Natural History Note

Attracting Predators without Falling Prey: Chemical Camouflage Protects Honeydew-Producing Treehoppers from Ant Predation

Henrique C. P. Silveira, Paulo S. Oliveira, and José R. Trigo*

Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, C.P. 6109, 13083-970 Campinas, São Paulo, Brazil

ABSTRACT: Predaceous ants are dominant organisms on foliage and represent a constant threat to herbivorous insects. The honeydew of sap-feeding hemipterans has been suggested to appease aggressive ants, which then begin tending activities. Here, we manipulated the cuticular chemical profiles of freeze-dried insect prey to show that chemical background matching with the host plant protects *Guayaquila xiphias* treehoppers against predaceous *Camponotus crassus* ants, regardless of honeydew supply. Ant predation is increased when treehoppers are transferred to a nonhost plant with which they have low chemical similarity. Palatable moth larvae manipulated to match the chemical background of *Guayaquila*'s host plant attracted lower numbers of predatory ants than unchanged controls. Although aggressive tending ants can protect honeydew-producing hemipterans from natural enemies, they may prey on the trophobionts under shortage of alternative food resources. Thus chemical camouflage in *G. xiphias* allows the trophobiont to attract predaceous bodyguards at reduced risk of falling prey itself.

Keywords: ant-treehopper interaction, cerrado savanna, chemical camouflage, cuticular profile, multitrophic interaction, mutualism.

Introduction

Interactions between predators and prey represent a strong pressure of natural selection, and antipredator adaptations occur worldwide in nature and in almost every taxonomic group. Avoiding detection by matching a background, named crypsis or camouflage, is a well-known defensive strategy of prey animals (Ruxton et al. 2004). Probably because vision is such an important part of our sensory systems, most documented cases of crypsis involve the low propagation of visual cues through inconspicuous coloration and morphology, usually associated with motionlessness. More recently, however, numerous examples of organisms have been reported in which crypsis is attained by the low dissemination of olfactory, auditory, or tactile cues (Ruxton 2009 and references therein). For example, Espelie et al. (1991) hypothesized that phytophagous insects could remain cryptic as a result of the similarity of their cuticular compounds with those of their host plants, a defensive mechanism called chemical crypsis or chemical camouflage. Empirical support for this hypothesis was provided by Portugal and Trigo (2005), who demonstrated that the similarity of cuticular compounds between larvae of the butterfly *Mechanitis polymnia* (Nymphalidae) and its host plant *Solanum tabacifolium* (Solanaceae) confers protection to caterpillars via chemical camouflage, reducing predation levels by foliage-dwelling ants.

The energy-rich honeydew produced by sap-feeding Hemiptera (e.g., membracids, aphids, and scales) functions as an efficient attractant of ant bodyguards, which in turn confer defense benefits to the trophobionts (Way 1963). Continuous attendance by honeydew-gathering ants can provide a range of benefits to hemipteran trophobionts, including protection from predators and parasitoids and increased fecundity (Stadler and Dixon 2008). Because foliage-dwelling ants can behave aggressively toward foreign insects, including herbivores (e.g., Davidson et al. 2003), it has been proposed that hemipteran honeydew would have an appeasement role by suppressing ant aggression and allowing the ants to begin tending activities (Hölldobler and Wilson 1990; Choe and Rust 2006; Stadler and Dixon 2008). Tending ants, however, can modify their behavior and actually consume their hemipteran partners, depending on the availability of alternative food resources (Way 1963; Buckley 1987; Sakata 1994; Offenberg 2001). Thus the dynamics of such ant-hemipteran interactions suggests that honeydew alone may not be sufficient to protect the trophobionts from ant predation on foliage. A dilemma is then created for honeydew-producing hemipterans: they need to attract pugnacious bodyguards for their own defense without falling prey themselves. This study shows how this problem is minimized by a tropical

trophobiont species. We manipulated the cuticular chemical profiles of potential insect prey to demonstrate that chemical background matching with the host plant protects a honeydew-producing treehopper against attacks by predaceous ants, regardless of honeydew supply. This is the first experimental demonstration that chemical resemblance with the host plant background hides a trophobiont species from predation by ants.

Our hypothesis is that honeydew-producing treehoppers presenting a high degree of similarity with the cuticular chemistry of their host plants would be protected against attacks from chemically oriented predators such as ants, regardless of the presence of honeydew. We tested three main predictions. (1) Treehoppers with high chemical similarity to their host plants should be less attacked by ants than those with low chemical similarity. (2) Switching the treehoppers to a nonhost plant should decrease their chemical similarity with the plant background and thus increase predation by ants. (3) Changing the chemical profile of a palatable (nontreehopper) insect to match the chemical background of a treehopper's host plant should reduce predation by ants compared with unchanged controls.

Methods

The Study System

We studied the gregarious honeydew-producing treehopper *Guayaquila xiphias* (Hemiptera: Membracidae), which inhabits the Brazilian cerrado savanna. The treehopper is tended day and night by 21 ant species that use honeydew droplets that have fallen on lower leaves and ground as cues to find the aggregations on the host plant *Schefflera vinosa* (Araliaceae; Del-Claro and Oliveira 1996, 1999). Tending ants are very aggressive near *G. xiphias* aggregations and ward off predators (spiders and syrphid flies) and parasitoids (wasps), which positively affects treehopper survival (Del-Claro and Oliveira 2000). Additionally, increased alertness and aggression by tending ants near the treehoppers can reduce plant damage by other herbivores (Oliveira and Del-Claro 2005).

Branches of the host plant *S. vinosa* were collected in the cerrado reserve of the Estação Experimental de Mogi Guaçu, state of São Paulo, southeast Brazil (22°49′S, 47°10′W). Plants and treehoppers were frozen at −20°C for the extraction of cuticular compounds to be used in bioassays and for chemical identification.

The ant *Camponotus crassus* (Formicinae) nests in dead and decaying logs and is one of the most frequent attendants to *G. xiphias* aggregations in the cerrado of Mogi-Guaçu (Del-Claro and Oliveira 1999). Because *C. crassus* is also an efficient predator of insect herbivores (Sendoya et al. 2009),

the species is a model generalist predator to test the chemical camouflage hypothesis. Colonies of *C. crassus* were collected in the same site as the branches of *S. vinosa* and in another cerrado reserve ∼70 km away. Captive colonies (30–50 workers) were reared in artificial nests consisting of three test tubes (2.2 cm diameter × 15 cm length, with water trapped behind a cotton plug) placed in a plastic container connected to a foraging arena (as in Portugal and Trigo 2005). The ants were fed daily on 50% sucrose-water solution as a carbohydrate source and three times a week with larvae of the mealworm *Tenebrio molitor* (Coleoptera: Tenebrionidae) as a protein source.

Extraction and Identification of Cuticular Compounds

Cuticular compounds of *G. xiphias* nymphs, of young stems of the host plant *S. vinosa*, of the nonhost plant *Solanum tabacifolium* (Solanaceae), and of *C. crassus* workers were extracted following Portugal and Trigo (2005). The extracts of cuticular compounds were analyzed using electron impact gas chromatography–mass spectrometry in a gas chromatograph (Hewlett Packard 6890) equipped with an automatic injector (Hewlett Packard 7683) and a column HP-5MS (5% phenyl methyl siloxane capillary 95%, 30 m × 250 μm × 0.25 μm; Hewlett Packard) directly coupled to a mass selective detector (Hewlett Packard 5973). All analyses were performed under the following conditions: 250°C temperature of injection; 70°–300°C to 2°C/min, 20 min at 300°C program temperature; helium 1 mL/min as carrier gas; ionization energy of 70 eV and a range of 40–600 amu. Alkanes were identified according to Howard (2001) and alcohols according to Wang et al. (2007), after derivatization with *N*-methyl-*N*-trimethylsilytrifluoruoacetamide (MSTFA; 100 μL MSTFA, 80°C, 1 h) according to Menéndez et al. (2005).

The similarity between the cuticular profiles of *G. xiphias* nymphs and stems of the host plant *S. vinosa*, of nymphs and stems of the nonhost plant *S. tabacifolium*, and of nymphs and *C. crassus* workers was estimated by Morisita's similarity index, which varies from 0% (no similarity) to 100% (full similarity; Krebs 1999).

Bioassays

To test our first prediction, we altered the cuticular profile of *G. xiphias* nymphs. Nymphs were freeze-dried in a Labconco Freezone 6 freeze-dry system for 48 h. The freeze-dried nymphs (body size ∼0.5 cm) were dipped in 10 mL of hexane for 10 min to remove the cuticular compounds (hereafter nymphs without cuticular compounds) and produce a low chemical similarity with the host plant. As controls, freeze-dried nymphs did not receive the hexane treatment, and their cuticular profile was kept intact (here-

after nymphs with cuticular profile intact). Prior paired tests with hexane-treated versus unchanged palatable larvae of the fall armyworm *Spodoptera frugiperda* (Noctuidae) have shown that the hexane decreases by 12% the number of *C. crassus* ants attacking the larvae (paired *t*-test, $t = 2.60$, df $= 9$, $P = .03$). Thus an increased quantity of ants attacking hexane-treated versus unchanged control nymphs (hexane free) would support the hypothesis of chemical camouflage. For the paired experiments on ant predation, one nymph without cuticular compounds and one control nymph were placed on the upper part of a young stem of *S. vinosa*, the preferred plant location of *G. xiphias* treehoppers (fig. 1*A*; see also Del-Claro and Oliveira 1999). The young stem (10 cm tall) was immersed in a 15-mL vial with water to prevent drying. Experimental nymphs were glued ventrally 1 cm apart from each other and on different sides of the stem to facilitate counting the ants (nymph location decided by flipping a coin). The adhesive had no apparent effect on ant behavior (Cascolar plastic glue; see also Oliveira et al. 1987). Ten experimental stems were prepared for the tests on ant predation, and one paired trial was performed for each of 10 different *C. crassus* colonies. We recorded the number of ants attacking each type of experimental nymph at the end of each minute during a 30-min period after the first ant had encountered a nymph (totaling 30 records). Ant attacks consisted of successive bites followed by tugging strikes aimed at removing the nymph. Trials terminated 30 min after starting the observations or on removal of any of the experimental nymphs by the ants. The sums of the numbers of ants recorded each minute

at either experimental nymph were ln $(x + 1)$ transformed to meet normality assumptions, and the means were compared by a paired *t*-test (Zar 1999).

Our second prediction was tested by comparing predation by ants on *G. xiphias* nymphs placed on the nonhost plant *S. tabacifolium* (low chemical similarity with treehoppers) versus predation on nymphs placed on the host plant *S. vinosa* (high chemical similarity with treehoppers). One freeze-dried nymph with its cuticular profile intact was glued to potted young stems of *S. tabacifolium* and *S. vinosa* ($n = 15$ for each plant), which were placed in pairs on the foraging arena of each of 15 colonies of *C. crassus*. The number of nymphs attacked and removed by ants from either plant of a pair was recorded after 24 h, and percentages were compared using a binomial test for two proportions (Zar 1999).

The third prediction was tested by changing the cuticular profile of a potential insect prey by treating it with a hexane cuticular extract from *G. xiphias* nymphs. We used second-instar larvae of *S. frugiperda* as potential prey (Portugal and Trigo 2005). Freeze-dried *S. frugiperda* larvae were dipped in 10 mL of hexane for 10 min to remove their cuticular compounds. Then they were treated topically with cuticular extract from *G. xiphias* nymphs diluted in 10 μL of hexane (hereafter larvae with *Guayaquila* cuticular compounds). Because part of the hexane extract could penetrate the body of moth larvae instead of remaining on the external cuticle, 10 times the larval equivalent was used to compensate for this loss (Portugal and Trigo 2005). The larval equivalent was calculated as in the study by Portugal and Trigo (2005) on the basis of the
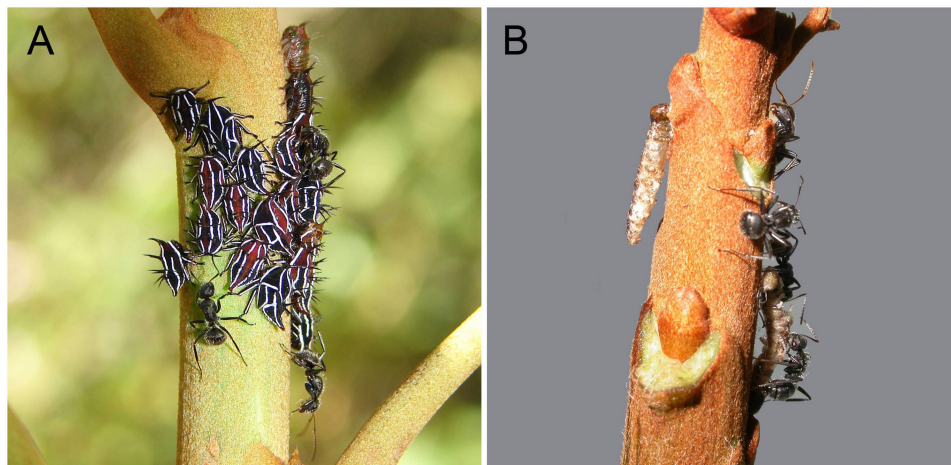

Figure 1: *A*, Workers of *Camponotus crassus* tending an aggregration of honeydew-producing *Guayaquila xiphias* treehoppers on a shrub of *Schefflera vinosa* in the Brazilian savanna (photograph courtesy of G. Bieber). *B*, Bioassay with freeze-dried *Spodoptera frugiperda* larvae glued on a young stem of *S. vinosa* and used in trials of predation by *C. crassus* ants. After removal of their cuticular compounds, the larva on the left was treated with cuticular extracts of *G. xiphias* nymphs, whereas the one under attack by the ants was treated with hexane only.

ratio of the dry weight of *S. frugiperda* larvae to the dry weight of *G. xiphias* nymphs. As controls, freeze-dried *S. frugiperda* larvae were dipped in 10 mL of hexane for 10 min to remove their cuticular compounds (hereafter larvae without cuticular compounds). *Spodoptera frugiperda* larvae with *Guayaquila* cuticular compounds had higher chemical similarity to *S. vinosa* than larvae without cuticular compounds. Experimental moth larvae of each group were glued in pairs on potted young stems of *Schefflera* ($n = 10$; fig. 1*B*), with each placed on the foraging arena of each of 10 *C. crassus* colonies. The number of ants attacking each group of experimental moth larvae was recorded during a 30-min period and compared as described above. In an additional experiment employing the same procedure, we used potted young stems of *S. tabacifolium* to record ant aggression toward *S. frugiperda* larvae coated with *G. xiphias* cuticular compounds versus larvae without cuticular compounds. In this case, both groups of moth larvae had low chemical similarity with the plant.

Results

The analyses by gas chromatography–mass spectrometry of the cuticular extracts of *Guayaquila xiphias* nymphs and of young stems of host (*Schefflera vinosa*) and nonhost (*Solanum tabacifolium*) plants revealed *n*-alkanes and primary alcohols as the main components (fig. 2; numbers in italic after the compounds below correspond to peaks in the chromatograms). Cuticles of treehopper nymphs and young stems of the host plant shared mainly the primary alcohols tetracosan-1-ol (*1*), hexaconsan-1-ol (*6*), octacontan-1-ol (*9*), and triacontan-1-ol (*15*); the *n*-alkanes heptacosane (*2*), nonacosane (*7*), and hentriacontane (*10*); an unknown compound (*5*); and unknown steroids (*13*, *18*); *n*-alkanes and alcohols eluted together (fig. 2). The branched methyl alkanes 13-, 11-methylnonacosanes (*8*) were present mainly in treehoppers; *S. vinosa* showed only traces of these compounds (fig. 2). The Morisita similarity index between the cuticular compounds of *G. xiphias* nymphs and young stems of *S. vinosa* was 81%. In contrast, the chemical similarity between treehopper nymphs and young stems of the nonhost plant *S. tabacifolium* was much lower (23%). *Camponotus crassus* workers showed mainly branched alkanes (*16*, *17*, *21*, *22*, *24*, and *25*) and the unidentified compounds *11*, *12*, *19*, *20*, and *23*, a completely different pattern of cuticular compounds than that found in *G. xiphias* nymphs (Morisita similarity indexes of <1%; see fig. 2).

In paired tests performed on the host plant *S. vinosa*, the number of ants attacking control nymphs with cuticular profile intact was significantly lower compared with nymphs without cuticular compounds (paired *t*-test, $t = -6.26$, df $= 9$, $P < .01$; fig. 3*A*). *Guayaquila xiphias*

freeze-dried nymphs were attacked and removed by ants at a higher percentage from the nonhost plant *S. tabacifolium* (73.33%) than from the host plant (26.67%; binomial test for proportions, $Z = 2.56$, $P = .01$; fig. 3*B*). In trials performed on *S. vinosa* host plants, ants attacked *Spodoptera frugiperda* larvae coated with *G. xiphias* cuticular compounds in lower numbers than moth larvae without cuticular compounds (paired *t*-test, $t = -6.97$, df $= 9$, $P < .01$; fig. 4). However, for trials performed on the nonhost plant *S. tabacifolium*, the quantity of ants attacking *S. frugiperda* larvae did not differ between caterpillars coated with *Guayaquila* cuticular profile and caterpillars without cuticular compounds (paired *t*-test, $t = 1.04$, df $= 8$, $P = .33$; fig. 4).

Discussion

Ants are important predators of herbivorous insects mainly as a result of their great abundance in various terrestrial habitats and most especially on tropical foliage (Davidson et al. 2003). Therefore, natural selection should favor the evolution of different kinds of strategies to escape ant predation or diminish ant-induced injury (Price et al. 1980; Sendoya et al. 2009). Production of exudate rewards by herbivorous insects has been suggested to appease foliage-dwelling predatory ants, which are then discouraged to attack or kill the trophobionts and, in turn, begin tending activities (Hölldobler and Wilson 1990; Stadler and Dixon 2008 and references therein). Our results suggest that an additional defensive strategy is involved in the protection of treehoppers against ant predation, irrespective of a possible appeasing role of honeydew. Because predation tests were performed using freeze-dried *Guayaquila xiphias* nymphs (thus without the honeydew reward), our results confirm that chemical background matching with the host plant does play a protective role. The hypothesis was further supported by the decreased numbers of ants attacking palatable moth larvae coated with *G. xiphias* cuticular compounds on *Schefflera vinosa* host plants. The low similarity between the chemical profiles of *G. xiphias* nymphs and *Camponotus crassus* discarded the possibility of chemical mimicry between the trophobionts and tending ants, as documented for other myrmecophilous insects (reviewed in Dettner and Liepert 1994).

Chemical camouflage as a defense strategy in phytophagous insects was first proposed by Espelie et al. (1991) for cases in which the herbivore matches the chemical background of its host plant (see also Ruxton 2009). More recently, Akino et al. (2004) showed that larvae of the geometrid moth *Biston robustum* resembling twigs of the plants on which they are commonly found were not attacked by predatory ants (*Lasius*, *Formica*), even after an-
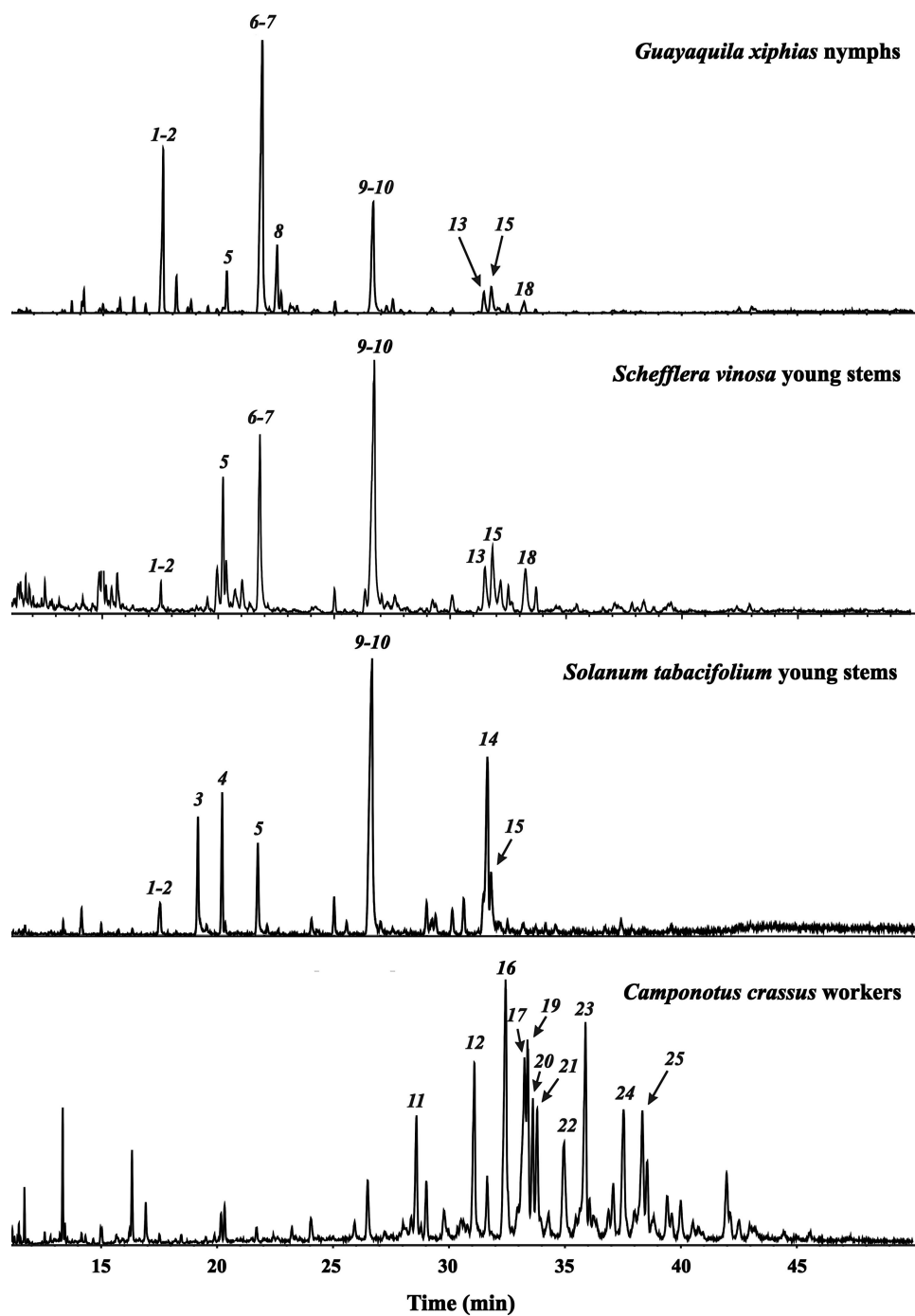
Figure 2: Chromatograms of the cuticular compounds of *Guayaquila xiphias* nymphs, *Schefflera vinosa* young stems, *Solanum tabacifolium* young stems, and *Camponotus crassus* workers. The numbers above each peak are described in "Results."

tennal contact. Chemical camouflage by the caterpillars against ants is achieved because larval cuticular chemicals resemble those of the twigs of the food plant as a result of ingestion of host leaves, indicating a diet-induced de-

fensive adaptation (Akino et al. 2004). Portugal and Trigo (2005) experimentally demonstrated chemical camouflage in larvae of the nymphalid butterfly *Mechanitis polymnia*. Although *C. crassus* ants walked on larvae and ignored
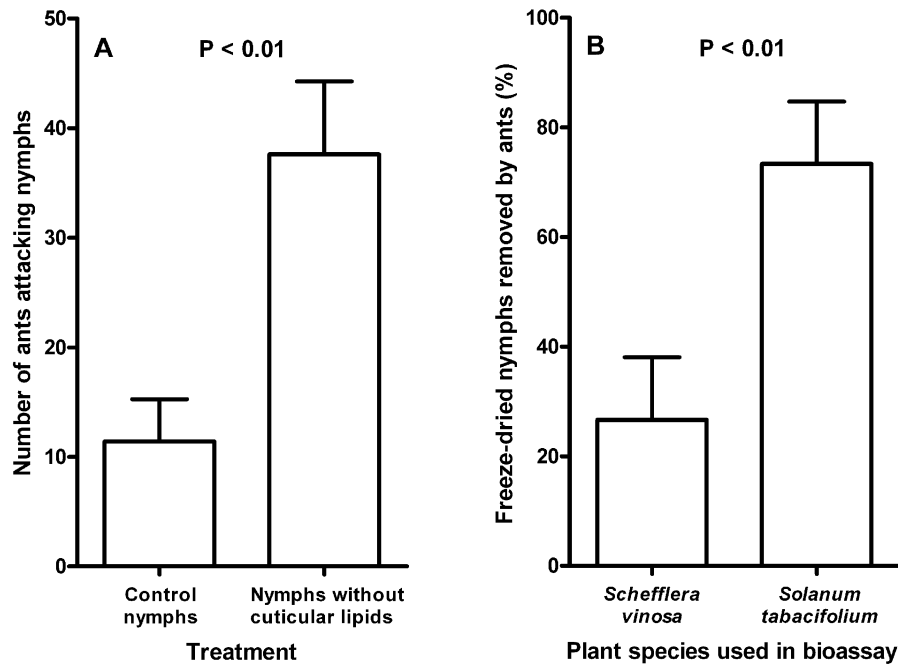
Figure 3: *A*, Quantity of ants attacking control *Guayaquila xiphias* nymphs with cuticular profiles intact versus nymphs without cuticular compounds. Experimental treehoppers were offered in pairs to *Camponotus crassus* ants allowed to forage on potted stems of the host plant *Schefflera vinosa*. Data are means + SE. Statistical analyses were performed on ln $(x + 1)$–transformed values. *B*, Percentage of *G. xiphias* freeze-dried nymphs attacked and removed by ants in the host plant *S. vinosa* and in the nonhost plant *Solanum tabacifolium*. The error bars are the binomial standard error to the percentages.

them in trials performed on the host plant (*Solanum tabacifolium*), they readily attacked caterpillars transplanted to a nonhost plant in a laboratory study. Additionally, when freeze-dried larvae of the fall armyworm *Spodoptera frugipera* were placed on *M. polymnia*'s host plant, they were readily attacked by the ants. In contrast, when coated with *Mechanitis* cuticular compounds, *Spodoptera* larvae were ignored by the ants (Portugal and Trigo 2005).

To our knowledge, the current study provides the first experimental demonstration that chemical background matching with the host plant hides a trophobiont from predation by ants. Whether *G. xiphias* treehoppers sequester compounds from plants or biosynthesize them de novo awaits further investigation (see Howard et al. 1980; Vander Meer and Wojcik 1982). The role of alcohols in species recognition is unusual in ants and remains to be investigated; ants generally recognize other organisms using hydrocarbons (Vander Meer and Wojcik 1982).

Foliage-dwelling ants are known to prey on honeydew-producing hemipterans, depending on the availability of alternative food resources (Buckley 1987; Sakata 1994; Offenberg 2001), and thus might have been important selective agents for the evolution of chemical camouflage in trophobiont species. Our experiments show that chemical background matching with the host plant is enough to reduce ant predation on foliage, irrespective of a possible appeasement role of honeydew. It is possible that the same kind of chemical camouflage also occurs in ant-tended lepidopteran larvae. More than 3 decades ago, Carroll and Janzen (1973) first suggested that honeydew-producing hemipterans could function as insect analogs of extrafloral nectaries, since both represent predictable food sources that elicit patrolling and deterring behavior by ant attendants against intruders. Our study extends Carroll and Janzen's suggestion by showing that, from the viewpoint of the ants, honeydew-producing *G. xiphias* treehoppers are indeed chemically analogous to a plant's secretory organ. This finding is relevant in view of the aggressive behavior of *C. crassus* toward insect herbivores on cerrado foliage and the fact that this ant species also frequently feeds on extrafloral nectaries and hemipteran honeydew (Del-Claro and Oliveira 1999; Sendoya et al. 2009). In fact, the high prevalence of foliage-dwelling ants in the cerrado savanna is partially due to the widespread occurrence on vegetation of predictable liquid food sources in the form of plant- and insect-derived secretions (Rico-Gray and Oliveira 2007). As a result, ants can be key participants in the selective processes operating at the plant-herbivore
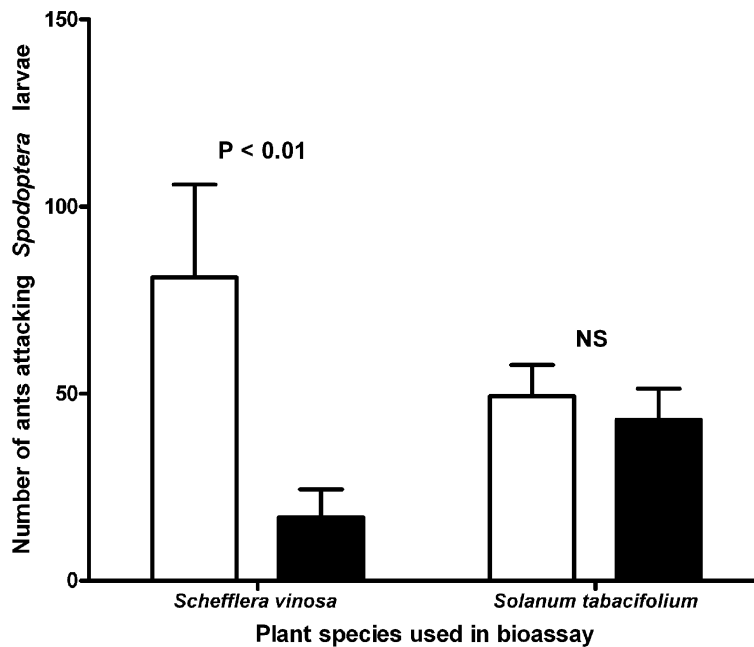
Figure 4: Quantity of *Camponotus crassus* ants attacking paired palatable moth larvae (*Spodoptera frugiperda*) coated (*solid bars*) or not coated (*open bars*) with cuticular compounds of *Guayaquila xiphias* nymphs and placed on potted stems of the host plant *Schefflera vinosa* and of the nonhost plant *Solanum tabacifolium*. Data are means $\pm$ SE. Statistical analyses were performed on ln $(x + 1)$–transformed values.

interface in cerrado, generating a range of interactions that may vary from antagonism to mutualism (Oliveira and Freitas 2004). Our experiments corroborate previous studies showing that the mutualism between ants and hemipteran trophobionts are tenuous and contextual in nature (see Stadler and Dixon 2008 and references therein). Given the important benefits that aggressive honeydew-gathering ants can provide to *G. xiphias* treehoppers (Del-Claro and Oliveira 2000), chemical camouflage resolves a crucial dilemma for this trophobiont: how not to become prey when attracting predators for its own defense. Additional studies with different chemically oriented visitors of extrafloral nectaries that can also act as predators of trophobionts will be necessary to evaluate the effectiveness and generality of chemical camouflage as a defense strategy in *G. xiphias.*

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