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Interspecific competition between endo- and ectoparasitoids attacking *Tuta absoluta*

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Abstract

Tuta absoluta is a major pest threatening tomato crops worldwide. In the Mediterranean basin, biological control mainly relies on zoophytophagous predators which coexist with larval parasitoids, the native ectoparasitoid *Necremnus tutae* and the recently established South American endoparasitoid *Dolichogenidea gelechiidivoris*. Although both are effective natural enemies of *T. absoluta*, their interactions remain poorly understood. Here, we explored the potential competitive outcomes between these two parasitoids through no-choice, choice, and behavior experiments. In single-species assays, *D. gelechiidivoris* exhibited high larval parasitism (92%) and effectively reduced *T. absoluta* densities, whereas *N. tutae* relied more on host-feeding and host-killing behaviors with lower parasitism (48%). When the parasitoids co-occurred, *T. absoluta* mortality increased to ~ 80% while parasitism for each species decreased by well over 50%. *Necremnus tutae* also showed a preference for host-feeding or killing larvae previously exposed to *D. gelechiidivoris*. This elevated larval mortality was likely driven by high probing activity from *D. gelechiidivoris* in combination with continued host-feeding and host-killing by *N. tutae*. Our findings demonstrated interspecific competition between the two larval parasitoids, emphasizing the importance of considering such dynamics when integrating them into biological control programs against *T. absoluta.*

Keywords *Dolichogenidea gelechiidivoris* · *Necremnus tutae* · Biological control · Coexistence · Extrinsic competition · Intrinsic competition

Introduction

Parasitoid wasps play crucial roles in insect communities by contributing to biodiversity and regulating herbivore populations (Boivin and Brodeur 2006). Their ecological significance has led to extensive research into their behavioral ecology, population dynamics, and biological control potential (Godfray and Shimada 1999; Hassell 2000). Parasitoids can function as primary carnivores that develop on herbivores, but also as secondary carnivores who can attack other parasitoids (hyperparasitism) (Boivin and Brodeur 2006; Poelman et al. 2022). As adults, they can also acquire energy from plant-derived food sources such as extrafloral and floral nectar, honeydew, and plant guttation (Wäckers et al. 2008; Heil 2015; Urbaneja-Bernat et al. 2024; Syropoulou et al. 2025). Within their communities, parasitoids coexist with other parasitoid species that have evolved comparable ecological strategies, leading them to exploit food sources, and occasionally the same host within the same habitat (Boivin and Brodeur 2006; Cusumano et al. 2012). These interspecific interactions can occur either during the adults' stage while searching for hosts or when their larvae develop within the same host (superparasitism) (Cusumano et al. 2012, 2016; Harvey et al. 2013), leading to interspecific competition that can impact the success of biological control programs (Boivin and Brodeur 2006).

The South American tomato pinworm, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), recently reinstated as *Phthorimaea absoluta* Meyrick (Chang and Metz 2021), poses a significant threat to tomato crops worldwide

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(Desneux et al. 2022). The primary method for controlling this pest remains the use of synthetic insecticides (Desneux et al. 2010; Mansour et al. 2018). However, the application of such insecticides is unsustainable, as the pest quickly develops resistance to different chemical compounds (Desneux et al. 2010, 2022). Moreover, these chemical applications can adversely affect humans and non-target organisms, including the key predators and parasitoids of *T. absoluta* (Arnó et al. 2011; Urbaneja-Bernat et al. 2025a). Therefore, significant efforts have been made to develop alternative control methods, such as biological control (Biondi et al. 2018). In the Mediterranean basin, biological control mainly relies on zoophytophagous predators, such as *Nesidiocoris tenuis* (Reuter) and *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) (Desneux et al. 2022), which primarily feed on *T. absoluta* eggs, but also exhibit low larval predation rates (Urbaneja et al. 2009). In this region, these predators coexist with larval parasitoids, such as the idiobiont ectoparasitoid *Necremnus tutae*, Ribes & Bernardo (Hymenoptera: Eulophidae), previously referred to as *Necremnus artynes* (Walker), a species native to this region with a high abundance in the field and wider geographical distribution (Gebiola et al. 2015). Additionally, *Dolichogenidea gelechiidivoris* Marsh (Hymenoptera: Braconidae), a larval koinobiont endoparasitoid native to South America, has been identified as an effective biological control agent against *T. absoluta* in tomato crops in Northeastern Spain (Denis et al. 2022). This species was likely unintentionally introduced into the region together with the pest. It was imported into Kenya from Peru in 2017 (Aigbedion-Atalor et al. 2020), and it was recently detected in tomato crops in Algeria (Krache et al. 2021).

Within this system, where *T. absoluta* is attacked by multiple larval parasitoids coexisting in the same agroecosystem, interactions among these parasitoids may influence their performance. For example, interspecific competitive interactions were observed when the endoparasitoid *D. gelechiidivoris* was combined with the ectoparasitoid *Bracon nigricans* Szépligeti (Hymenoptera: Braconidae), resulting in reduced population growth of *D. gelechiidivoris* (Mama Sambo et al. 2023). Similarly, Savino et al. (2016) reported that when the ectoparasitoid *Dineulophus phthorimaeae* De Santis (Hymenoptera: Eulophidae) and the endoparasitoid *Pseudapanteles dignus* (Muesebeck) (Hymenoptera: Braconidae) coexisted on *T. absoluta*, both species altered their searching activity in the presence of the other species. However, the efficacy of *P. dignus* was not affected by competition, maintaining comparable parasitism rates regardless of the presence of *D. phthorimaeae*.

Necremnus tutae exhibits strong host-killing and -feeding on *T. absoluta* larvae (Zhang et al. 2022a, 2022b). This idiobiont ectoparasitoid prefers to parasitize 2nd-3rd instar larvae (Zhang et al. 2022a), while the koinobiont endoparasitoid *D. gelechiidivoris* shows a preference for 1st-2nd instar larvae (Aigbedion-Atalor et al. 2020). The classification of parasitoids as koinobionts or idiobionts serves as a practical indicator for assessing their potential as biological control agents as well as their ability to compete within a specific group of parasitoids (Mills 2006). In general, koinobionts allow their hosts to continue development after parasitism, making it possible for another parasitoid species to find, attack, and use the same resource (Marktl et al. 2002; Wang et al. 2008; Magdaraog et al. 2012). In contrast, idiobionts are often considered superior to koinobionts since they paralyze hosts during oviposition, thus reducing the likelihood of other parasitoids exploiting the same resource (Strand 2000).

The presence of *D. gelechiidivoris* in Mediterranean tomato crops brings a new ecological layer to the trophic interactions shaping the community of natural enemies of *T. absoluta*. While previous studies have evaluated its interactions with predatory mirid bugs such as *N. tenuis* (Aigbedion-Atalor et al. 2021) and the larval parasitoid *B. nigricans* (Mama-Sambo et al. 2023), the competitive interactions between *N. tutae* and *D. gelechiidivoris* remain unexplored. The main objective of this study is to determine the competitive interactions between an endoparasitoid and an ectoparasitoid of *T. absoluta*. We hypothesize that the idiobiont *N. tutae* will be a more effective competitor than the koinobiont parasitoid *D. gelechiidivoris*. To test this, we conducted no-choice, choice, and behavior experiments to evaluate i) parasitoid killing on parasitized larvae from the other parasitoid, ii) their preference to parasitize or kill on unparasitized larvae or those exposed previously to the other parasitoid, and iii) their overall behavior when either introduced alone or with the other parasitoid in the system. Understanding these dynamics will be valuable to optimize integrated pest management (IPM) strategies and enhance *T. absoluta* biological control in Mediterranean tomato crops where both parasitic wasp species are present.

Materials & methods

Plants and insects

All experiments and insect rearing were carried out in a climatic chamber at the facilities of the Institut de Recerca i Tecnologies Agroalimentàries (IRTA) in Cabrils, Barcelona, Spain. Environmental conditions were maintained at 25 ± 1 °C, with relative humidity (RH) of 70 ± 10%, and a photoperiod of 16:8 h (L:D). Pesticide-free tomato (*Solanum lycopersicum* L. (Solanaceae)) plants (cv. Rentita; Samen Hoffmann, Germany) were grown by sowing seeds on a 70/30 peat-perlite substrate in seed-raising plastic trays of 28 cells (7.5 × 7.5 cm) and maintained in a greenhouse.

Once seedlings reached 20–30 cm in height, they were transferred to the laboratory to initiate insect colonies and bioassays. The herbivore and the parasitoid colonies were established using individuals collected from commercial tomato fields infested with *T. absoluta* in Northeastern Spain (41°30′59.6″N, 2°24′03.7″E, Maresme County) and refreshed annually. *Tuta absoluta* larvae were reared on caged tomato plants (47.5 cm × 47.5 cm × 47.5 cm; BugDorm-2; MegaView Science, Taiwan). Separate cages were used to maintain each parasitoid species colony, with adult females and males of *D. gelechiidivoris* and *N. tutae* introduced (2 host:1 parasitoid ratio), respectively. Parasitoids were fed with 1 M sucrose solution. The tested concentration of sucrose was selected based on previous studies (Benelli et al. 2017; Urbaneja-Bernat et al. 2020, 2023). To obtain individuals for the bioassays, leaflets with parasitized *T. absoluta* larvae (1st-3rd instar) were maintained in aerated cages until parasitoids emerged. Parasitic wasps used for all experiments were mated females 1–3 d old for *D. gelechiidivoris* and 2–5 d old for *N. tutae* following each parasitoid species' oviposition peak (Arnó et al. 2018; Urbaneja-Bernat et al. 2024).

Extrinsic and intrinsic competition with no-choice

To evaluate extrinsic competition between *D. gelechiidivoris* and *N. tutae*, *T. absoluta* larvae were dissected 5 days after parasitoid exposure to determine the outcome of adult competition within each host larva. Intrinsic competition between the immature stages of both parasitoid species was assessed by recording emergence outcomes (*T. absoluta, D. gelechiidivoris,* or *N. tutae*) 17–20 days after exposure. Both experiments were conducted under no-choice conditions. The experimental setup consisted of a plastic Petri dish (14 cm diameter), with a hole in the lid, covered with a fine mesh (7 cm diameter). One tomato leaflet (3.5 ± 0.1 cm^2) infested with five *T. absoluta* 2nd instar (L_2) larvae was placed in each Petri dish. The 2nd larval instar (L_2) was selected as it represents the shared preferred host stage between the two parasitoids used in this study. The infestation was performed by transferring the larvae onto the leaflet and allowing all larvae to mine into the leaf tissues for 2 h prior to the start of the experiment. To maintain leaf turgidity and ensure larval survival, the leaflet petiole was sealed with Parafilm® and placed into a 1.5 mL Eppendorf® tube filled with distilled water (Fig. S1a). There were six treatments, each replicated 15 times: (i) *T. absoluta* larvae alone (herbivore control), (ii) one *D. gelechiidivoris* female introduced alone for 24 h (endoparasitoid control), (iii) one *N. tutae* female introduced alone for 24 h (ectoparasitoid control), (iv) one *N. tutae* female introduced 24 h after *D. gelechiidivoris,* (v) one *D. gelechiidivoris* female introduced 24 h after *N. tutae*, and (vi) one *D. gelechiidivoris* and one *N. tutae* introduced simultaneously for 24 h.

Before the experiment, female parasitoids were fed on a 1 M sucrose solution. During the experiment, sucrose droplets were offered on a Parafilm® square piece (1 cm^2), while distilled water was supplied through a small cotton wool. The experiment was carried out in a climatic chamber under the controlled abiotic conditions mentioned above. To evaluate the extrinsic competition, Petri dishes were maintained in the climatic chamber for 5 days. Subsequently, alive *T. absoluta* larvae were introduced in a polypropylene 100 mL container for 24 h with distilled water and sodium hypochlorite solution (1:49 mL) (Urbaneja-Bernat et al. 2025b). After this period, *T. absoluta* larvae were dissected under a stereomicroscope (ZEISS Stemi 508) to determine the parasitism rate (number of parasitized larvae relative to the total number of larvae). For the endoparasitoid *D. gelechiidivoris*, parasitism was determined by observing internal parasitoid stages after dissection following the Urbaneja-Bernat et al. (2025b) monitoring techniques, whereas for the ectoparasitoid *N. tutae*, parasitism was assessed by visual inspection of eggs or larvae attached externally to the host. The number of alive and dead *T. absoluta* larvae (natural mortality or due to host-feeding or host-killing of parasitoids) was also recorded. Natural mortality was differentiated from host-feeding as larvae subjected to host-feeding were dry due to hemolymph consumption, whereas naturally dead larvae remained intact. For the intrinsic competition, Petri dishes were maintained until the development of *T. absoluta* larvae and the emergence of *D. gelechiidivoris, N. tutae,* and *T. absoluta* adults. Water in the Eppendorf® tubes and fresh tomato leaflets were periodically renewed to maintain suitable conditions throughout the experiment. After 17–20 days, *D. gelechiidivoris* and *N. tutae* progeny and number of *T. absoluta* adults as well as *T. absoluta* larvae that did not emerge were recorded.

Choice experiment

To assess whether female parasitoids exhibit a preference for unparasitized hosts or hosts previously parasitized by the other species, a choice experiment was conducted. Two tomato leaflets (3.5 ± 0.1 cm^2 each) were placed on opposite sides of a plastic Petri® dish (14 cm diameter) with a hole in the lid, covered with a fine mesh (7 cm diameter) (Fig. S1b). Each leaflet was infested with five 2nd instars (L_2) *T. absoluta* larvae. A single female parasitoid was released in the center of the dish and allowed to oviposit for 24 h. Water and food were provided as described in the previous bioassay, and parasitoids were pre-fed with sucrose prior to the experiment.

Two treatments were evaluated, each with 15 replicates. (i) A dual-choice assay in which one leaflet with five unparasitized *T. absoluta* larvae *vs.* one leaflet with five larvae previously exposed to parasitism by a *D. gelechiidivoris* female for 24 h were offered to a single *N. tutae* female, and (ii) a dual-choice assay in which one leaflet with five unparasitized *T. absoluta* larvae *vs.* one leaflet with larvae previously exposed to parasitism by a *N. tutae* female for 24 h was offered to a single *D. gelechiidivoris* female. Parasitoid females remained in the experimental setup for 24 h. In the leaflets previously exposed to *D. gelechiidivoris*, parasitism by the endoparasitoid reached 82%, with 10% of larval mortality. In the leaflets previously exposed to *N. tutae*, parasitism by the ectoparasitoid reached 34%, and larval mortality was 43.3%. These percentages represent parasitism and mortality levels prior to the introduction of the second parasitoid in the choice experiment. Dishes were then maintained in a climatic chamber for 5 days, with regular replenishment of water in the Eppendorf® tubes. The number of parasitized larvae by *N. tutae* or *D. gelechiidivoris* was determined by visual inspection of dead larvae to detect ectoparasitization and larval dissection of alive larvae as mentioned in "Extrinsic and intrinsic competition with no-choice" section. *Tuta absoluta* larval mortality was also recorded.

Behavior experiment

A behavioral experiment was conducted to assess interspecific competition and behavioral interactions between females of *D. gelechiidivoris* and *N. tutae* when introduced either alone or simultaneously. Observations were realized in a custom-built enclosed chamber designed to minimize external visual interference and provide uniform, diffuse illumination (Fig. S1c). The observation arena consisted of a 7 cm diameter glass Petri dish placed on a white paper background to enhance contrast. A USB digital microscope camera (Jiusion model, with up to 1000 × magnification) was placed vertically above the arena to allow continuous video recording of parasitoid activity. Video recordings were later reviewed manually, and behavioral events were categorized according to the definitions described below. Each Petri dish contained a single tomato leaflet (3.5 ± 0.1 cm^2) infested with five 2nd instar (L_2) *T. absoluta* larvae. Experiments were conducted under constant ambient laboratory lighting (300 lx). Behavioral observations were continuously recorded for 3 h per replicate. After each recording, Petri dishes were cleaned using 70% ethanol, rinsed with distilled water, and air-dried at room temperature. The same treatments as in the no-choice experiments (except herbivore control) were used, resulting in five treatments with 15 replicates each: (i) simultaneous release of *D. gelechiidivoris* and *N. tutae*, (ii) introduction of *D. gelechiidivoris* 24 h after *N. tutae*, (iii) introduction of *N. tutae* 24 h after *D. gelechiidivoris,* (iv) *D. gelechiidivoris* with unparasitized larvae, and (v) *N. tutae* with unparasitized larvae. For each parasitoid species, the frequency (number) and duration of the following behaviors were counted: (i) resting, (ii) host-feeding, iii) ovipositing, (iv) probing, (v) searching, and (vi) host-killing, following the descriptions of these behaviors in Urbaneja-Bernat et al. 2023. "Host-feeding" was defined as feeding on exuded hemolymph from parasitoid-induced punctures. "Probing" was defined as inserting the ovipositor into a host without egg deposition or host-feeding. "Host-killing" (or host-stinging) was defined as directly killing a host larva with the ovipositor without oviposition (Abram et al. 2019). "Ovipositing" was confirmed when an egg was laid following probing. To verify probing or ovipositing events/behaviors, all larvae were dissected 1 day after the experiment to confirm the presence or absence of parasitoid egg.

Statistical analysis

For the no-choice experiments, generalized linear models (GLMs) with binomial distributions and logit link functions were used to analyze the proportions of dead and alive *T. absoluta* larvae, as well as parasitized larvae by *D. gelechiidivoris* and *N. tutae*. The same model structure was used to assess adult emergence of *T. absoluta*, *D. gelechiidivoris* and *N. tutae*. For the choice experiment, paired Student's t-tests were performed to compare larval mortality and parasitism percentages between the two leaflets within each treatment.

In the behavioral experiment, a GLM assuming a Poisson's distribution and log link function was used to compare the number of occurrences (frequency) of probing, oviposition, and host-feeding/host-killing (combined as a single category) events between treatments. Additionally, GLMs with a binomial distribution and logit link function were employed to analyze the proportion of time each parasitoid species spent performing each behavior (searching, probing, resting, ovipositing, and host-feeding/host-killing) calculated over the total recorded observation time (3 h per replicate). When statistical differences were found in GLMs, post hoc pairwise comparisons were conducted using the Tukey method for multiple comparisons. Data normality was assessed using the Shapiro–Wilk test, which indicated non-normal distributions ($P < 0.05$); therefore, GLMs were applied for the analyses. All statistical analyses were performed in RStudio software (R version 4.4.2) with a nominal significance of 5% ($P < 0.05$). The packages emmeans (Lenth and Lenth 2018) and car (Fox and Weisberg 2018) were used.

Results

Extrinsic and intrinsic competition with no-choice

For the extrinsic competition experiment, the presence of *D. gelechiidivoris* and *N. tutae* significantly affected the proportion of *T. absoluta* larvae that remained alive ($\chi^2 = 333.98$; $df = 5$; $P < 0.001$). The highest proportion of surviving larvae was recorded in the control treatment, followed by treatments where parasitoids were introduced either alone or sequentially. In contrast, the lowest proportion of alive larvae occurred when both parasitoids were introduced simultaneously (Table 1). Larval mortality also differed among treatments ($\chi^2 = 218.36$; $df = 5$; $P < 0.001$). The proportion of dead larvae was highest when *D. gelechiidivoris* and *N. tutae* were introduced simultaneously, followed by treatments in which *N. tutae* was present either alone or in combination with *D. gelechiidivoris*. The lowest mortality was observed in the control and in the treatment where *D. gelechiidivoris* was introduced alone. However, host-feeding by *D. gelechiidivoris* ($\chi^2 = 5.65$; $df = 2$; $P = 0.059$) and *N. tutae* ($\chi^2 = 2.19$; $df = 2$; $P = 0.34$), as well as host-killing by *N. tutae* ($\chi^2 = 0.62$; $df = 2$; $P = 0.73$) and *T. absoluta* natural mortality did not differ among treatments ($\chi^2 = 4.63$; $df = 5$; $P = 0.46$) (Table 1).

Parasitism by *D. gelechiidivoris* was significantly affected by the presence of *N. tutae* ($\chi^2 = 173.68$; $df = 3$; $P < 0.001$). Females parasitized more *T. absoluta* larvae when introduced alone compared to when *N. tutae* was present regardless of whether it was introduced before, after, or simultaneously. Similarly, parasitism by *N. tutae* was influenced by the presence of *D. gelechiidivoris* ($\chi^2 = 40.62$; $df = 3$; $P < 0.001$). The proportion of larvae parasitized by *N. tutae* was highest when females were introduced alone or before *D. gelechiidivoris*, and lowest when both parasitic wasps were introduced simultaneously. *Tuta absoluta* larvae parasitized by both species were not recorded.

For intrinsic competition, *T. absoluta* adult emergence was significantly affected by parasitoid introduction ($\chi^2 = 236.73$; $df = 5$; $P < 0.001$). The proportion of emerged adults was highest in the control and consistently reduced in treatments involving parasitoids. The proportion of not emerged (undeveloped) larvae was also significantly influenced by parasitoid presence ($\chi^2 = 62.87$; $df = 5$; $P < 0.001$). The highest proportion of undeveloped larvae occurred when both parasitoid species were introduced simultaneously, or when *N. tutae* was present alone or sequentially with *D. gelechiidivoris*, whereas the lowest proportion was recorded in the control and in the treatment with *D. gelechiidivoris* alone. The emergence of *D. gelechiidivoris* progeny was affected by the presence of *N. tutae* ($\chi^2 = 111.73$; $df = 3$; $P < 0.001$). The presence of *N. tutae* reduced *D. gelechiidivoris* emergence compared to when it was introduced alone. In contrast, *N. tutae* emergence was not significantly influenced by the presence of *D. gelechiidivoris* ($\chi^2 = 3.01$; $df = 3$; $P = 0.392$) (Table 2).

Choice experiment

When *D. gelechiidivoris* females were given a choice, they parasitized significantly more larvae that had not been previously exposed to *N. tutae* (80%) than those that had (13.3%) ($t = 14.35$; $df = 14$; $P < 0.001$) (Fig. 1A). In contrast, larval mortality was significantly higher in the leaflet

Table 1 Outcomes of extrinsic competition between *Dolichogenidea gelechiidivoris* (Dg) and *Necremnus tutae* (Nt) when parasitizing *Tuta absoluta* larvae

Treatment	Extrinsic competition								
	Alive	Natural mortality	*Dolichogenidea gelechiidivoris* host-feeding	*Necremnus tutae* host-feeding	*Necremnus tutae* host-killing	Total mortality	*Dolichogenidea gelechiidivoris* parasitism	*Necremnus tutae* parasitism	Parasitized by both parasitoids
Control	0.99 ± 0.01 **a**	0.01 ± 0.01 **a**	–	–	–	0.01 ± 0.01**c**	–	–	–
Dg alone	0.05 ± 0.02 **b**	0.03 ± 0.02 **a**	0 **a**	–	–	0.03 ± 0.02 **c**	0.92 ± 0.03 **a**	–	–
Nt alone	0.12 ± 0.03 **b**	0.01 ± 0.01 **a**	–	0.25 ± 0.06 **a**	0.14 ± 0.04 **a**	0.4 ± 0.05 **b**	–	0.48 ± 0.05 **a**	–
1°Dg + 2°Nt	0.01 ± 0.01 **b**	0.01 ± 0.01 **a**	0.03 ± 0.02 **a**	0.36 ± 0.04 **a**	0.12 ± 0.05 **a**	0.52 ± 0.05 **b**	0.19 ± 0.06 **b**	0.28 ± 0.06 **a**	0
1°Nt + 2°Dg	0.08 ± 0.03 **b**	0 **a**	0.05 ± 0.02 **a**	0.28 ± 0.04 **a**	0.09 ± 0.04 **a**	0.43 ± 0.05 **b**	0.15 ± 0.04 **b**	0.35 ± 0.03 **a**	0
DgNt simultaneously	0 **c**	0 **a**	–	–	–	0.8 ± 0.06 **a**	0.08 ± 0.04 **b**	0.12 ± 0.05 **b**	0

Data (mean ± SE) represent the proportion of *T. absoluta* larvae that remained alive, died (host-feeding/host-killing, natural mortality), or were parasitized by either or both parasitoid species under each treatment. Treatments included single and simultaneous exposures of hosts to both parasitoids (1°Dg + 2°Nt, 1°Nt + 2°Dg, and DgNt). Parasitism rates by each species were recorded. In the simultaneous treatment, no host-feeding or host-killing was reported because the source of mortality could not be attributed to a specific species. Different letters within a column indicate significant differences among treatments (Tukey's test, $P < 0.05$)

Table 2 Outcomes of intrinsic competition between *Dolichogenidea gelechiidivoris* (Dg) and *Necremnus tutae* (Nt) when parasitizing *Tuta absoluta* larvae

Treatment	Intrinsic competition			
	Tuta absoluta emergence	Not emerged	*Dolichogenidea gelechiidivoris* emergence	*Necremnus tutae* emergence
Control	0.91 ± 0.03 **a**	0.09 ± 0.03 **b**	–	–
Dg alone	0.11 ± 0.03 **b**	0.09 ± 0.03 **b**	0.8 ± 0.03 **a**	–
Nt alone	0.15 ± 0.03 **b**	0.37 ± 0.04 **a**	–	0.48 ± 0.04 **a**
1°Dg + 2°Nt	0 **c**	0.45 ± 0.04 **a**	0.13 ± 0.04 **b**	0.42 ± 0.03 **a**
1°Nt + 2°Dg	0.07 ± 0.03 **b**	0.37 ± 0.05 **a**	0.17 ± 0.04 **b**	0.39 ± 0.02 **a**
DgNt simultaneously	0.03 ± 0.02 **b**	0.53 ± 0.05 **a**	0.1 ± 0.03 **b**	0.34 ± 0.04 **a**

Data (mean ± SE) represent the proportion of *T. absoluta* larvae that emerged, not emerged or the emergence of each parasitoid species from parasitized larvae. Treatments included single and simultaneous exposures of hosts to both parasitoids (1°Dg + 2°Nt, 1°Nt + 2°Dg, and DgNt). Different letters within a column indicate significant differences among treatments (Tukey's test, $P < 0.05$)

that was first offered to *N. tutae* (62.7%) than in the leaflet that never contacted this last parasitoid (13.3%) ($t = 5.67$; $df = 14$; $P < 0.001$). In the choice test of *N. tutae*, the ectoparasitoid caused higher larval mortality in individuals previously exposed to *D. gelechiidivoris* (65.3%) than in those without prior exposure (30.7%) ($t = 4.84$; $df = 14$; $P < 0.001$). Parasitism was higher in larvae without prior exposure to *D. gelechiidivoris* (46.7%) compared to those previously exposed (25.3%) ($t = 2.54$; $df = 14$; $P = 0.023$) (Fig. 1B).

Behavior experiment

For *D. gelechiidivoris,* the percentage of time spent searching ($\chi^2 = 0.806$; $df = 2$; $P = 0.668$), resting ($\chi^2 = 0.711$; $df = 2$; $P = 0.701$), probing ($\chi^2 = 0.051$; $df = 2$; $P = 0.975$),

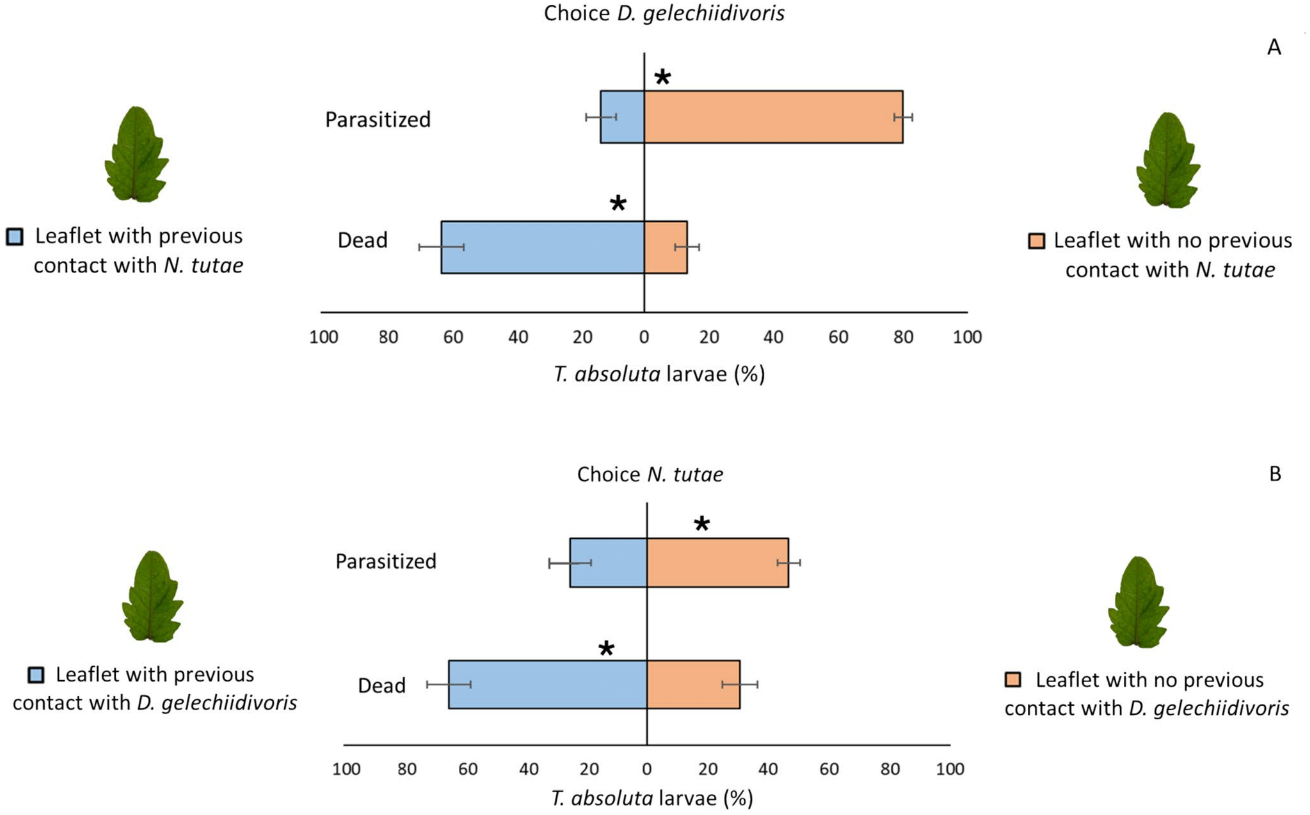

Fig. 1 Percentage (± SE) of *Tuta absoluta* larvae parasitized or dead on each tomato leaflet: **A** parasitism by *Dolichogenidea gelechiidivoris* and **B** parasitism by *Necremnus tutae*. An asterisk (*) indicates significant differences between leaflets (*t*-test, $P < 0.05$)

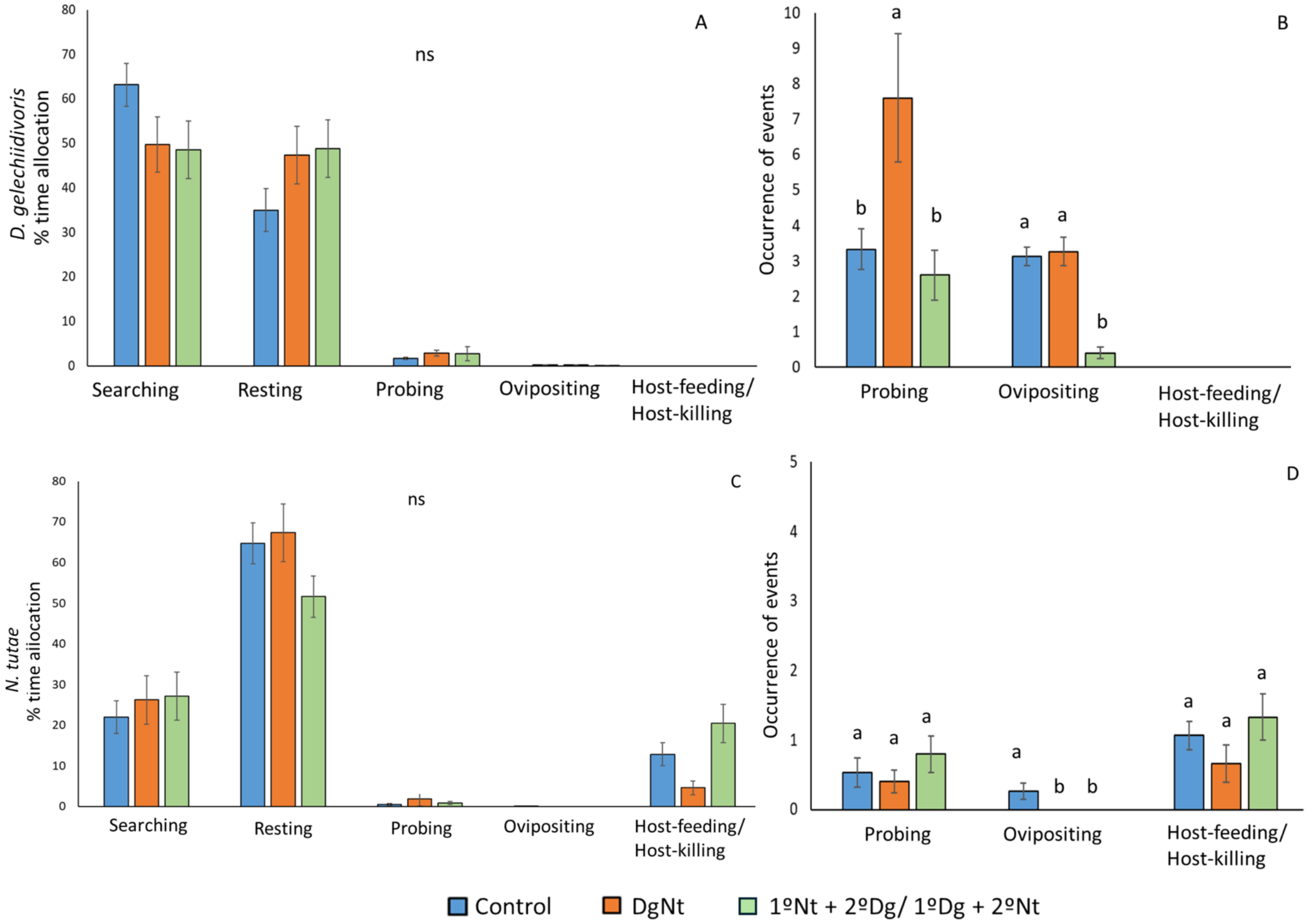

Fig. 2 Proportion of the time spent engaged in five host-finding behavioral categories (mean ± SE), and number of times that *Tuta absoluta* larvae were probed, oviposited, and host-fed/host-killed by *Dolichogenidea gelechiidivoris* (Dg) (**A**, **B**) and *Necremnus tutae* (Nt) females (**C**, **D**) when introduced alone (Control), simultaneously (DgNt), or 24-h post-introduction of the other species (1°Nt + 2°Dg, 1°Dg + 2°Nt). There were no significant (ns) differences in the percentage of time allocation observed in the treatments. For each behavior, different letters indicate significant differences among treatments (Tukey's test, $P < 0.05$)

and ovipositing ($\chi^2 = 0.028$; $df = 2$; $P = 0.986$) was not affected by the presence of *N. tutae* in the system. No host-feeding or host-killing activity was recorded (Fig. 2A). In contrast, the number of *T. absoluta* larvae that *D. gelechiidivoris* females probed ($\chi^2 = 45.69$; $df = 2$; $P < 0.001$), and oviposited ($\chi^2 = 45.44$; $df = 2$; $P < 0.001$) was influenced by the presence of *N. tutae*. Specifically, females probed more than twice as many larvae when introduced simultaneously with *N. tutae* compared to when introduced alone (control) or after *N. tutae*. Oviposition was also higher when females were introduced alone or simultaneously, than when introduced after *N. tutae* (Fig. 2B).

Similarly, for *N. tutae*, the percentage of time spent searching ($\chi^2 = 0.12$; $df = 2$; $P = 0.940$), resting ($\chi^2 = 0.89$; $df = 2$; $P = 0.642$), probing ($\chi^2 = 0.14$; $df = 2$; $P = 0.934$), ovipositing ($\chi^2 = 0.006$; $df = 2$; $P = 0.997$), and host-feeding/host-killing ($\chi^2 = 1.829$; $df = 2$; $P = 0.401$) was not dependent on the presence of *D. gelechiidivoris* (Fig. 2C). The number of *T. absoluta* larvae in which *N. tutae* females oviposited was significantly influenced by the presence of *D. gelechiidivoris* ($\chi^2 = 8.79$; $df = 2$; $P < 0.05$), whereas the number of larvae probed ($\chi^2 = 2.12$; $df = 2$; $P = 0.347$) and host-fed/host-killed ($\chi^2 = 3.44$; $df = 2$; $P = 0.179$) was not affected (Fig. 2D).

Discussion

Our study demonstrated that interspecific competition between the exotic *D. gelechiidivoris* and the native *N. tutae* within the same system can reduce the parasitism efficiency of both species. When tested alone, *D. gelechiidivoris* achieved very high parasitism levels (92%), effectively suppressing *T. absoluta* population. In contrast, *N. tutae* exhibited lower parasitism levels (48%), consistent with its tendency to rely more on host-feeding and host-killing, particularly during the 2nd instar (L_2) larval stage (Zhang et al. 2022a). The presence of *N. tutae* led to a 50% reduction in *D. gelechiidivoris* parasitism, indicating strong interference. This likely occurred because *N. tutae* either reduced host availability before *D. gelechiidivoris* could parasitize or directly attacked larvae already parasitized by *D. gelechiidivoris*. Although limited, host-feeding or host-killing activity was also recorded by *D. gelechiidivoris* when combined with *N. tutae*, confirming previous findings of this behavior when the parasitoid was provided with floral nectar (Urbaneja-Bernat et al. 2024). Interestingly, we did not observe any cases of larvae parasitized by both species, suggesting that the ectoparasitoid outcompeted the endoparasitoid within the same host. These results are consistent with theoretical expectations that idiobiont ectoparasitoids, through host paralysis and venom injection, can eliminate immature stages of endoparasitoids developing within the host (van Alphen and Visser 1990; Harvey et al. 2013). However, under field conditions, Denis et al. (2022) reported that *D. gelechiidivoris* emerged from 11.5% larvae previously ectoparasitized, indicating that successful development of the endoparasitoid may still occur under more complex and environmental variable conditions. Notably, in the no-choice extrinsic competition experiment, a percentage (~ 65%) of the larvae host-killed by *N. tutae* already contained larvae of *D. gelechiidivoris*, thus confirming this lethal interference with the endoparasitoid's success. The strong interference of *N. tutae* with *D. gelechiidivoris* aligns with results from previous studies. According to Mama Sambo et al. (2023), the presence of the native ectoparasitoid *B. nigricans* decreased *D. gelechiidivoris* parasitism by nearly 50%, a pattern also attributed to intense host-feeding and host-killing activity of this ectoparasitoid.

In the choice experiment, we observed that both parasitoids prefer to parasitize larvae that had not previously been exposed to the other species. However, *N. tutae* tended to host-feed or host-kill on larvae previously exposed to *D. gelechiidivoris* which were highly likely to be parasitized given the high parasitism levels recorded prior to its introduction, thereby interfering with the success of the endoparasitoid. This behavior is typical of ectoparasitoids like *B. nigricans* that lack host discrimination and gain fitness both from host resources and from eliminating competitors (Biondi et al. 2013; Idriss et al. 2018). It is also possible that the mortality and physiological alterations induced by the first introduced parasitoid on *T. absoluta* larvae influenced the behavioral decisions of the second parasitoid. In particular, the reduction in host survival and the potential alteration of larval cues (including VOCs) could interfere with how the second species evaluates and selects hosts, which is also a scenario that both parasitic wasps can encounter under greenhouse and open-field conditions. For this reason, this host-mediated effect needs further investigation. Such patterns are consistent with well-known interference behaviors among parasitoid females, where a later-arriving intruder may eliminate the offspring of a previous female through ovicide, larvicide, or destructive host-feeding to secure the host for itself (Ode et al. 2022).

When both parasitoids coexisted, *T. absoluta* larval mortality increased (host-feeding or host-killing), although parasitism by each species declined. Initially, we attributed this increased mortality primarily to *N. tutae*. However, behavioral observations revealed that *D. gelechiidivoris* markedly increased its probing activity in the presence of *N. tutae* adults. According to Cebolla et al. (2018), excessive probing or overstinging can indirectly cause host mortality without resulting in successful oviposition. The likelihood of this parasitoid behavior may depend on the geographical origin of the interacting parasitoid species. Overstinging is often more frequent in non-coevolved parasitoids than in coevolved ones, as their host evaluation process may not accurately reflect host suitability due to the absence of a shared evolutionary history (Schlaepfer et al. 2005). Although *D. gelechiidivoris* and *T. absoluta* share a common native origin, the recent establishment of *D. gelechiidivoris* in the north-east Mediterranean region makes it ecologically non-coevolved with the native *N. tutae*. Therefore, the elevated probing activity observed may reflect a degree of maladaptation in its interactions with native parasitoids. Although this excessive probing may reduce the reproductive efficiency of *D. gelechiidivoris*, it may still contribute to pest suppression, as repeated probing can increase host mortality through host damage. Host-feeding by *D. gelechiidivoris* was not recorded during the 3-h behavioral observations, which may reflect the limited observation period, as parasitoids were exposed to hosts for longer durations (e.g., 24 h) in other experimental assays. Altogether, the combined effects of excessive probing by *D. gelechiidivoris* and host-feeding and host-killing behavior by *N. tutae* likely explain the high *T. absoluta* mortality rates observed when both parasitic wasp species were present.

In the behavioral study, we also detected differences in time allocation patterns between the two parasitoid species. *Dolichogenidea gelechiidivoris* exhibited consistently high levels of searching activity regardless of the presence of *N. tutae*, whereas *N. tutae* was less active and spent a greater proportion of time resting. This pattern contrasts with the findings of Savino et al. (2016), who reported that the ectoparasitoid *D. phthorimaeae* increased its searching activity when competing with the endoparasitoid *P. dignus*, while the searching behavior of *P. dignus* remained unaffected. One possible explanation is that both parasitoids included in the previous study were native to the region and had coevolved with *T. absoluta*, potentially leading to more intense direct competition. In our case, *N. tutae* is native to the Mediterranean, whereas *D.*

gelechiidivoris has only recently become established in the region (Denis et al. 2022), and this difference in evolutionary history may help explain the weaker behavioral response we observed.

In conclusion, our original hypothesis, that *N. tutae* strongly interferes with the success of *D. gelechiidivoris* was supported, regardless of whether *N. tutae* entered the system before, after, or simultaneously with *D. gelechiidivoris.* The reverse effect, however, was only detected when both parasitoid species were introduced at the same time. Nevertheless, their combined presence can still contribute to *T. absoluta* suppression, although their reproductive performance is compromised under direct competition. We suggest that coexistence between these two parasitoids in the field may depend on the availability of different larval instars, as *D. gelechiidivoris* is more efficient at parasitizing early instars (Aigbedion-Atalor et al. 2020), whereas *N. tutae* primarily targets later developmental stages (Zhang et al. 2022a). Future studies should examine potential coexistence scenarios under field conditions within IPM programs, exploring additional factors that may influence the strength and outcome of their interaction (e.g., extrinsic and intrinsic), such as larval stage preferences, parasitoid nutritional status (e.g., nectar, plant guttation, and honeydew), and parasitoid age, which may ultimately modulate the intensity of their competitive interactions.

Author contributions

All authors contributed to the study conception. AS and PUB designed research. AS conducted experiments and analyzed data. JA acquired research funding. AS drafted the initial manuscript. All authors read, revised and approved of the manuscript.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding authors on reasonable request.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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