



RESEARCH ARTICLE - ANTS

Whiteflies Provide Honeydew to *Camponotus* ants Without Receiving Reciprocal Favor

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Abstract

The notion that tending ants provide protection to honeydew-producing hemipterans is widely accepted. Nevertheless, there have been debates about whether or not this protection can always disrupt the biological control of hemipterans. Although various hemipteran species interact with tending ants, most studies have focused on the mutualism between ants and aphids. Woolly whitefly *Aleurothrixus floccosus* (Maskell) is an important pest of citrus whose nymphs are frequently tended by ants such as *Camponotus*. However, it is unknown whether or not ants in this genus alone can disrupt biological control of woolly whitefly by protecting this pest's nymphs from natural enemies. We investigated the impact of *Camponotus* ants on the biological control of woolly whitefly in the field by excluding or allowing the access of ants to whitefly nymph colonies in different tangerine trees. Furthermore, in a laboratory study we also assessed the behavior of *Camponotus* ants in response to woolly whitefly's common predator cues (visual and scent). In summary, this field-laboratory study suggests that there is no mutualism between tending *Camponotus* ants and the whitefly *A. floccosus*; rather it indicates commensalism as an alternative interaction. Interactions as this may provide more benefits for the host plant, whereby *Camponotus* ants can reduce sooty mold by removing honeydew from the leaves and favor pest biological control by leaving the whiteflies unprotected.

Introduction

The mutualism between tending ants and honeydew-producing hemipterans has been widely recognized (Way, 1963; Völkl et al., 1999; Flatt & Weisser, 2000; Queiroz & Oliveira, 2001; Oliveira & Freitas, 2004; Del-Claro et al., 2006; Muller et al., 2016). Nevertheless, although many hemipterans are known to interact with tending ants more attention has been given to the aphid-ant mutualism (Floate & Whitham, 1994; Kaplan & Eubanks, 2002; Stadler & Dixon, 2005; Muller et al. 2016). Some attention has also been given to ant-membracids interactions in the neotropics (Del-Claro & Oliveira, 1999; Del-Claro, 2004; Fagundes et al., 2013). In general, various hemipteran species produce an aminoacid-poor, but carbohydrate-rich excretion namely honeydew, which is the main driver of these mutualistic relationships (Buckley,

1987; Hölldobler & Wilson, 1990). Tending ants can provide benefits to hemipterans by protecting them from predators, parasitoids and fungal infections (Banks, 1962; Way, 1963; Samways, 1983; Völkl, 1992; Kaplan & Eubanks, 2002; Del-Claro & Oliveira, 2000; Byk & Del-Claro, 2010; Zhang et al., 2013), thus suggesting a potential to disrupt biological control of such hemipterans.

The magnitude of the mutual benefits between ants and hemipterans is highly influenced by the ecological settings in which they occur (Cushman & Whitham, 1989, 1991; Cushman & Addicott, 1991; Del-Claro & Oliveira, 2000). More specifically, the level of ant attendance can be influenced by both the host plant and hemipteran species (Hendrix et al., 1992). Ants respond most intensively to honeydew containing high amounts of melezitose (Kiss, 1981; Völkl et al., 1999). For example, Fischer & Shingleton (2001) reported that



aphids *Chaitophorus populialbae* (Boyer de Fonscolombe) were often tended by ants because its honeydew had high proportions of melezitose, whereas the species *C. populeti* (Panzer) were untended because of its melezitose-poor honeydew. Furthermore, the intensity of ant-hemipteran mutualism is positively correlated with the quantity of honeydew required by the ants (Hölldobler & Wilson, 1990; Bristow, 1991; Bonser et al., 1998), suggesting that ants with high sugar demand provide longer attendance and protection to honeydew-producing hemipterans, which in turn may mediate the disruption of biological control.

Extrafloral nectar can also attract ants to plants, which can mediate some plant protection whereby the ants ward off some herbivores (Heil & McKey, 2003). Nevertheless, extrafloral nectar is known to attract more generalist ants whereas honeydew attracts more specialized ants (Bluthgen et al., 2000), which have a more narrow relationship with the honeydew-producing insects.

Woolly whitefly *Aleurothrixus floccosus* (Maskell) (Hemiptera: Aleyrodidae) is an important pest of citrus. The sessile nymphal stages produce wax filaments and occupy the undersurface of the leaves. The nymphs also excrete honeydew which favors the growth of sooty mold and the attraction of tending ants such as the argentine ant (DeBach & Rose, 1976; Belay et al., 2011). Other ants that have been documented to often tend woolly whitefly nymphs in the Neotropics are *Camponotus* spp. (Queiroz & Oliveira, 2001; Rodrigues & Cassino, 2011; Alves et al., 2015). However, it is still unknown whether ants in this genus alone can significantly disrupt woolly whitefly biological control by protecting them from natural enemies. A week prior to the beginning of our experiments, an unsprayed citrus orchard located at the Instituto Federal Goiano, Campus Morrinhos, GO, Brazil, was noticed to be highly infested with woolly white flies. At that same time great numbers of *Camponotus* ants were observed either walking within the tree canopies or tending the woolly whitefly colonies on every infested citrus tree. Thus, thereafter we set up a field experiment in that citrus orchard to investigate whether or not *Camponotus* ants could disrupt the biological control of the woolly whitefly nymphs by protecting them from natural enemies. Furthermore, in a laboratory study we also assessed the behavior of *Camponotus* ants in response to woolly whitefly's predator cues.

Materials and Methods

Field experiment

This experiment was conducted in a 5-year old unsprayed citrus orchard composed of tangerine trees cultivar 'Ponkan', and located at Instituto Federal Goiano - Campus Morrinhos, in the state of Goias, Brazil. The orchard had 465 trees spaced 5m along row and 7 m between rows. There was also an irrigation system of micro sprinklers running along the tree rows (south-north lengthwise). This field experiment had two

treatments and ten replicates, which were set up in a completely randomized design. Treatments were comprised by I) woolly whitefly nymph colonies freely accessible to ants and natural enemies (with ants), and II) woolly whitefly nymph colonies inaccessible to ants, but accessible to natural enemies (without ants). Each replicate was composed of a 1-m long middle branch infested with woolly whitefly nymphs. For treatment II, the base of each branch on the tree was spread weekly with tangle foot to prevent ants reaching the nymph colonies, and thus allowing access only to parasitoids and flying predators. Prior to the experiment each experimental tree branch (from all treatments) was trimmed to avoid connectivity with other branches, which was specifically important to prevent ants from other parts of the tree reaching the nymph colonies in treatment II. In addition, before the experiment the number of woolly whitefly nymphs (all stages) in each branch was adjusted to 400 individuals distributed among 5-10 leaves close to each other. The possible presence of woolly whitefly eggs was not investigated because of the difficulty of doing so in the field.

The number of woolly whitefly nymphs, ants and natural enemies was evaluated weekly in each replicate during the course of six weeks (5 October - 9 November, 2013). To do so, each evaluator approached the branch with care and looked first for motile forms of natural enemies, which were visually identified to taxon level and recorded. Thereafter, the number of ants and whitefly nymphs was counted on the infested leaves. However, after the experiment started we did not control for adult woolly whiteflies that might eventually come to the experimental branch and oviposit there contributing to an increase in nymph density. We did so because the initial 400 nymphs (all stages) might hatch in a short period of time not allowing enough time for predation to occur on repeated dates. In addition, we conducted weekly a targeted search on non-experimental trees for ants associated with woolly whitefly colonies, which were collected and placed in a glass vial containing preserving alcohol 70% for later identification.

Behavior experiment in the laboratory

In this experiment we assessed the behavior of ants in response to visual/scent and visual cues from predators. The predators used were adults of *Cycloneda sanguinea*(L.) (Coleoptera: Coccinellidae). This predator was chosen because it appeared to be one of the most common species during a random search on non-experimental trees infested with woolly whitefly. This lab experiment had three treatments and 15 replicates, which were carried out at five different dates (n = 3 replicates of each treatment/date). The treatments were as follow: I) no predator cue (no coccinellid), II) visual + scent cues from predator (live coccinellid), and III) visual cue from predator (drawn coccinellid). Each replicate consisted of a clear-plastic cup (13 x 10 cm: h x d) closed with a lid that had an orifice (3 cm in diameter) covered by organza fabric, which allowed ventilation. Each cup (arena) had inside an 8

cm-long citrus stem with four leaves infested with woolly whitefly nymphs placed inside a small glass vial (50 ml) with water and sealed with cotton. In addition, all replicates had a two-hour starved *Camponotus* sp. ant.

The ants were collected manually with the aid of a camel brush from citrus leaves infested with woolly whitefly nymphs two hours prior to the experiment and kept individually in plastic vials in the absence of food and water. Likewise, adults of *C. sanguinea* (both sexes) were collected manually from infested trees twenty four hours prior to the experiment and kept in plastic cups containing a small cotton ball wet with a honey/water solution (30% honey). For treatment II, two adult *C. sanguinea* were released at the bottom of the cup (arena) three minutes prior to the experiment, which was expected to provide both scent and visual cues to the ant. For treatment III, the figures of three adult ladybeetles were accurately and equidistantly painted on the inner walls of each cup using water soluble paint (dark red and black), which were expected to provide the predator visual cue. This experiment was carried out in the laboratory at temperature of 27 °C, R.H. of 70% and under fluorescent lights.

During the experiment each ant was carefully placed on an infested leaf with the aid of a fine paint brush and allowed two minutes to settle. Ants that did not stay on the leaves for these first two minutes were discarded. Thereafter, the following ant behavioral categories were measured during 10 minutes: number of times it left the citrus stem/leaves to explore the arena, number of times it attacked the coccinellid, time spent resting on citrus stem/leaves and arena, time spent moving on citrus stem/leaves and arena. Resting was defined as the time that the ant remained stationary; moving represented the time spent walking, regardless of direction. These measurements were taken by direct observation, where one person informed the beginning and the end of each behavioral category while another person recorded the time in which that occurred. Subsequently, the broken times (s) were summed for each behavioral category.

Statistical analyses

Field experiment: Differences in woolly whitefly nymph density between treatments were assessed using repeated measures analyses of variance (PROC MIXED). Covariance structures for the mixed model repeated measures were constructed, and Bayesian Information Criterion (BIC) were used to assess that the UN covariance structure provided the best fit for the data. Date was considered a random factor in these models.

Behavior experiment: Treatments were blocked through time and 3 replicates of each treatment were run per day for a total of 15 replicates at the end of the 5-day experiment. However, the data were pooled for all dates at the time of analyses. Ant behavioral data were organized for analysis into the following categories: (1) time spent walking on the citrus stem/leaves; (2) time spent resting on the citrus stem/leaves; (3) time spent walking on the arena; (4) time spent resting on

the arena; (5) total time walking; and (6) total time resting, regardless of place. Thereafter, a separate MANOVA was carried out for each data category. For the data regarding the number of times each ant left the infested leaves to explore the arena a simple analysis of variance (PROC GLM) was carried out to test for differences among treatments. All analyses were carried out using the software SAS (SAS, 2008).

Results

Field experiment

There was no significant treatment ($F = 0.30$, $P = 0.60$), time ($F = 1.47$, $P = 0.25$) or treatment*time interaction effect ($F = 0.90$, $P = 0.49$) on the number of whitefly nymphs per replicate during the course of the experiment. In general, it was noticed only a slight increase trend for whitefly nymph density towards the last three weeks of the experiment in both treatments (Fig 1) suggesting that adult whiteflies continued to reproduce on the replicates (citrus branches) after the experiment had started. The fact that whitefly nymphs did not reach higher densities in treatment I (with ants) indicates that these ants may not be able to significantly disrupt the biological control of this pest by inhibiting natural enemy attack. In fact, it was noticeable that biological control was able to maintain the whitefly nymphs at a very slow rate of increase in both treatments, therefore preventing further outbreaks (Fig 1).

Despite the fact that the field evaluations constituted a “snapshot” in time, the presence of *Camponotus* ants tending whitefly nymphs in treatment I (with ants) was very common during the weekly evaluations (Table 1). Likewise, a diverse group of generalist predators was found associated with the nymph colonies during the evaluations. The main predator taxa encountered (larvae and adults) were coccinellids, lacewings, spiders and syrphids (Table 1). There was no sign of nymph parasitism nor the presence of adult parasitoids associated with whitefly nymph colonies. The species of ants associated with the whitefly nymphs identified by Dr. Marco Antonio Oliveira were *Camponotus femoratus* (Fabricius, 1804) and *Camponotus blandus* (Smith, 1858).

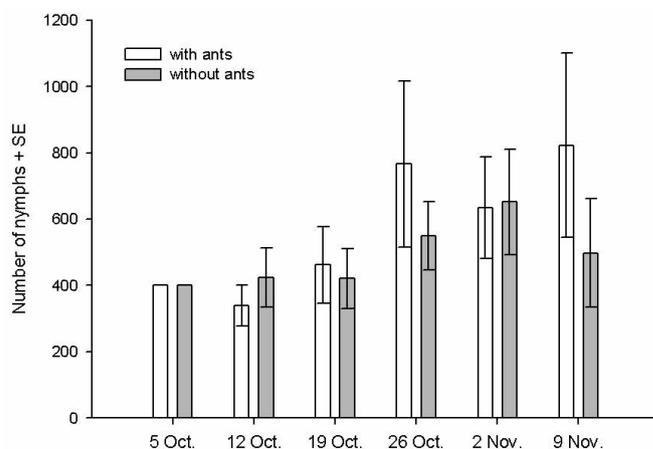


Fig 1. Number of woolly whitefly nymphs per replicate (citrus branch) at different dates.

Table 1 - Total number of ants and predators found associated with woolly whitefly nymphs on citrus at different dates.

Date	12 Oct.		19 Oct.		26 Oct.		2 Nov.		9 Nov.	
	with ant	no ant								
Ants	22	0	12	0	3	0	14	0	11	0
Coccinellid	1	1	0	0	1	0	0	1	0	0
Lacewing	1	2	0	2	1	0	1	3	0	0
Spider	0	2	0	0	0	0	0	0	0	0
Syrphid	1	2	1	0	1	0	2	1	0	0

Natural enemies, including both larval and adult stages.

Behavior Experiment

There was no significant treatment effect on time spent by ants walking on the stem/leaves ($F = 1.36, P = 0.27$) or arena ($F = 0.77, P = 0.47$). Likewise, there was no significant treatment effect on time spent by ants resting on the stem/leaves ($F = 0.74, P = 0.48$) or arena ($F = 1.76, P = 0.19$). In general, ants spent more time on the arena compared to the stem/leaves (Fig 2), suggesting little engagement in whitefly nymph protection. There was no treatment effect on the total amount of time spent by ants walking ($F = 1.64, P = 0.20$) or resting ($F = 2.30, P = 0.11$), regardless of place (Fig 3). Nonetheless, it appears that ants tended to spend more time in activity than resting (Figs 2 and 3). In addition, there was no significant treatment effect on the number of times the ants left the stem/leaves to explore the arena ($F = 2.00, P = 0.15$). The ants left the stem/leaves in the treatment 'live coccinellid' 3.53 ± 0.70 times, in treatment 'drawn coccinellid' 2.50 ± 0.62 times, and in the treatment 'no coccinellid' 4.80 ± 1.10 times. Ten of all experimental ants were observed to feed on whitefly nymph honeydew during the experiment. Only one experimental ant was observed to attack a live ladybeetle during the experiment. Five of all experimental ants inspected the drawn (painted) ladybeetles by moving its antennae to and fro upon the drawing.

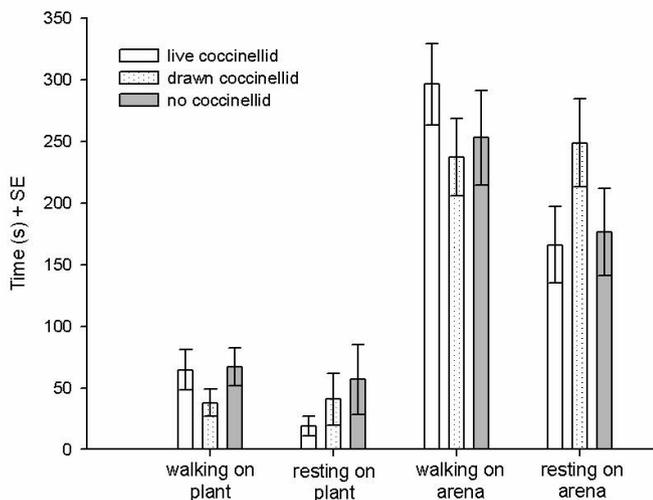


Fig 2. Time spent walking and resting by *Camponotus* ants on the stem/leaves and arena (cup) of three treatments: live coccinellid (scent and visual cues), drawn coccinellid (visual cue only), and no coccinellid (no predator cue).

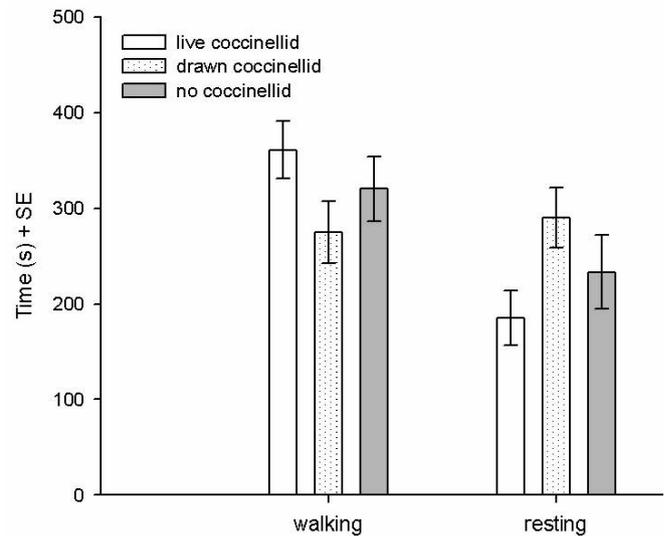


Fig 3. Total time spent walking and resting by *Camponotus* ants in three treatments: live coccinellid (scent and visual cues), drawn coccinellid (visual cue only), and no coccinellid (no predator cue).

Discussion

It has been widely accepted that certain ant species associated with honeydew-producing hemipterans can disrupt the biological control of the latter (Vinson & Scarborough, 1991; Queiroz & Oliveira, 2001; Kaplan & Eubanks, 2002). However, the magnitude of mutual dependence between ants and hemipterans plays an important role in the equilibrium of this relationship, which in turn may indirectly affect biological control. In this study we investigated whether or not *Camponotus* ants that feed on honeydew can disrupt the biological control of the woolly whitefly *Aleurothrix floccosus*. Furthermore, we assessed the behavior of tending *Camponotus* ants in response to woolly whitefly's predator cues.

Our results show that the field population of woolly whiteflies increased equally little in both treatments during the course of six weeks, suggesting that the ants were not able to disrupt biological control when they had free access to whitefly nymph colonies. Although the presence of *Camponotus* ants associated with the experimental whitefly nymph colonies was common in treatment I (with ants), there were times during the evaluation when ants were absent from some of the replicates in this treatment. This suggests that these ants may not have a very narrow relationship with the woolly whitefly,

and thus do not take turns or stay continuously with the nymph colonies. Because *Camponotus* ants are omnivorous (Fowler & Roberts, 1980, Cannon & Fell, 2002; Feldhaar et al., 2007), and honeydew is a suboptimal and ephemeral food source (Wäckers et al., 2008) it may be more advantageous for them not to attend continuously the whitefly nymphs, and had better forage at additional locations for alternative food. Moreover, the honeydew quality depends on the host plants species, whereby nutritionally-poor plants may mediate lower levels of ant attendance to hemipteran colonies (Nemec & Starý, 1990; Hendrix et al., 1992). However, this has yet to be empirically investigated for our particular scenario.

A study conducted by Alves et al. (2015) reports that *Camponotus* ants were observed warding off stingless bees that would come to feed on the honeydew of the whiteflies *Aleurothrixus aepim* (Goeldi) attacking cassava plants. However, unlike in our study they did not quantify the biological control of whiteflies nor assessed the response of the ants to other natural enemies (e.g., predators).

The main generalist predators found associated with the whitefly nymph colonies in our study were coccinellids, syrphids, lacewings, and spiders. With the exception of spiders, all the other three predators have been documented to feed on whiteflies (Ghahhari & Hatami, 2000; Queiroz & Oliveira, 2001). Because the predators we surveyed were in or near the whitefly colonies, we have a reasonable degree of confidence that they were preying on whitefly nymphs. However, our samples were taken only during the day, so nocturnal predators such as earwigs and others may have escaped notice. The more mobile predators (i.e., Coccinellidae) may also have been underrepresented in relation to the Syrphidae, which are relatively sessile once settled in a colony. The relatively low encounter rate of predators in association with the nymph colonies may not, therefore, reflect the impact of predators; these samples constitute a “snapshot” in time, rather than the cumulative effect of predation.

There was no significant difference among treatments in regards to the number of times each ant left the infested stem/leaves to explore the arena during the behavior experiment. In general, the ants spent more time on the arena than on stem/leaves, regardless of experimental treatment. This suggests that neither scent nor visual cues from coccinellids were able to induce a protection behavior on ants for guarding the whitefly nymphs. This may be so because guarding whitefly nymphs and attacking predators such as coccinellids require a substantial amount of energy and implies a risk of getting intoxicated from coccinellid chemical defense, therefore not justifying the necessity of attending continuously the whitefly nymphs. Nevertheless, this has yet to be empirically demonstrated. In any case, coccinellids are known to defend themselves from hemipteran-tending ants by using behavioral, physical and chemical mechanisms (Pasteels et al., 1973; Richards, 1985; Majerus et al., 2007). Because we tested only coccinellids, it is unknown whether or not these *Camponotus* ants could respond in the same way to other predator species.

Most of the studies regarding ant-hemipteran association have been done in temperate regions, and these have focused mostly on aphids (Bretton & Addicott, 1992; Floate & Whitham, 1994; Flatt & Weisser, 2000; Kaplan & Eubanks, 2002; Stadler & Dixon, 2005). By contrast, most of the work regarding ant-hemipteran interactions in the Neotropics involves plant hoppers (Wood, 1984; Dansa & Rocha, 1992; Del-Claro & Oliveira, 1999, 2000; Del-Claro, 2004; Fagundes et al., 2013), whereas very few concern white flies (Queiroz & Oliveira, 2001; Rodrigues & Cassino, 2011; Alves et al., 2013). In general, studies of this nature have congruent results indicating that tending ants can disrupt the biological control of honeydew-producing hemipterans by protecting them from predators and parasitoids. For example, Queiroz & Oliveira (2001) observed higher densities of whiteflies *Aleurothrixus aepim* Goeldi on *Croton floribundus* (Euphorbiaceae) when these plants were freely accessed by ants, possibly because these ants protected the whiteflies from its natural enemies. By contrast, our results show that the biological control of the woolly whitefly *A. floccosus* is not significantly affected by *Camponotus* ants. This difference between our studies may be due to the fact that we investigated a different whitefly and plant species, and moreover, besides *Camponotus* ants their experiment had also the presence of other ant species (e.g., fire ants). Our results raise the question whether the biological control disruption could be an exception rather than the rule, which has been advocated by many insect ecologists.

In summary, this field-laboratory study provides an interesting piece of natural history information that suggests that there is no mutualism between tending *Camponotus* ants and the woolly whitefly *A. floccosus* attacking citrus plants; rather it indicates commensalism as an alternative interaction. Interactions as such may provide more benefits for the host plant whereby *Camponotus* ants can reduce sooty mold by removing honeydew from the leaves and favor biological control by leaving the whiteflies unprotected. If these plants can reciprocally provide shelter and alternative food for these omnivorous ants, and this outweighs the benefit of feeding on honeydew, natural selection should lead to a more narrow relationship between those plants and ants. Nevertheless, further studies are needed to confirm this.

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