

Timid spider uses odor and visual cues to actively select protected nesting sites near ants

Running head: Ants as protector species of spiders

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Abstract

Associations in which a more vulnerable species gains protection by seeking out the company of a pugnacious ‘protector’ species capable of deterring predators are documented among mixed-species groups from various taxa, but experimental studies are rare. We consider an unusual arthropod-based example in which the associate species, *Phintella piantensis*, is a jumping spider (Salticidae) that associates with the territorial weaver ant *Oecophylla smaragdina*, which in turn is a potential predator of *Phintella*. However, the predator we consider in this mixed-species association is *Scytodes* sp., a spitting spider (Scytodae) that often targets salticids as prey. *Scytodes* adopts a strategy of building its web over salticid nests and then preying on resident salticids when they leave or return to their nests. Our experiments show that, on the basis of olfactory cues, *Scytodes* is deterred from the vicinity of *O. smaragdina*. *Phintella* builds dense ant-proof nests to minimize the risk of being killed by *Oecophylla*, and we show that olfactory as well as visual cues of ants elicit nest building by *Phintella*. We propose that *Phintella* actively chooses to situate nests in the vicinity of weaver ants as defense against a specific ant-averse predator that singles out salticids as preferred prey.

Introduction

Mixed-species associations may often be a consequence of each species being independently attracted to specific features of the environment (the ‘similar-habitat hypothesis’; see Quinn et al. 2003), but there are many instances in which one or more members of a mixed-species group exploit other members of the group. Well-known examples include kleptoparasites associating with other species from which they steal food, and Batesian mimics associating with their models (Allan and Elgar 2001; Ruxton et al. 2004; Iyengar et al. 2008; Jackson and Nelson 2012). Collective vigilance, enhanced by species with differently specialized sensory systems, also drives mixed-species associations through the anti-predator benefits that one species gains from another that warns of approaching predators that might otherwise have gone undetected (Hodge and Uetz 1992; Stensland et al. 2003; Caro 2005; Campobello et al. 2012).

The anti-predator benefits of living in mixed-species groups have often been considered in the context of the ‘protector-species hypothesis’. According to this hypothesis, individuals of one species, often called the ‘timid’ or ‘associate’ species, benefit by associating with, or nesting near, another species (the ‘protector’ species) that aggressively repels potential predators of the timid species (Burger 1984; Quinn and Kokorev 2002; Quinn et al. 2003; Campobello et al. 2012). While many of these nesting associations come from birds, protective associations are relatively widespread and, particularly in the tropics, often involve hymenopterans (ants and wasps) as protector species (see Quinn and Ueta 2008).

This study differs from previous work in several respects. Firstly we have adopted an experimental approach where many other studies are descriptive, relying on surveys of patterns of habitat use as evidence of associations for which a protective function is deduced (e.g., Somavilla et al. 2013). Additionally, although typical examples attributed to the protector-species hypothesis have come from birds, the species we consider are all

arthropods. We investigate an ant that as a potential protector species, whereas the associate species and the predator are spiders. Although rarely quantified, there are cases where the protector species is sometimes a potential predator of the associate species (reviewed by Quinn and Ueta 2008). In this study we show that the ant is also a predator of the associate species.

The associate species, *Phintella piatensis* (hereafter *Phintella*), is a jumping spider (Salticidae). For many salticids, the company of ants can be exceedingly dangerous (Nelson et al. 2004), and yet there are numerous examples of specialized salticid-ant relationships, including species that specialize on eating ants (myrmecophagic species) and ant mimics (myrmecomorphic species) that tend to be found in the company of the ants they mimic (Allan et al. 1996; Cushing 1997, 2012; Allan and Elgar 2001; Edmunds 2006; Nelson and Jackson 2009; Jackson and Nelson 2012). Despite being neither myrmecophagic nor myrmecomorphic, *Phintella* appears nonetheless to be myrmecophilic, or attracted to the vicinity of ants. More than 90% of *Phintella* individuals found in a field study (Nelson and Jackson 2009) were in the company of ants, including the Asian weaver ant, *Oecophylla smaragdina* (hereafter *Oecophylla*). That *Phintella* was often associated with *Oecophylla* is interesting because this ant is a formidable predator of arthropods, including salticids (Nelson et al. 2004). Yet, when kept with *Oecophylla* in laboratory experiments, *Phintella*'s survival rate was considerably higher than the survival rates of non-myrmecophilic salticids, being instead similar to the survival rates of myrmecomorphic and myrmecophagic salticids (Nelson et al. 2005).

Phintella's ability to survive in the company of *Oecophylla* appears to be partly related to nest structure, which ensure that they are well protected from *Oecophylla* and other ants. Typical salticid nests are cocoon-like silken structures, but *Phintella*'s nest has an unusually tough and dense weave that makes it difficult for ants to tear open (Nelson and

Jackson 2009). Another unusual feature is that *Phintella*'s nest has hinged flaps of silk at each end that function as swinging doors, such that *Phintella* temporarily raises a flap when entering or leaving its nest, and ants rarely attempt to enter through these doors (Nelson and Jackson 2009).

The web-building 'spitting' spider *Scytodes* sp. (Scytodidae; hereafter *Scytodes*) is the predator we consider in this study, and its natural diet is dominated by salticids (Li et al. 1999). In the Philippines *Phintella* lives on large waxy leaves and *Scytodes* lives on the same leaves. From *Phintella*'s perspective, *Scytodes* is an especially dangerous predator because, uniquely among spiders, the species from the genus *Scytodes* attack their prey from a distance by spitting. To spit, the scytodid forcefully expels sticky gum from its fangs. This gum holds the prey sealed to the substratum long enough for *Scytodes* to approach and complete the capture sequence by injecting venom and wrapping the prey with silk from its spinnerets (Gilbert and Rayor 1985; Nentwig 1985).

In the field we have often seen *Scytodes* in webs that were spun over salticid nests, including *Phintella*'s, suggesting that positioning webs over salticid nests is a predatory strategy by which *Scytodes* can attack and capture salticids that are leaving or returning to their nests. However, *Scytodes* was never seen in the close company of *Oecophylla*, leading us to hypothesize that, by nesting near *Oecophylla* nests, *Phintella* uses this species as a protector – a counter-ploy against *Scytodes*' salticid-specific prey-capture tactic.

On the basis that this nesting association is not driven by chance, our specific interest in designing these experiments was to ascertain the sensory cues used both by the prey, *Phintella*, and by the predator, *Scytodes*, to detect *Oecophylla*. Because of the different sensory systems of salticids and scytodids we suggest that *Phintella* uses olfactory and visual cues from *Oecophylla* when making nest-site choices, whereas *Scytodes* bases web-site choices on olfactory, but not visual, cues. Salticids have well-developed capacity for

chemoreception (e.g., Nelson et al. 2012), including the detection of airborne volatile compounds (olfaction). However, the most distinctive characteristic of salticids is their eyesight, which supports remarkable capacity for seeing object detail (Harland et al. 2012). This means that, even when restricted to relying on solely visual cues, salticids can readily determine from a distance the presence, identity and location of prey and potential predators, including ants (Harland et al. 1999; Nelson and Jackson 2006). *Scytodes*, however, has minute eyes and we can assume that this spider has poor capacity for seeing object detail.

This study aims to combine field data with experimental work to determine the cost posed by the ants on the associate, as well as to determine how both the predator and the associate determine the presence of ants, and what effect this has on their behavior.

Methods

General

Our research was carried out at the International Rice Research Institute (IRRI) in Los Baños, the Philippines, where we had a laboratory and access to nearby field sites in tropical rain forest and neighboring agricultural plots where *Phintella*, *Oecophylla* and *Scytodes* were abundant. In addition to laboratory experiments described below, we recorded field data from 174 instances of observing *Scytodes* ‘targeting’ a salticid, where ‘targeting’ means that either an adult female or a large juvenile (sex undetermined) was in a web that was covering a salticid nest with the salticid either alive in the nest or dead out in the web. These were ‘ad hoc’ observations made whenever we saw a *Scytodes* web over a salticid nest, and were merely used to determine whether ants were ever nearby these targeted nests.

Laboratory experiments started at 0900 h and ended 24 h later (laboratory photoperiod, 12:12; lights on at 0800 hours). For laboratory studies, we established cultures derived from spiders collected from the field. In all experiments, the spiders were 2nd

generation virgin adult females (*Scytodes* body length c. 8 mm; *Phintella* body length 3-5 mm) that had matured 2-4 weeks before being used. All of the ants used in experiments were major workers (hereafter, just ‘workers’) of *Oecophylla* from colonies maintained in glass terrariums. Maintenance feeding was based on using a variety of flies (Diptera) and moths (Lepidoptera) collected from the field as necessary. For normal maintenance, spiders were fed to satiation three days a week. However, immediately before experiments began, each *Scytodes* was subjected to a 7-day fast.

Artificial leaves (hereafter, simply ‘leaves’) were made by cutting green cardboard into ellipses, which were bent to give them a slightly concave shape like that of natural leaves. No individual leaf, spider, or insect was used in more than one experimental trial and none of the spiders used in experiments had prior experience with other spiders, or with insects used as stimuli.

Data were analyzed using Fisher exact tests and 2 x 2 or 2 x 3 chi-square tests of independence, or binomial tests. Bonferroni adjustments were made whenever multiple comparisons were made with the same dataset.

Cues for nest and web building

Our experimental apparatus consisted of four chambers with removable tops: leaf chamber, visual-stimulus chamber and two odor chambers (see Fig. 1 for dimensions). All chambers were made of transparent glass, except that the top inner side of the glass visual-stimulus chamber was painted white. All components of the apparatus were cleaned between trials by first wiping with 80% ethanol followed by distilled water and then drying.

An introduction hole in the leaf chamber was used for inserting the test spider and four other holes were used for airflow (Fig. 1); the function of the two inflow and two outflow holes was to permeate the leaf chamber with odor emanating from ants that were

being held in the odor chambers. The airflow holes and the introduction hole were each 5 mm in diameter and the center of each hole was 10 mm above the floor of the leaf chamber. Above each inflow and each outflow hole, another 5 mm hole was used to secure wires on which a leaf was suspended. Each of these holes was plugged with a rubber stopper containing a hole from which a 2 mm diameter wire extended to the corresponding hole in the opposite side of the leaf chamber. The leaf was placed on top of these wires during tests.

Each odor chamber had an inflow hole centered on one side and an outflow hole centered on opposite side, allowing air to be pumped through the odor chambers and into the leaf chamber (Fig. 1). Airflow was adjusted to 1500 ml/min (Matheson FM-1000 flowmeter) and a cardboard barrier between the leaf chamber and the two odor chambers hid the odor source from the test spider's view. The airflow system was running in all tests, regardless of whether there were odor sources in the odor chambers. The odor source, when present, was five *Oecophylla* workers placed in each odor chamber. Otherwise the odor chambers were left empty. Silicone tubing connected the various parts of the apparatus (Fig. 1) and nylon netting over each opening in the tubing blocked passage by ants and spiders.

To acquire a leaf on which a *Phintella* nest was present, a *Phintella* individual was first put with a leaf (concave side up) in a Petri dish (diameter 140 mm) and left for 4 days to build a nest. On rare occasions, rudimentary additional nests were present on the leaf, but these were destroyed before the leaf was put inside the leaf chamber. If *Phintella* failed to build a normal nest after 4 days, the leaf was discarded and the individual was not used again. For tests, the resident *Phintella* was always in its nest at 0900 h, when testing began. In tests where an unoccupied nest was required, a paintbrush was used to prod *Phintella* out of its nest 1 h prior to placing the leaf in the leaf chamber.

Regardless of whether it was empty or housing insects, the visual-stimulus chamber sat on top of the leaf chamber. Sometimes the insects were eight living *Oecophylla* workers.

Other times, we put eight mounts in the leaf chamber (Fig. 1). Experimental mounts were eight dead, stationary *Oecophylla* workers and control mounts were eight dead, stationary leafhoppers (*Nephrotettix nigropictus*). The leafhoppers, taken from stock cultures at IRRI, were used to determine whether *Phintella*'s behavior was affected simply by the presence of nearby arthropods, rather than ants in particular. Each mount was made by using carbon dioxide to immobilize the insect, placing it in 70% ethanol for 60 min, gluing it in a life-like posture on the center of a small disc-shaped piece of cork, and then spraying it with an aerosol plastic adhesive (Crystal Clear Lacquer, Atsco Australia Pty). Mounts were positioned in two rows along the inner top of the chamber (facing the center) and were held in place with double-sided sticky tape stuck on the underside of the cork disc.

The odor chambers were connected to the leaf chamber and the airflow was turned on 60 min before a test was initiated by inserting the test spider into the leaf chamber. Test spiders were placed in a glass tube (each end plugged with a rubber stopper) for 15 min before opening the introduction hole. Connecting the tube allowed the spider free access to the leaf chamber. Having unplugged one end of the glass tube, the test spider's entry into the arena defined the beginning of a test. However, if the test spider had not entered after 5 min, the other stopper was removed and a paintbrush was used to gently coax the spider into the leaf chamber. The test spider's entry into the arena defined the beginning of a test. When the test spider was *Phintella*, we recorded 24 h later whether a nest had been built. When the test spider was *Scytodes*, we recorded 24 h later whether a web had been built. We also made intermittent observations of the spiders during the day.

With Experiments 1-3 (N = 60 for each), we determined whether the presence of a nest built by *Phintella* influenced the web-building decisions of *Scytodes*. With these experiments, we also investigated whether the presence of a resident *Phintella* individual mattered and whether cues (visual or olfactory) from ants influenced *Scytodes*' web-building

decisions. The objective in Experiments 4-6 (N = 60 for each), was to determine whether cues from ants (visual or olfactory) influenced *Phintella*'s nest-building decisions (for details, see Table 1).

Survival in the presence of ants

For *Scytodes* and for *Phintella*, we compared survival in the presence versus absence of *Oecophylla* workers in three separate experiments: 1. *Scytodes* alone in web on leaf, 2. *Phintella* alone in nest on leaf, and 3. *Scytodes* in web over nest in which there was a resident *Phintella*. For each experiment (N = 40 for each), we tested spiders in the presence of ants (10 *Oecophylla* workers that had been introduced into the leaf chamber immediately prior to test initiation) and in the absence of ants. All testing started at 0900 h and, 24 h later, we recorded whether the resident *Phintella* or *Scytodes* was still alive. Intermittent casual observations of the spiders' behavior were made during the day.

Occupied *Phintella* nests were obtained as described above and occupied webs were obtained similarly, except that *Scytodes* instead of *Phintella* was left with the leaf in the Petri dish. For experiment 3 (*Scytodes* in web over occupied *Phintella* nest), we first used the established procedure for acquiring a leaf with an occupied nest and then we put a *Scytodes* into the Petri dish for 24 h, during which time it built a web over the occupied nest. The resulting nests and webs on the leaf, along with the spiders, were placed in the leaf chamber before each experiment began and in ant tests, before inserting the ants.

Results

Field data

From the 174 instances of *Scytodes* 'targeting' a salticid, we never found *Oecophylla* on the leaf containing the targeted salticid nest, nor was *Oecophylla* common in the vicinity of the leaf in

any of these instances. Although other ants were sometimes present in small numbers on or near the leaf, these ants were always considerably smaller than *Scytodes*. Yet, as documented in an earlier study (Nelson and Jackson 2009), it was common to find *Phintella* on leaves in trees where *Oecophylla* was common, including sometimes with many *Oecophylla* being on the same leaf as the nest, or even on the nest.

Several salticid species, including *Phintella*, were targeted by *Scytodes* (Fig. 2). The median, 1st and 3rd quartiles for the number of targeted salticid individuals were, respectively, 8, 4 and 11.75. For the number of salticids found dead in *Scytodes*' web, the median, 1st and 3rd quartiles were, respectively, 2, 1 and 4.25. A total of four *Phintella* individuals were targeted, and two of these were dead, placing *Phintella* at the median of salticids found dead in *Scytodes* webs.

Cues for nest and web building

A 3 x 2 chi-square test revealed that the presence of *Phintella* inside a nest had a significant effect on how many *Scytodes* individuals built webs ($\chi^2_2 = 20.9$, $P < 0.001$), with 85% of the *Scytodes* individuals building webs when there were occupied *Phintella* nests present compared with 48% and 52% building webs when there were no salticid nests or only unoccupied nests present, respectively (Experiment 1, Table 1). The number of *Scytodes* that built webs on leaves where there were no nests compared with the number that built webs on leaves where there were empty *Phintella* nests was not significantly different ($\chi^2 = 0.13$, $P = 0.72$) and were pooled. Further comparison with the number of *Scytodes* that built webs on leaves occupied by *Phintella* demonstrated that *Scytodes* were significantly more prone to build webs on *Phintella*-occupied leaves ($\chi^2 = 20.73$, $P < 0.001$).

Significantly more web-building by *Scytodes* over nests occupied by *Phintella* was observed in the presence of ants in the visual-stimulus chamber (Experiment 2, $P < 0.001$,

binomial test, Table 1.), but there was no difference in *Scytodes*' behavior with visual cues of ants present to when there were not as long as the leaf had a *Phintella* -occupied nest (Experiment 1, Treatment 3, compared with Experiment 2, $\chi^2 = 0.52$, $P = 0.47$). When *Phintella* -occupied nests and ant odor was present, *Scytodes* was significantly less likely to build a web over the nest (Experiment 3, $P < 0.001$, binomial test), and there was a significant reduction in the number of *Scytodes* that built webs over nests occupied by *Phintella* when there were no ants present (Experiment 1, Treatment 3, compared with Experiment 3, $\chi^2 = 64.61$, $P < 0.001$, Table 1).

Significantly more *Phintella* individuals built nests on leaves when living ants could be seen (Experiment 4, $\chi^2 = 39.47$, $P < 0.001$), or smelled (Experiment 5, $P = 0.03$, binomial test) than when there were no ant cues present (Table 1). To determine whether simply the presence of nearby arthropods, rather than ants in particular, influenced *Phintella*'s nest-building decisions, we compared findings from using dead ants as mounts to findings from using dead leafhoppers as mounts. Significantly more ($\chi^2 = 7.6$, $P = 0.006$; Experiment 6, Table 1) *Phintella* built nests in the presence of ant mounts (92%) than in the presence of leafhopper mounts (68%).

We also found that significantly more *Phintella* individuals built nests in the presence of ant odor than in the absence of any ant cues (Experiment 4, Treatment 2, compared with Experiment 5, $\chi^2 = 9.64$, $P = 0.002$). Yet the effect of smelling ants was significantly less pronounced than the effect of seeing live ants on how many *Phintella* individuals built nests (Experiment 4, Treatment 1, compared with Experiment 5, $\chi^2 = 12.57$, $P < 0.001$). When ants could be seen but not smelled, movement was an important variable: seeing active living ants elicited nest-building behavior by significantly more *Phintella* individuals than seeing dead ants mounted in a life-like posture (Experiment 6, Treatment 1, compared with Experiment 4, Treatment 1, $\chi^2 = 10.21$, $P = 0.001$).

Survival in the presence of ants

In the presence of ants, significantly more *Scytodes* individuals died than when there were no ants present and yet, when *Scytodes* was absent, there was no significant difference in the number of *Phintella* individuals that survived in the presence instead of the absence of ants (Table 2). Additionally, when *Phintella* was in its nest and *Scytodes* was in a web built over the nest, the number of *Scytodes* individuals that were killed by ants was significantly more than the number of *Phintella* individuals killed by ants ($P < 0.001$, Table 2). Casual observation suggested that *Oecophylla* had minimal difficulty moving through *Scytodes*' webs, and although *Scytodes* spat at *Oecophylla* individuals that came close, spitting was ineffective as defense against a group of *Oecophylla*.

Discussion

Being social and often aggressively territorial, ants may often be sought out by less pugnacious species, even when these are considerably larger than the ants themselves (as found among birds that associate with ants, see Quinn and Ueta 2008). Due to its territorial and aggressive nature (Hölldobler 1983, Crozier et al. 2010), *Oecophylla* is commonly used as a biocontrol agent, especially in mango plantations (e.g., Offenberg et al. 2013), where many of our spiders were found. In this study we show that at least some species of myrmecophilic salticids may use ants for protection against predators that would otherwise pose a significant threat to the salticid. Our results suggest that *Oecophylla* provides *Phintella* with benefits in terms of reduced predation by *Scytodes*. We also found that positioning webs over salticid nests seems to function for *Scytodes* as an effective and specialized tactic by which to prey on salticids.

Although they were largely quiescent during the day, we sometimes saw *Scytodes* tapping *Phintella* nests during tests. As foreleg tapping is used by *Scytodes* as a primary means to localize prey (Gilbert & Rayor 1985), perhaps this was to determine whether the salticid was in residence. When tapping occurred, the resident *Phintella* sometimes became momentarily active and this may have informed *Scytodes* that the nest was occupied, after which, at night, it could spin a web over the nest. Certainly, in our experiments, *Scytodes* built webs over nests on leaves specifically when *Phintella* was inside, suggesting that the presence of a resident salticid is an important web-building cue for *Scytodes*. This mechanism would readily allow the scytodid to attack and kill the salticid as it passes through the web when it attempts to move out of the relative safety of its nest during the daytime.

Our field data suggest that, once *Scytodes* has spun a web over the nest, a resident *Phintella*'s risk of being killed by *Scytodes* is comparable to the risk experienced by other salticid species, as might be expected. However, by associating with *Oecophylla*, *Phintella* appears to minimize the risk of being targeted by *Scytodes*. Findings from our survival experiments imply that the vicinity of *Oecophylla* is especially dangerous for *Scytodes* and considerably less dangerous for *Phintella*. Moreover, *Phintella*'s response to cues from *Oecophylla* in experiments appeared to be almost the opposite to those of *Scytodes*. Cues from *Oecophylla* elicited nest-building behavior in *Phintella* but inhibited *Scytodes*' web-building behavior. Consistent with scytodids having minute eyes and relying primarily on mechanosensory and chemosensory input for prey and predator detection (Gilbert and Rayor 1985; Li et al. 1999; Li 2002; Li and Jackson 2005), we found evidence of *Scytodes* relying primarily on olfactory cues to sense *Oecophylla*'s presence. In contrast, nest building by *Phintella* was elicited by ant odor, by seeing mounts made from dead *Oecophylla*, and they especially often built nests when they could see active, living ants. As there was a dramatic difference in *Phintella*'s propensity to build a nest on a leaf in otherwise identical 'habitat'

except for the presence of ants, the similar habitat hypothesis seems an unlikely explanation for these findings.

Numerous species of spiders associate with ants (reviewed in Cushing 1997, 2012), and some of these are costly to the ants. For example, the zodariid spider *Habronestes bradleyi* uses airborne chemical cues (alarm pheromones) from the ant *Iridomyrmex purpureus* to locate the ants on which they prey (Allan et al. 1996). However, associations with ants are often mutualistic, with ants often protecting other arthropods in return for honeydew secretions, as found among many myrmecophilic lycaenid butterflies and in the well-studied aphid-ant associations (e.g., Fiedler and Maschwitz 1989; Saarinen 2006; Mooney and Mandal 2010), but these can also turn parasitic (e.g., Martins et al. 2013). However, Quinn and Ueta (2008) conclude that nesting associations, even when the protected species are birds and the protector species are ants, are typically commensal in nature. The *Oecophylla-Phintella* association we describe shows no sign of being mutualistic. While we did not explicitly test costs for the ants in this nesting association, it seems likely that this, too, is a commensal relationship. Populations of *Oecophylla* are enormous in comparison to the number of associated *Phintella*, suggesting that any impact of *Phintella* on *Oecophylla* is minimal. However, joining *Oecophylla* appears to be a double-edged sword for *Phintella* because, besides being a lethal threat to *Scytodes*, *Oecophylla* is also one of *Phintella*'s potential predators (Nelson et al. 2005; Nelson and Jackson 2009).

'Protector species' appears to be an appropriate term for *Oecophylla* when we consider *Phintella* as an associate species and *Scytodes* as a predator of the associate species. Yet this salticid-ant relationship contrasts with better-known examples from the avian literature (see Quinn and Ueta 2008). With the bird examples, the protector species is often not a predator of the associate species' predators. Additionally, the prey being protected by associating with the protector species is often the associate species' eggs or hatchlings, with

the adults of the associate species having little or no risk of being killed by the predator or the protector species (e.g., Bogliani et al. 1999; Quinn and Kokorev 2002; Campobello et al. 2012). However, the most striking contrast may pertain to the level of specificity. With bird examples, the predator can usually be envisaged as a generalized threat, but *Scytodes* uses a predatory tactic (building a web over occupied salticid nests) as an especially effective method of targeting specifically salticids as prey.

As an abundant predator that targets salticids with a specialized prey-capture method, *Scytodes* may have been a significant driver behind the evolution of myrmecophily in *Phintella*. Besides *Scytodes*, it is safe to assume that *Phintella* has other potentially significant predators, including predators that can be envisaged as generalized threats. Many of these other predators may be averse to the company of *Oecophylla*, which may thereby contribute to *Phintella*'s defense against a variety of predators. Our results suggest that nesting associations with territorial ants whereby the ant does not receive any benefit may be more common among arthropods than is currently appreciated. We expect that a closer look at ant-other arthropod relationships will yield numerous examples similar to ours and provide a better understanding of the complexities of microhabitat choice and its ecological ramifications.

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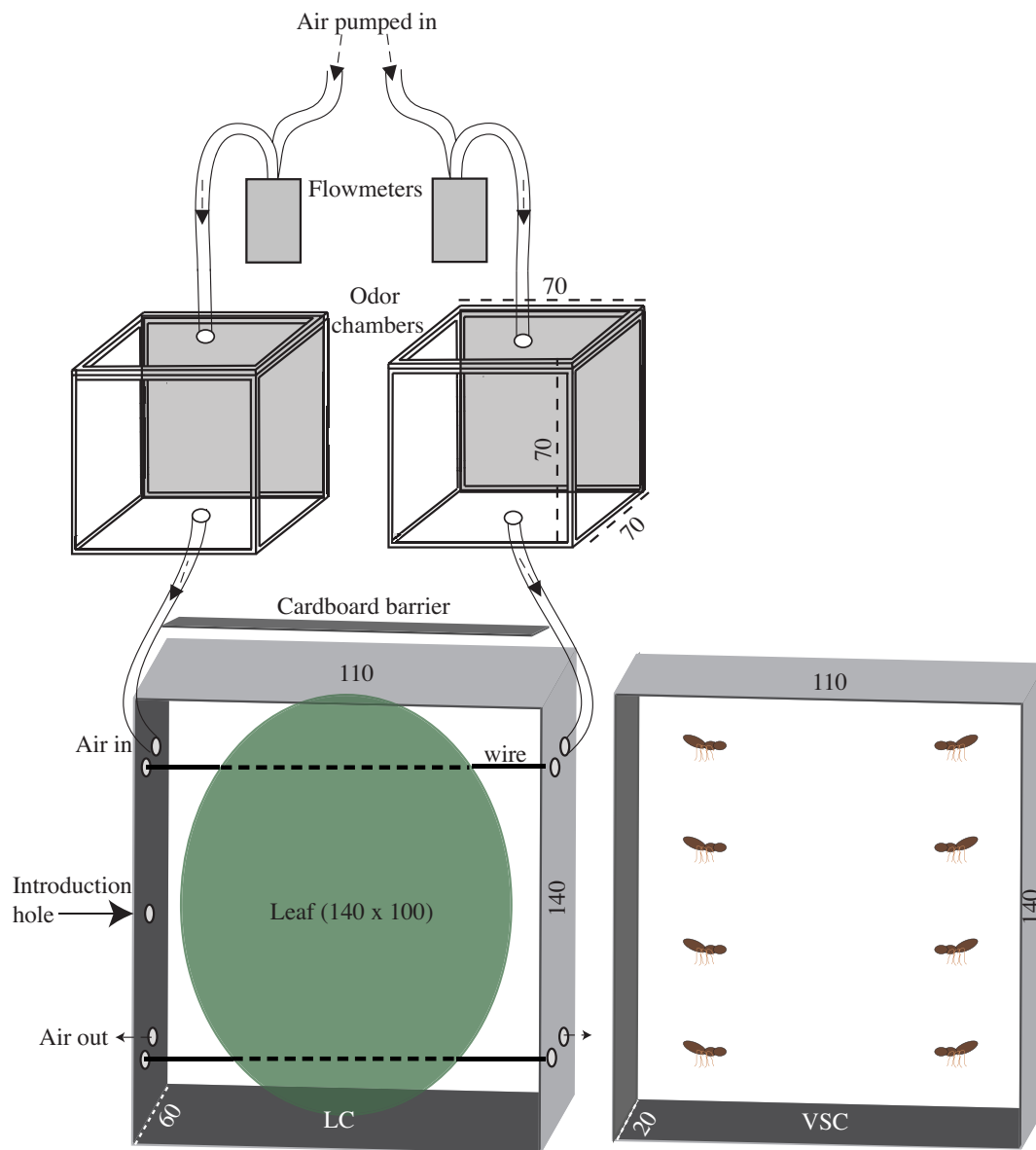


Fig. 1 Apparatus (not to scale) used for determining how different cues influence nest and web building behavior of *Phintella* and of *Scytodes*, respectively. Dashed arrows indicate direction of airflow from the pumps through the odor chambers and then the leaf chamber (LC), which is placed horizontally on a laboratory bench. Visual-stimulus chamber (VSC) sits on top on the leaf chamber during testing, but is shown displaced to the side. VSC depicted with ant mounts stuck to inner top of chamber, facing center of chamber. Cardboard barrier blocks the test spider's view of odor chambers. All dimensions given in mm

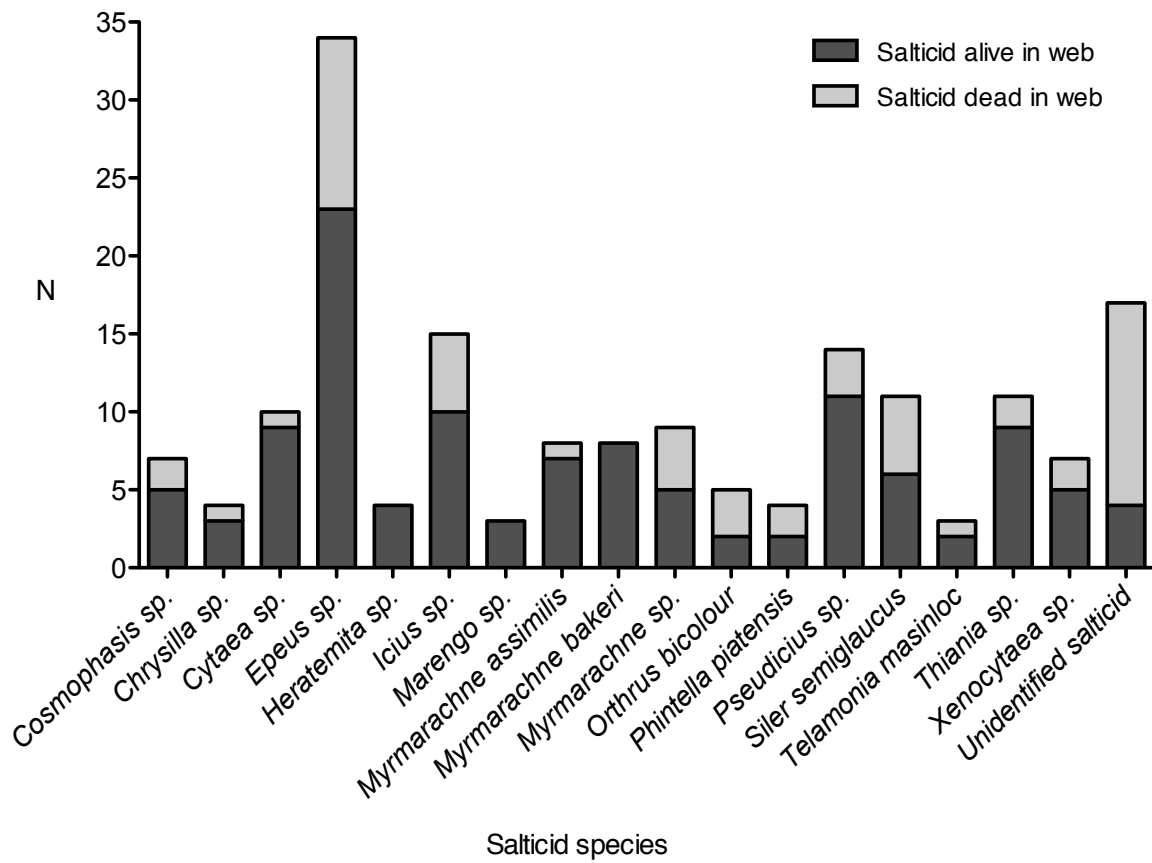


Fig. 2 Salticids with which *Scytodes* individuals were found in webs built over the nests (N = 174)

- 1 **Table 1** Experiments measuring propensity of spiders to build webs (¹*Scytodes*) or nests (²*Phintella*) in the presence or absence of visual or odor cues
- 2 from *Oecophylla smaragdina* ants, salticids or leafhoppers.

| Experiment number and hypothesis | Test spider | Treatment | Built web ¹ /nest ² | Did not build web ¹ /nest ² |
|---|------------------|---|---|---|
| 1. Does the presence of <i>Phintella</i> in a nest influence <i>Scytodes</i> ' decision to build a web? | <i>Scytodes</i> | 1. Leaf with no nest and no <i>Phintella</i> | 29 | 31 |
| | | 2. Leaf with nest but no <i>Phintella</i> | 31 | 29 |
| | | 3. Leaf with nest occupied by <i>Phintella</i> | 51 | 9 |
| 2. Does seeing ants influence <i>Scytodes</i> ' decision to build a web? | <i>Scytodes</i> | Leaf with nest occupied by <i>Phintella</i> ; living ants could be seen but not smelled | 48 | 12 |
| 3. Does ant odor influence <i>Scytodes</i> ' decision to build a web? | <i>Scytodes</i> | Leaf with nest occupied by <i>Phintella</i> ; living ants could be smelled but not seen | 7 | 53 |
| 4. Does seeing ants influence <i>Phintella</i> 's decision to build a nest? | <i>Phintella</i> | 1. Bare leaf present and living ants could be seen but not smelled | 55 | 5 |
| | | 2. Bare leaf present and no visual or odor stimulus present | 22 | 38 |
| 5. Does ant odor influence | <i>Phintella</i> | Bare leaf present and living ants could be smelled but | 39 | 21 |

| | | | |
|--|------------------|--|----|
| <i>Phintella</i> 's decision to build a nest? | | not seen | |
| 6. Does the static appearance of ants suffice to influence <i>Phintella</i> 's decision to build a nest? | <i>Phintella</i> | 1. Bare leaf present and ant lures could be seen (no stimulus odor) | 41 |
| | | 2. Bare leaf present and leafhopper lures could be seen (no stimulus odor) | 26 |
| | | | 19 |
| | | | 34 |

3

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7 **Table 2** Spider survival in the presence (Present) or absence (Absent) of *Oecophylla smaragdina* ants. Fisher exact tests, all df = 1.

| Experiment | Survival | Present | Absent | P |
|---|--|---------|--------|---------|
| 1. <i>Scytodes</i> in web; no <i>Phintella</i> nor its nest | <i>Scytodes</i> lived | 1 | 20 | <0.0001 |
| | <i>Scytodes</i> died | 19 | 0 | |
| 2. <i>Phintella</i> in nest; no <i>Scytodes</i> nor its web | <i>Phintella</i> lived | 18 | 20 | 0.49 |
| | <i>Phintella</i> died | 2 | 0 | |
| 3. <i>Scytodes</i> in web built over occupied <i>Phintella</i> nest | Both lived | 2 | 5 | 0.17 |
| | Both died | 3 | 0 | |
| | <i>Scytodes</i> lived; <i>Phintella</i> died | 0 | 15 | <0.0001 |
| | <i>Phintella</i> lived; <i>Scytodes</i> died | 15 | 0 | |

