

ORIGINAL ARTICLE

Mediterranean ants can increase nymph mortality in the stink bug *Nezara viridula* without interfering with its egg parasitoid *Trissolcus basal*

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Funding information

Italian Ministry for Education

Abstract

Ants (Hymenoptera: Formicidae) play a relevant ecological role across terrestrial ecosystems. Recent studies suggest that the presence of ants in crops could lead to a decrease in the populations of insect pests, but how these actions can vary along the different trophic levels is not well known. The southern green stink bug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae), is a cosmopolitan agricultural pest which is regularly found on horticultural agroecosystems closely associated with its main egg parasitoid, *Trissolcus basal* (Wollaston) (Hymenoptera: Scelionidae). We conducted laboratory experiments to test whether two Mediterranean ant species, the generalist predators *Crematogaster scutellaris* (Olivier) and *Tapinoma magnum* Mayr, attack *N. viridula* eggs or nymphs, and whether they interfere with the parasitization activity of *T. basal*. The experiment showed that both ant species significantly increased the mortality of *N. viridula* nymphs, whereas they do not attack their eggs and do not interfere with the egg parasitoids. Our results suggest that ants and egg parasitoids may have an integrable role in biocontrol strategies against this pest.

KEYWORDS

agricultural pest, biocontrol agent, biological control, *Crematogaster scutellaris*, crop protection, Formicidae, Hemiptera, Hymenoptera, Pentatomidae, Scelionidae, southern green stink bug, *Tapinoma magnum*

INTRODUCTION

Ants (Hymenoptera: Formicidae) are key ecological actors across terrestrial ecosystems (Hölldobler & Wilson, 1990; Lach et al., 2010; Parker & Kronauer, 2021). Their widespread presence in agroecosystems yields a range of services, e.g., ants produce chemical secretions that may limit certain plant pathogens (Offenberg & Damgaard, 2019), they have positive effects on soil bioturbation and nutrients (Lach et al., 2010; Taylor et al., 2019), and most ants are generalist predators that may suppress several agricultural pests, mostly arthropods but also weeds (Way & Khoo, 1992; Lach et al., 2010; Baraibar et al., 2011; Offenberg, 2015). On the other hand, ants are also known to cause ecosystem disservices to agricultural activities, e.g., they may

facilitate mutualistic honeydew-producing hemipteran pests or prey upon insects that are beneficial to biological control programs and may cause damage by consuming seeds of cultivated species (Way, 1963; Baraibar et al., 2011; Offenberg, 2015). Many ants also attack non-prey insects because of territorialism or other forms of aggressiveness (Le Moli et al., 1994; Katayama & Suzuki, 2005; Dejean et al., 2009). Furthermore, they release persistent chemical cues which may attract/recruit nestmates and repel or have a deterrent effect on other insects (Grasso et al., 1998, 1999, 2005; Abandonon et al., 2009; Van Mele et al., 2009; Giannetti et al., 2022). Direct attacks against plants, on the other hand, are essentially restricted to the leafcutter ants that inhabit the American continents (Swanson et al., 2019) and some granivorous species (Rico-Grey & Oliveira, 2007).

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Stink bugs (Hemiptera: Pentatomidae) are a large group of insects which includes several agricultural pests, of which ants have proved to be effective predators in some cases (e.g., Kryspin & Todd, 1982; Yang, 1984; Van Den Berg et al., 1995; Jones et al., 2001; Hosetti & Rudresh, 2012; Castracani et al., 2017; Bulgarini et al., 2021; Kamiyama et al., 2021). The southern green stink bug, *Nezara viridula* (L.), is a cosmopolitan pest species whose geographic origin may reside in the Mediterranean region and/or the African continent (Jones, 1988). This highly polyphagous insect is considered one of the most important pentatomid pests worldwide (Conti et al., 2021). The egg parasitoid *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) is a key natural enemy of *N. viridula* and it is used in biocontrol programs across the world (Colazza & Bin, 1995; Esquivel et al., 2018). Ant activity may interfere with the action of parasitoids under various circumstances: this is mostly observed for those parasitoids that attack ant-mutualist aphids or coccids (Martinez-Ferrer et al., 2003; Chen et al., 2014), but parasitoids of insect species that are prey for ants can also be repelled (Appiah et al., 2014).

Three tropical ants are known as important predators of *N. viridula*, attacking both eggs and nymphs: the Asian weaver ant, *Oecophylla smaragdina* (Fabricius), and two invasive species, the fire ant *Solenopsis invicta* Buren and the big-headed ant, *Pheidole megacephala* (Fabricius) (Krispyn & Todd, 1982; Yang, 1984; Van Den Berg et al., 1995; Jones et al., 2001). Furthermore, *Monomorium minimum* (Buckley), *Pheidole dentata* (Mayr), and *Tetramorium guineense* (Bernard) are known to be nymph predators (Lockwood & Story, 1986). However, it is unknown whether ants from temperate regions can act as predators of *N. viridula* eggs or nymphs. Moreover, the interactions among ant species, *N. viridula*, and parasitoids like *T. basalis* were never investigated. To fill these gaps, we conducted laboratory experiments investigating the interactions between two Mediterranean ant species, eggs and nymphs of *N. viridula*, and females of the egg parasitoid *T. basalis*. The two ant species we chose as models are widespread in agroecosystems (Campolo et al., 2015; Giannetti et al., 2021; Bazzato et al., 2022; Schifani et al., 2022): *Crematogaster scutellaris* (Olivier) and *Tapinoma magnum* Mayr. The two ants are both very disturbance-tolerant species with large colonies, and their workers actively forage on a wide variety of plants, feeding on honeydew and acting as generalist predators (Campolo et al., 2015; Castracani et al., 2017; Seifert, 2018; Giannetti et al., 2022). At the same time, they are representatives of very different ant lineages with distinct behavioral and morphological adaptations. *Crematogaster scutellaris* is an arboreal-nesting species with monomorphic workers that apply their venom topically with a spatulate stinger, whereas *T. magnum* is a ground-nesting species, characterized by highly polymorphic but on average smaller workers which at short range can spray a toxic secretion produced by their anal glands (Seifert, 2018). We tested whether these ants would increase the mortality of

the stink bug nymphs, damage their eggs, or interfere with the parasitoids.

MATERIALS AND METHODS

Plant and insects rearing

Seeds of broad bean plants, *Vicia faba* L. cv. 'Aguadulce Supersimonia' (Fabaceae), were immersed in a slurry of water and soil (1:4 vol/vol) for 24 h, to promote root nodulation. The seeds were then individually seeded in plastic pots (9 × 9 × 13 cm) that were filled with a mixture of agriperlite (Superlite; Gyproc Saint-Gobain, Milan, Italy), vermiculite (Silver; Gyproc Saint-Gobain), and sand (1:1:1 vol/vol/vol). The seeds were germinated, and the plants were grown in a climate-controlled chamber (24 ± 2 °C, 55 ± 10% r.h., L12:D12 h, with light intensity 400 μmol photons m⁻² s⁻¹). The plants were watered daily and 1 week after germination they were fertilized with an aqueous solution of fertilizer (1.4 g L⁻¹; N-P-K=5-15-45; Plantfol, Valagro, Italy). Plants of 20–25 cm tall were used for the experiments.

Nezara viridula was reared in wooden cages (50 × 30 × 35 cm), ventilated with mesh-covered holes (5 cm diameter), in an environmental room (24 ± 1 °C, 70 ± 5% r.h., L16:D8). Stink bugs were fed with a diet of seasonal fresh vegetables and sunflower seeds. Food was changed every 2–3 days, and separate cages were used for nymphs and adults. Paper towels were placed inside each adult cage as an ovipositional substrate. Egg masses collected daily were used to maintain the stink bug colony, which was from time to time refreshed with field-collected bugs.

The *T. basalis* colony was established from wasps emerging from naturally laid *N. viridula* egg masses collected from cultivated fields and surrounding uncultivated areas near Palermo (Sicily, Italy). Adult parasitoids were reared in 16-mL glass tubes (density = 50–60 wasps per tube), fed with a solution of honey and water, and kept in an incubator at the same environmental conditions described for the stink bugs. Egg masses of *N. viridula* collected from the colony were exposed to parasitoids for 48 h, then the wasps were removed, and the parasitized eggs were stored for incubation.

Crematogaster scutellaris and *T. magnum* laboratory colonies were established from samples of about 2000 workers from colonies collected near Palermo. Both colonies were temporarily reared in plastic cages (75 × 35 × 20 cm) for the duration of the experiment under the same environmental conditions described for the stink bugs. They were fed with a honey–water solution. Ants used during each experimental trial were not re-used in following tests.

Experimental setup

Experiments were conducted under controlled conditions of 24 ± 1 °C, 66 ± 1.4% r.h., and L16:D8 photoperiod,

using 30 × 30 cm insect cages. In the center of each cage, we placed a *V. faba* plant with its plastic pot. On one corner of the cage, we placed a plastic cup (8 cm high, 6.5 cm diameter) filled for 1/3 with broken twig pieces and, at its upper internal margins, covered for 1 cm with an ant-repelling substance (50% glycerin oil, 50% petroleum jelly) to prevent ants from escaping. In each plastic cup, we also inserted a 10-cm-long wooden stick, whose upper end was leaning on the plant. The plastic cup was meant to offer a shelter to the ants during the experiments, allowing them to move towards the plant along the wooden stick, without dispersing in all other directions thanks to the repellent substance. After each experiment, the insect cages and plastic cups were washed with clean water, and the plants, the content of the plastic cups, and the wooden sticks were replaced with new ones. We conducted three tests for each experiment, running 15 replicates per test: one with *C. scutellaris*, one with *T. magnum*, and a control test with no ants.

Experiment 1: effects of ant activity on stink bug nymph mortality

On an apical leaf of each plant, we placed with a clip a 1 × 3 cm filter paper with an artificially made egg mass of 15 eggs attached with a glue stick (Pritt; Henkel, Hemel Hempstead, UK). We then waited for 6–10 h after the eggs hatched and counted the *N. viridula* nymphs (mean ± SD = 12.4 ± 2.8). The experiment then started with the introduction of 50 ants in each plastic cup, and lasted 24 h, during which the cage was kept closed. At the end, we collected the stink bug nymphs, checking how many of them were still alive.

Experiment 2: effects of ant activity on stink bug eggs and parasitoid oviposition and survival

We first introduced on each plant three *N. viridula* virgin females for 24 h to allow them to walk over the plant to contaminate it with chemical footprints that are relevant cues exploited by *T. basalis* in its searching behavior (Colazza et al., 1999). We used a glue stick to attach *N. viridula* egg masses (50–100 eggs each) on 1 × 3 cm filter papers and used a clip to put one of them on the apical leaf of each plant. To start the experiment, we introduced 50 ants into each plastic cup, and three *T. basalis* females (24–48 h old). Each experiment lasted 24 h, during which the cages were kept closed, after which we removed the egg masses and the parasitoids and checked whether the latter were alive or dead. The egg masses were incubated until the eggs hatched, or parasitoids emerged. We discriminated between eggs from which parasitoids emerged and the rest from which stink bugs emerged or that did not hatch.

Statistical analysis

The normality of the data and equality of their variance between treatments were tested by means of Shapiro–Wilk and Levene's tests, respectively. To evaluate the differences between treatments concerning stink bug nymph mortality and the egg parasitization rate, we relied on Kruskal–Wallis tests followed by Dunn's post hoc tests for pairwise comparisons if significant differences between treatments had been detected. As no more than one parasitoid died in each trial, data on parasitoid mortality were binomial and differences between treatments were analyzed using a generalized linear model (GLM). All statistical analyses were conducted with the software R v.4.2.0 and RStudio-2022.02.2–485 (R Core Team, 2022).

RESULTS

Experiment 1: effects of ant activity on stink bug nymph mortality

Stink bug mortality rate differed between treatments ($H = 12.24$, d.f. = 2, $P = 0.002$). In particular, the treatment with no ants was different from the other two (no ants vs. *C. scutellaris*: $P = 0.023$; no ants vs. *T. magnum*: $P = 0.003$), whereas there were no differences between the treatment with *C. scutellaris* vs. *T. magnum* ($P = 0.49$). Stink bug mortality was $0 \pm 7\%$ in the treatment with no ants, and $17 \pm 32\%$ in the treatments with ants (median ± interquartile range; Figure 1A–C).

Experiment 2: effects of ant activity on stink bug eggs and parasitoid oviposition and survival

Stink bug eggs were not removed by ants and their shell was not damaged after the experiments in which they were exposed to ants. There was no effect of treatment on the parasitization rate and the consequent number of stink bugs that hatched ($H = 0.27$, d.f. = 2, $P = 0.87$) (Figure 1D, E). Furthermore, there was also no treatment effect on the number of dead parasitoids ($0.24 < P < 0.70$).

DISCUSSION

Our results show that native Mediterranean ants may act as antagonists of *N. viridula* nymphs, significantly increasing their mortality. Furthermore, we found no evidence of interference between ants and the parasitization activity of *T. basalis* on *N. viridula* eggs. As these ants do not appear to prey upon stink bug eggs, they may be even less likely to interact with parasitoids directly. Although we cannot rule out that increasing the number of ants per plant even more would eventually have posed some problems to the

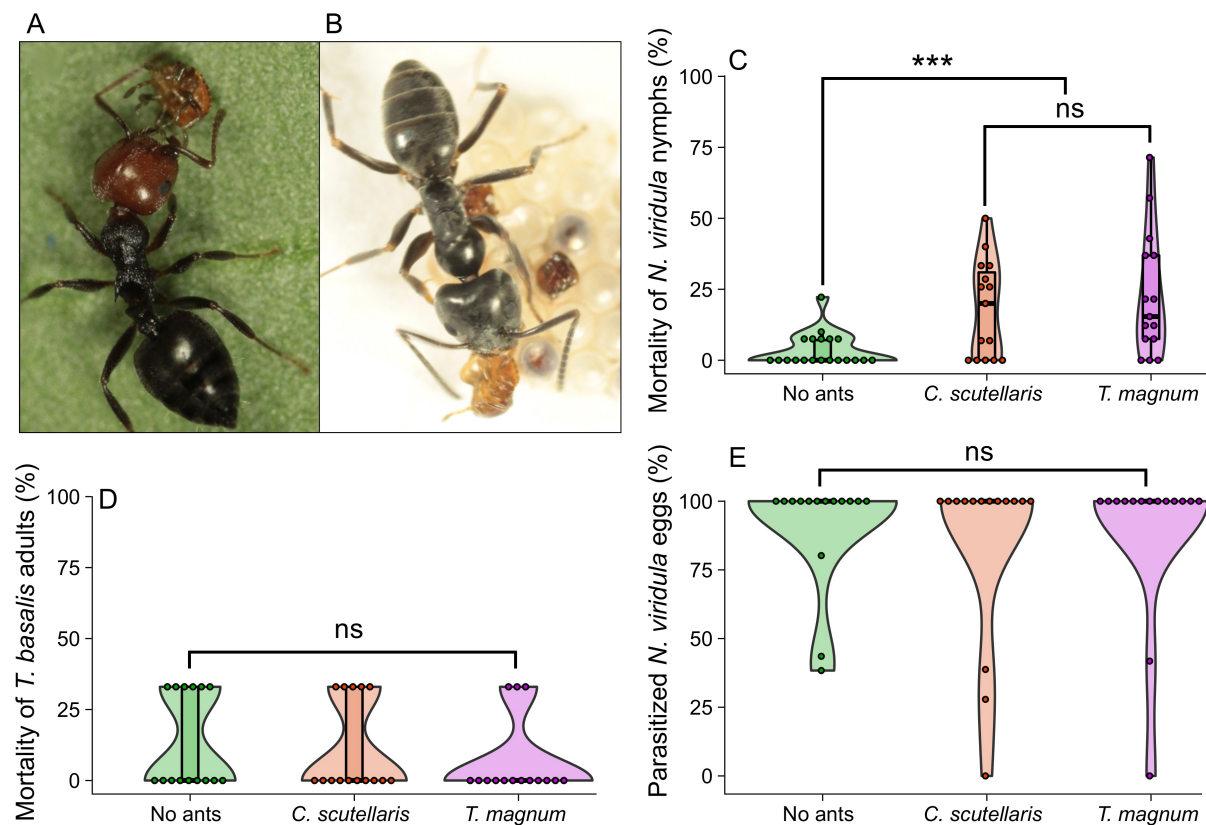


FIGURE 1 Interactions between the ants (A) *Crematogaster scutellaris* and (B) *Tapinoma magnum*, the stink bug *Nezara viridula*, and its egg parasitoid *Trissolcus basalis*. Mortality (%) of (C) stink bug nymphs and (D) the parasitoids. (E) Parasitization rate (%) of stink bug eggs. Asterisks indicate significant treatment effects (Kruskal-Wallis tests followed by Dunn post-hoc tests for pairwise comparisons: $P < 0.001$; ns, $P > 0.05$). Note that the ants in A and B are attacking stink bug nymphs.

parasitoids, and perhaps further increase stink bug mortality, we would not expect such high concentrations to occur under natural conditions.

The fact that we did not record egg predation by the ants, unlike what was observed for *O. smaragdina* (Yang, 1984; Hosetti & Rudresh, 2012), may be due to the relatively smaller size of the ant species we used for the experiments. *Crematogaster scutellaris*, as well as the native European ant *Lasius niger* (L.), are similarly unable to attack the eggs of the brown marmorated stink bug, *Halyomorpha halys* Stål, whereas they do prey upon its nymphs (Castracani et al., 2017; Bulgarini et al., 2022), highlighting a similar pattern among Mediterranean ants interacting with various stink bug species. Larger Mediterranean ant species may be able to prey upon *N. viridula* eggs, but they are seemingly less frequent in agroecosystems than eggs of species such as *C. scutellaris* and *T. magnum* (Mansour et al., 2012; Campolo et al., 2015; Giannetti et al., 2021; Bazzato et al., 2022; Schifani et al., 2022). On the other hand, ants may increase nymphal mortality through different mechanisms, which require further investigation. In addition to suffering from direct attacks (Castracani et al., 2017), disturbance may prompt young nymphs to break aggregations, which leads to a higher risk of death by desiccation and

may even expose them to other predators (Lockwood & Story, 1986).

Ants are often reported to either displace or favor parasitoids, often due to specialized myrmecophilic adaptations by either the hosts or the parasitoids themselves (Pierce & Mead, 1981; Völkl, 1992), whereas in our experiments we witnessed a substantial neutrality between the two actors. The lack of direct interference with *T. basalis* and the lack of interest for *N. viridula* eggs by *C. scutellaris* and *T. magnum* opens the possibility of using these ants as complementary tools along with *T. basalis* in the control programs against *N. viridula*. In this perspective, it is notable that the activity of both ants and *T. basalis* can be enhanced or manipulated by using natural and artificial nectars, favoring their presence on target plants, increasing their survivability, and, in the case of ants, even distracting them from tending coccids or aphids (Offenberg, 2001; Rahat et al., 2005; Schifani et al., 2020). Habitat characteristics may significantly contribute to determining whether ants or parasitoids play a more significant role in controlling *N. viridula* and other stink bugs (Wright & Diez, 2011).

Crematogaster scutellaris and *T. magnum* are already known to play an interesting role in the control of other insect pests, including brown marmorated stink bug, *H. halys*, but also horse-chestnut leaf miner, *Cameraria*

ohridella Deschka & Dimić, Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), codling moth, *Cydia pomonella* (L.), and the ambrosia beetle *Xylosandrus compactus* (Eichhoff) (Radeghieri, 2004; Campolo et al., 2015; Castracani et al., 2017; Giannetti et al., 2022; Schifani et al., 2023). Considering the significant behavioral, morphological, and phylogenetic differences between the ant species known to prey upon *N. viridula* nymphs so far, we expect that several other ants may play a similar role (Offenberg, 2015). However, even superficially similar species may still differ markedly in their attitude towards both stink bugs and their parasitoids (Chen et al., 2014). Further assessments are required to quantify the predatory role of Mediterranean ants on stink bug nymphs in agricultural fields, where generalist species such as *C. scutellaris* and *T. magnum* are expected to co-occur frequently with *N. viridula*.

AUTHOR CONTRIBUTIONS

Enrico Schifani: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); resources (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Ezio Peri:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – review and editing (lead). **Daniele Giannetti:** Conceptualization (equal); methodology (equal); resources (supporting); writing – review and editing (supporting). **Tuğcan Alinç:** Investigation (supporting); resources (lead); writing – review and editing (supporting). **Stefano Colazza:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – review and editing (lead). **Donato Antonio Grasso:** Conceptualization (lead); funding acquisition (equal); methodology (equal); project administration (lead); supervision (lead); validation (equal); writing – review and editing (supporting).

ACKNOWLEDGMENTS

We thank Rihem Moujahed (University of Palermo) for assisting us with plant and insect rearing.

FUNDING INFORMATION

The work benefited from the equipment and framework of the COMP-HUB Initiative, funded by the ‘Departments of Excellence’ program of the Italian Ministry for Education, University and Research (MIUR, 2018–2022).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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How to cite this article: Schifani E, Peri E, Giannetti D, Alinç T, Colazza S & Grasso DA (2023) Mediterranean ants can increase nymph mortality in the stink bug *Nezara viridula* without interfering with its egg parasitoid *Trissolcus basalus*. *Entomologia Experimentalis et Applicata* 171: 739–744. <https://doi.org/10.1111/eea.13357>