, $P < 0.001$; Figure 4a) after removal from experimental pitchers. The mean larval abundance of *Tripteroides* spp. reduced significantly after *M. nepenthicola* was introduced on the third day ($\chi^2 = 20.0$, df = 2, $P < 0.001$; Figure 4b). There was no change in larval abundance of *Tripteroides* spp. when *Thomisus nepenthiphilus* was introduced (Figure 4b) and a significant decrease in predator weight was observed ($\chi^2 = 20.0$, df = 2, $P < 0.001$; Figure 4a). Hence, *T. nepenthiphilus* was excluded from further field manipulative experiments as it did not feed on mosquito larvae.

Significant reductions in the larval abundance of *E. schuitemakeri* ($\chi^2 = 15.0$, df = 2, $P < 0.001$; Figure 4d) and *Lestodiplosis* spp. ($\chi^2 = 16.8$, df = 2, $P < 0.001$; Figure 4f) were observed after *M. nepenthicola* was introduced. Although *M. nepenthicola* had significant weight changes throughout the experiment (feeding on *E. schuitemakeri*: $\chi^2 = 18.6$, df = 2, $P < 0.001$ (Figure 4c); feeding on *Lestodiplosis* spp.: $\chi^2 = 18.7$, df = 2, $P < 0.001$ (Figure 4e)), a significant mass increment after the spider's introduction was only observed when feeding on *E. schuitemakeri* (Figure 4c).

Field experiments

A total of 42 pitchers were involved in statistical analyses. Over 4 wk (i.e. wk 3 to 6), dipteran larval abundance significantly changed when *M. nepenthicola* was introduced or removed (*Tripteroides* spp.: $\chi^2 = 20.7$, df = 3, $P < 0.001$; *Culex* spp.: $\chi^2 = 19.0$, df = 3, $P < 0.001$; *E. schuitemakeri*: $\chi^2 = 33.7$, df = 3, $P < 0.001$; *Lestodiplosis* spp.: $\chi^2 = 24.2$, df = 3, $P < 0.001$), with a general decrease in prey abundance in the spider's presence and concomitant increase after the spider's removal (Figure 5).

DISCUSSION

Our study is one of the first to demonstrate the influence of a terrestrial phytotelm forager on key phytotelm organisms via direct predation: *Misumenops nepenthicola*, but not *T. nepenthiphilus*, significantly influences phytotelm dipteran larval abundance in *N. gracilis*. This supports the ecological importance of cross-habitat-capable predators in influencing phytotelm insect larvae numbers (Greeney 2001, Romero & Srivastava

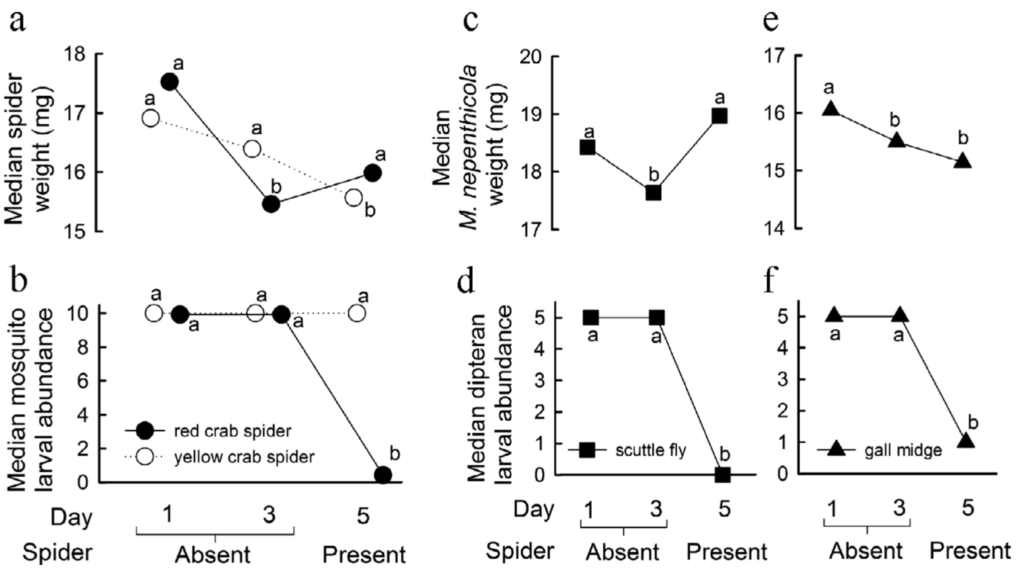

Figure 4. Effects of spider's absence and presence on dipteran larval abundance and spider's corresponding weight. Effects of absence (days 1 and 3) and presence (day 5) of the red crab spider *Misumenops nepenthicola* (filled circles) and the yellow crab spider *Thomisus nepenthiphilus* (unfilled circles) and their corresponding weight (median) (a) relating to the abundance of the mosquito larvae *Tripteroides* spp. (b). Effects of absence (days 1 and 3) and presence (day 5) of *M. nepenthicola* and its corresponding weight (median) (c, e) relating to the abundance of the larvae of the scuttle fly *Endonepenthia schuitemakeri* (squares) (d) and gall midge *Lestodiplosis* spp. (triangles) (f). All spiders were introduced on day 3 only after experimental larval abundances were recorded for that day. For all data, n = 10 replicates. Different letters represent significant difference within experiments/species at $P < 0.001$, applying post hoc Friedman test.

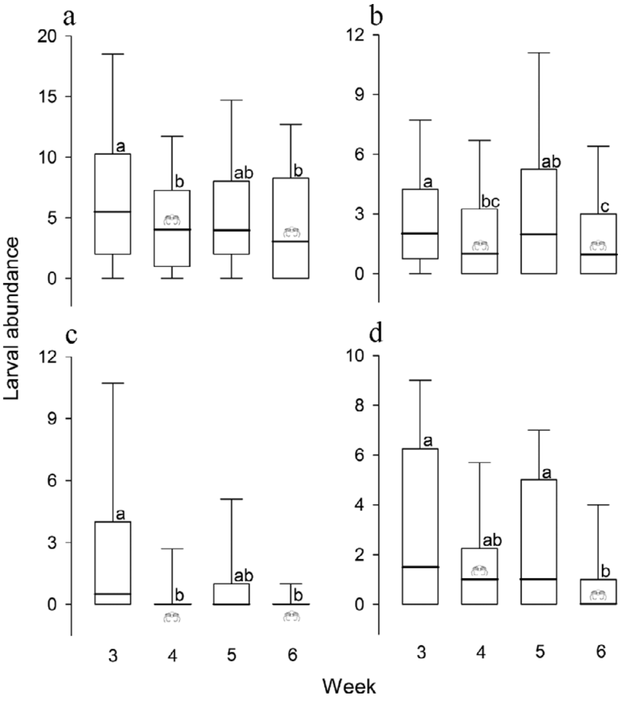

Figure 5. Box-plots on predation of *Misumenops nepenthicola* on dipteran larvae. Effects of absence (wk 3 and 5) and presence (wk 4 and 6) of *M. nepenthicola* (presence indicated by spider inserts) on larval abundance of mosquitoes *Culex* spp. (a) and *Tripteriodes* spp. (b), scuttle fly *Endonepenthia schuitemakeri* (c) and gall midge *Lestodiplosis* spp. (d). Central bar: median; hinges: 25 and 75%; whiskers: 5 and 95%. For all data, n = 42 replicates. Different letters represent significant difference within species at $P < 0.001$, applying post hoc Friedman test.

2010), suggesting this spider's role in regulating larval abundance in *N. gracilis*.

Evidence of aquatic dipteran larval predation

The decrease in mosquito larval abundance and increase in spider mass reported here support earlier claims on the aquatic foraging capability of *M. nepenthicola* (Clarke 1998, Moran 1993). A small pit on the ventral abdomen of *M. nepenthicola* allows storage of a small reserve supply of air that facilitates aquatic foraging and possibly predator avoidance. Like all crab spiders, *M. nepenthicola* possesses eyes that provide excellent spatial resolution (Land 1985). Its relatively longer legs possibly allow swift and safe locomotion into and out of the pitcher fluid since the pitcher inner wall is usually lined with numerous draglines. In contrast, *T. nepenthiphilus* did not affect mosquito larval abundance; a significant weight decline meant it is not capable of aquatic foraging. No cannibalism in mosquito larvae was recorded, since their numbers did not differ after 3 and 5 d during laboratory experiments. Although the aquatic foraging ability of *M. nepenthicola* is further established with lower abundances of *E. schuitemakeri* and *Lestodiplosis* spp. larvae after its introduction, results of the latter's abundance did not concur with spider weight change: spiders lost weight with decreased *Lestodiplosis* spp. abundances. We believe that the total amount of *Lestodiplosis* biomass consumed was inadequate to sustain an increase in spider mass, given that they are half the size (2 mm) of *E. schuitemakeri* and *Tripteroides* (both 4 mm).

Future directions

Though *M. nepenthicola* is described as a nepenthebiont, empirical data supporting its symbiotic relation with *N. gracilis* is lacking. Clarke (1997) proposed that the entire in-fauna of *Nepenthes* pitchers is in a symbiotic interaction with the plant as these organisms contribute to the more efficient breakdown of prey items within the pitchers. Additionally, Phillipps *et al.* (2008) explained that while *M. nepenthicola* feeds on insects, the plant may benefit from the spider's waste products, suggesting this spider's symbiotic interaction with *N. gracilis* (also see Clarke *et al.* 2009, Romero *et al.* 2006). In the mutualistic interaction between the ant *C. schmitzi* and its host pitcher plant, *N. bicalcarata*, Clarke & Kitching (1995) reported that, while providing this ant with a domicile within the swollen tendrils of the pitchers, the host in fact benefits from the comminution of larger prey items by the ants, which the plant extracts from the pitcher fluid. Without this ant-assisted breakdown, the pitcher will likely become anoxic as the rate of decay outruns that of digestion (Clarke & Kitching 1995). Also, these ants prey on organisms within the pitcher, possibly acting as a top predator within the contained food web (Kitching 2001). Likewise, by regulating the abundance of dipteran larvae in the pitcher fluid via direct predation, *M. nepenthicola* can reduce the potential amount of prey putrefaction in *N. gracilis* that can disrupt the plant's digestive system.

The predation of *M. nepenthicola* on various dipteran species suggests that it can regulate dipteran larval populations and indirectly affect the food chain and ecosystem within pitchers. Several well-studied food webs of *N. gracilis* (Clarke & Kitching 1993, Phillipps *et al.* 2008, Tan 1997) have proposed *M. nepenthicola* as a higher trophic level consumer and possibly an apex predator in pitcher phytotelmata (Figure 1). Our results support this possibility: *M. nepenthicola* can influence the population of key organisms in *N. gracilis.* Future research should focus on this spider's potential to alter food web and community structure (e.g. altering the balance between aquatic detritivores and predators) and the ecosystem functions these dipteran larvae provide. We also propose that future ecological studies of phytotelm communities include investigating the potential of terrestrial phytotelm dwellers, particularly those with aquatic foraging ability, to influence the aquatic organisms' populations and hence food web and ecosystem functions. Finally, with global warming altering predator–prey interactions (Traill *et al.* 2010), we urge that future phytotelm dipteran studies should take into consideration the effect of abiotic factors, in particular temperature (Hoekman 2010), in influencing pitcher community structure and ecosystem function.

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