



Predation of *Pterostichus melanarius* on cocoons of soybean gall midge, *Resseliella maxima*

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Abstract The soybean gall midge, *Resseliella maxima* Gagné (Diptera: Cecidomyiidae), feeds on soybean, *Glycine max* (L.) Merrill (Fabales: Fabaceae), causing significant injury and yield losses. *Pterostichus melanarius* Illiger (Coleoptera: Carabidae), a generalist predator introduced to North America, has been reported to prey on *R. maxima* larvae under laboratory conditions. Understanding the feeding preference of *P. melanarius* on different prey life stages is important to evaluate its role in the biological control of *R. maxima*. Three laboratory experiments were conducted to assess predatory behaviors. In a no-choice test, *P. melanarius* adults fed on both *R. maxima* free (i.e., not cocooned) larvae and cocooned

larvae, showing significant differences in prey consumption between *R. maxima* developmental stages over time. A choice test revealed a preference of *P. melanarius* adults for free larvae over cocooned larvae within the first hour, although this preference was not significant after 24 h. In an experiment examining the effect of soil on predation rates, *P. melanarius* adults consumed larvae and cocooned pupae placed either without soil, on the soil surface, or at a 1 cm depth, and predation rates were influenced by prey stage and the presence and depth of soil. These findings indicate that *P. melanarius* adults can feed on cocooned life stages, but that the presence of soil may hinder predation.

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Introduction

Soybean gall midge, *Resseliella maxima* Gagné (Diptera: Cecidomyiidae) was described in 2019 in the Midwestern USA as a new species that feeds on stems of soybean, *Glycine max* (L.) Merrill (Fabales: Fabaceae) (Gagné et al. 2019). Infestation of soybean plants by this insect pest typically begins when soybean plants have 2–3 fully developed trifoliolate leaves, when females oviposit at the base of the plants in natural cracks that occur during plant growth (McMechan et al. 2021a). After hatching, the

larvae of *R. maxima* enter the stem and feed beneath the plant's epidermis, with larvae moving into the phloem, xylem, and pith as time passes (Gagné et al. 2019). Injury to these plant tissues can lead to wilting, plant death, and yield losses (McMechan et al. 2021a; Helton et al. 2022). Once mature, the larvae drop from the plants, burrow into the soil, build silken cocoons, and then either immediately pupate or overwinter as larvae before pupation in the spring (McMechan et al. 2021b). Adults eventually emerge out of the soil (McMechan et al. 2021b).

Resseliella maxima is present in seven soybean-producing states (i.e., Iowa, Kansas, Minnesota, Missouri, Nebraska, North Dakota, and South Dakota) (<https://soybeangallmidge.org>), which together account for more than 43% of the total soybean production in the USA (USDA 2024). Yield losses caused by infestations of *R. maxima* can exceed 92% within the first 30 m from the field edges and can reach up to 31% in the interior of the field (McMechan et al. 2021a). The expanding range of *R. maxima* and its potential to cause yield losses to soybean press for the identification of potential management methods for this pest. Foliar insecticides and granular at-plant insecticides have shown some suppression of the pest. However, their effects are inconsistent and likely not sufficient for effective control (Cooper and McMechan 2024; Hodgson and Helton 2021; McMechan 2021; Montenegro et al. 2022). Cultural control, such as hilling, can be highly effective at reducing *R. maxima* infestation and yield loss, but this practice requires specialized equipment and is not common in soybean production (McMechan et al. 2023; Gupta and McMechan 2025). Soybean genotypes are being screened for resistance to *R. maxima* to provide a foundation for development of host plant resistance (Sever 2021).

Biological control of *R. maxima* is also being assessed. A new species of wasp, *Synopeas maximum* Awad & Talamas (Hymenoptera: Platygasteridae) was identified and described as a parasitoid of *R. maxima* (Melotto et al. 2023a), but its parasitism rate in the field is relatively low (Melotto et al. 2023b). A second wasp, *Synopeas ruficoxum* Buhl (Hymenoptera: Platygasteridae) recently had its parasitoid-host association with *R. maxima* confirmed, although its distribution and parasitism rate remain unknown (von Gries et al. 2025a). The role of predators was investigated in soybean fields in southwest Minnesota, and

Pterostichus melanarius (Illiger) (Coleoptera: Carabidae) was the most abundant among the ground-foraging predatory species found (Melotto et al. 2023c). Adults of *P. melanarius* feed on *R. maxima* larvae under laboratory conditions (Melotto et al. 2023c), and *P. melanarius* exhibits a preference for *R. maxima* larvae over an alternative prey species as well as a Type I (i.e., linear) functional response across *R. maxima* densities (von Gries et al. 2025b).

Pterostichus melanarius is an exotic, omnivorous generalist predator unintentionally introduced to North America that feeds on insects, nematodes, plant tissue, and spores (Pollet and Desender 1985; Busch et al. 2021). It is also an opportunist, feeding on the most abundant prey (Pollet and Desender 1985; Busch et al. 2021). In the field, when third instar larvae of *R. maxima* drop to the ground, they may become more vulnerable to attacks from ground-foraging predators such as *P. melanarius*. Given that *R. maxima* larvae burrow into the soil and form cocoons, it raises the question of whether *P. melanarius* adults can locate and open these cocoons to consume the larva or pupa inside. Thus, this study was conducted to evaluate: (1) the consumption rate of *P. melanarius* on cocooned *R. maxima* larvae (no-choice test), (2) the feeding preference of *P. melanarius* adults between free (i.e., not cocooned) *R. maxima* larvae and cocooned *R. maxima* larvae (choice test), and (3) the ability of *P. melanarius* adults to find and feed on buried cocooned *R. maxima* pupae (soil test). This information will provide insights on the role of *P. melanarius* as a biological control agent of *R. maxima*.

Material and methods

No-choice test

Pterostichus melanarius adults were collected as described in Melotto et al. (2023c), using dry pit-fall traps (11.5 cm diameter × 14 cm length) in a soybean field near Luverne, Minnesota, USA in July and August of 2023. *Pterostichus melanarius* were separated from the by-catch, transported to the laboratory in coolers, then kept in an environmental growth chamber at 25 ± 2 °C with a L:D 16:8 photoperiod. They were placed in clear round plastic containers (18.7 cm diameter × 7.62 cm height; Pioneer

Plastics, Dixon, Kentucky, USA). Each container had a polystyrene plastic vial (33.7 ml) filled with deionized water and a small cotton ball at the tip as a water source, along with an *ad libitum* supply of dog food (Pro Plan Puppy Sensitive Skin & Stomach Salmon & Rice Formula Dry Dog Food; Purina, Nestlé Purina PetCare Company, St. Louis, Missouri, USA) and paper towels to create a sheltered environment. Beetles remained in the environmental growth chamber for 5–20 days prior to further processing, depending on collection timing and experimental scheduling. Before experiments, *P. melanarius* adults were subjected to a starvation period of 48 h to standardize hunger levels. This was done by placing individual *P. melanarius* in tight-fitted Petri dishes (50 mm diameter×9 mm height) with small cotton balls moistened with deionized water, and maintained in an environmental growth chamber with the same conditions described above.

Resseliella maxima were obtained from soybean plants collected from commercial fields near Luverne, Minnesota, USA and Sioux Falls, South Dakota, USA. The soybean plants were brought back to the laboratory, and what are assumed to be the third instar larvae (orange-colored) of *R. maxima* were collected with the help of a soft-bristled brush after dissecting the soybean stems with a scalpel (von Gries et al. 2025b). For treatments involving free larvae, stems were collected five or six days before setting up the experiment, but larvae were only extracted from the stems on the same day the experiments were set up. For production of cocooned *R. maxima*, stems were collected from the field 12 days before setting up the experiment. The process for obtaining *R. maxima* cocoons was modified from the methods described by Košťál and Havelka (2000) and Des Marteaux et al. (2012) and optimized for *R. maxima* (P. Anderson, unpublished data) by placing the collected larvae in polystyrene plastic vials (33.7 ml) containing moistened sand and sealing them with a plastic cap. Vials containing *R. maxima* were kept in environmental chambers with a temperature of 20 ± 2 °C and a L:D16:8 photoperiod. After ten days, cocoons containing *R. maxima* larvae were collected from the vial by emptying its contents into a clear round plastic container and using a plastic squeeze bottle filled with deionized water to wash and separate the sand particles. The cocoons were then removed with tweezers and placed on filter paper to dry.

The no-choice test was performed in 9 cm Petri dishes kept on a laboratory bench at room temperature (~25 °C) with constant lighting. One of two prey treatments was placed in each dish: five cocooned larvae or five free larvae of *R. maxima*. One starved *P. melanarius* adult was added to each dish (Fig. 1a). The experiment was conducted over two temporal blocks, with 4–6 replications of each treatment per block for a total of ten replications of each treatment. Within each treatment, five replicates were performed with female *P. melanarius* adults and five with male *P. melanarius* adults (Lindroth 1966; von Gries et al. 2025b). The overall feeding period lasted 24 h after the addition of *P. melanarius* adults to the dishes, with assessment of the number of remaining cocooned larvae or free larvae recorded at 1 and 24 h by visually inspecting the Petri dishes.

Choice test

Pterostichus melanarius adults were collected, maintained and starved as described above for the no-choice test. *Resseliella maxima* were obtained from soybean plants collected from a commercial field near Sioux Falls, South Dakota, USA. *Resseliella maxima* free larvae and cocooned larvae were obtained as described above for the no-choice test.

The choice test was performed using the same Petri dish and at the same conditions described above for the no-choice test. Five cocooned larvae and five free larvae of *R. maxima* were placed in each Petri dish, with each prey type positioned on opposite sides of the dish. One starved *P. melanarius* adult was added to each dish (Fig. 1b). The experiment was conducted with a total of ten repetitions, with five repetitions having female *P. melanarius* adults and five having male *P. melanarius* adults. The total feeding period lasted for 24 h after the addition of *P. melanarius* adults to the dishes, with assessment of the number of remaining cocooned larvae and free larvae recorded at 1 and 24 h by visually inspecting the Petri dishes.

Soil test

Pterostichus melanarius adults were collected from a commercial soybean field near Luverne, Minnesota, USA in June of 2024, and maintained and starved as described above for the no-choice test. *Resseliella maxima* were obtained from soybean plants

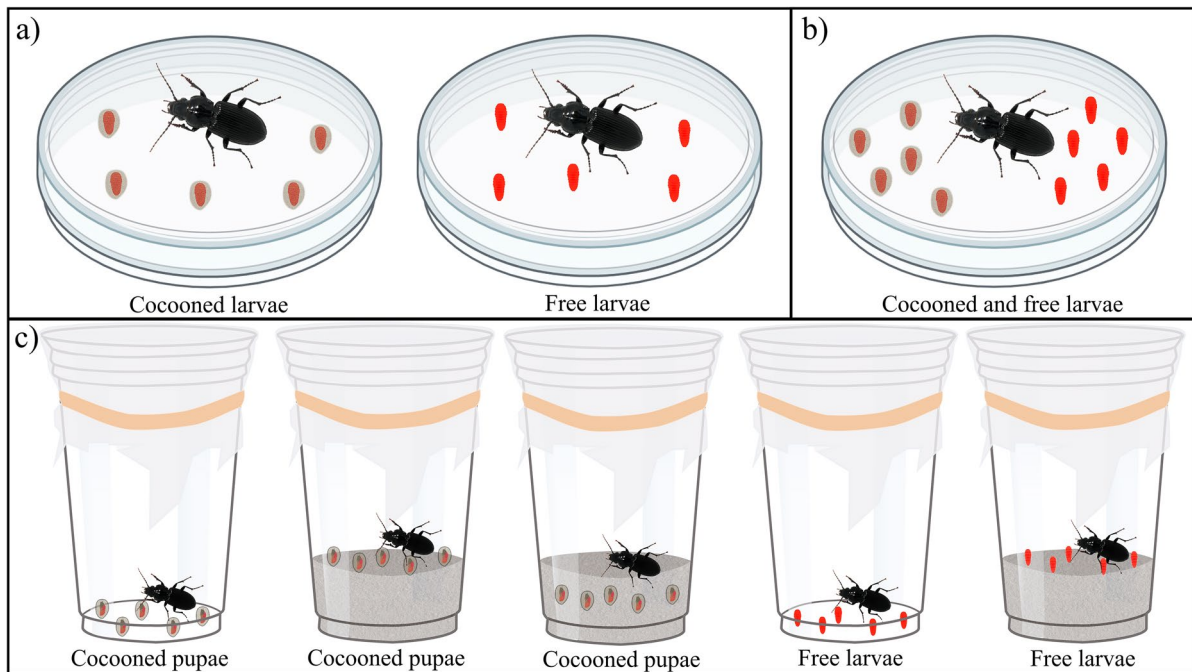


Fig. 1 Experimental setup for predation trials using *Pterostichus melanarius* and *Resseliella maxima*: **a** No-choice test: *P. melanarius* adults were placed in Petri dishes with either *R. maxima* free larvae or cocooned larvae. **b** Choice test: *P. melanarius* adults were placed in Petri dishes and given a simulta-

neous choice between *R. maxima* free larvae or cocooned larvae. **c** Soil test: *P. melanarius* adults were placed in cups, with and without soil, containing either *R. maxima* free larvae or cocooned pupae, covered with a plastic sheet and secured with a rubber band

from a laboratory colony of *R. maxima* maintained at the University of Minnesota, USA. *Resseliella maxima* larvae were collected from soybean stems on the same day the experiments were set up, following the methods described above for the no-choice test. For production of *R. maxima* cocoons, stems were obtained from the colony 12 days before setting up the experiment. The process for obtaining *R. maxima* cocoons was carried out as described previously in the no-choice test. The cocoons used in this study contained *R. maxima* pupae, likely because the larvae collected from the laboratory colony had not been exposed to overwintering cues and therefore continued development to the pupal stage (in contrast to the field-collected individuals which would have likely ceased development in the overwintering stage [cocooned larvae]).

The experiment was performed in 266.16 ml (88.9 mm top diameter×57.15 mm bottom diameter×101.6 mm height) clear plastic cups (Clear cups, Great Value, USA), closed on top using a 15 cm square clear plastic sheet, cut from a zip-top

storage bag, secured with a rubber band. Soil used as substrate was collected from the same field from which *P. melanarius* were collected. The soil was dried for 48 h in a chamber at 60 °C and then sifted (sieve number 20, 0.84 mm) to remove any material larger than the prey. Before setting up the experiment, water was added to moisten the soil: 520 ml of water for every 2 kg of soil. In this experiment, five treatments were tested: (1) cocoons with no soil, (2) cocoons placed on the surface of the soil, (3) cocoons placed 1 cm deep in the soil, (4) free larvae with no soil, and (5) free larvae with soil. Five individual prey were used in each arena. In treatments with soil as substrate, a 3 cm deep layer of soil was used in each arena. For the treatment using free larvae with soil, larvae were placed on the surface of the soil because they typically burrow into the soil, and do not remain on the surface like the cocoons. For the treatment with cocoons 1 cm into the soil, a 2 cm deep layer of soil was initially added in the cup, the cocoons were placed on the surface of this layer, and the remaining 1 cm deep layer of soil was added after the cocoons

were placed. One *P. melanarius* was placed into each arena and they were closed on top as described above (Fig. 1c). The experiment was performed with 20 arenas (i.e., repetitions) of each of the five treatments. To assess the effectiveness of recovering cocoons and free larvae from the soil, five additional predator-free replicates of cocoons (buried at 1 cm) and of free larvae were also conducted, but not included in statistical analyses. Five individuals were placed in each of these replicates, and all individuals were recovered after 24 h.

The arenas were kept in a controlled environment, with a temperature of 26 ± 2 °C and a L:D16:8 photoperiod. After 24 h, *P. melanarius* were removed from each arena, and prey consumption was evaluated by quantifying the remaining *R. maxima*. Quantification was done by transferring the soil to a sieve (sieve number 20, 0.84 mm) and washing the soil with deionized water until only *R. maxima* remained in the sieve. All remaining *R. maxima* for each repetition were examined under a microscope to determine if the cocoons were open and/or if the larvae were partially consumed. *Resseliella maxima* that were missing or partially consumed were considered eaten.

Statistical analysis

For the no-choice test, the proportion of *R. maxima* consumed by *P. melanarius* adults was analyzed separately for 1- and 24-h time assessments with bias-reduced (package *brglm2* version 0.9.2, method=*brglmFit*; Kosmidis 2023) generalized linear models with a Binomial distributions and a logit link function (package *stats* version 4.3.2, function *glm*; R Core Team 2025). The proportion of *R. maxima* consumed was used in the model as the response variable and stage (free larvae versus cocooned larvae) was included as a fixed factor. The significance of estimates was obtained with a Type II Wald χ^2 test (package *car* version 3.1–2, function *Anova*; Fox and Weisberg 2019), and model fit and presence of influential observations (outliers) were verified visually with diagnostic plots (package *performance* version 0.10.9, function *check_model*; Lüdtke et al. 2021). The presence of one influential observation was detected for 24 h and therefore this replicate was removed from all analyses. Models followed assumptions after removal of the outlier.

For the choice test, the difference in consumption between the number of *R. maxima* free larvae and the number of cocooned larvae by *P. melanarius* adults was tested against 0 with a Wilcoxon signed rank test (package *stats* version 4.5.2, function *wilcox.test*; R Core Team 2025), because the assumption of normality was violated for the 24 h assessment. The assumption of normality was assessed with a Shapiro–Wilk normality test (package *rstatix* version 0.7.2, function *shapiro_test*; Kassambara 2023).

For the soil test, the proportion of *R. maxima* consumed by *P. melanarius* adults was analyzed with bias-reduced (package *brglm2* version 0.9.2, method=*brglmFit*; Kosmidis 2023) generalized linear models with Bbinomial distributions and a logit link function (package *stats* version 4.3.2, function *glm*; R Core Team 2025). The proportion of *R. maxima* consumed was used in the model as the response variable and treatment was included as a fixed factor. The significance of estimates was obtained with a Type II Wald χ^2 test (package *car* version 3.1–2, function *Anova*; Fox and Weisberg 2019) and model fit was verified visually with diagnostic plots (package *performance* version 0.10.9, function *check_model*; Lüdtke et al. 2021). Furthermore, pairwise comparisons of treatments were conducted using estimated marginal means with Tukey's adjustment ($p < 0.05$) (package *emmeans* version 1.8.9; Lenth 2023).

Results

No-choice test

Pterostichus melanarius adults consumed both stages (i.e., free and cocooned larvae) of *R. maxima*. Under laboratory conditions, we observed *P. melanarius* adults detecting *R. maxima* cocoons, opening them, and feeding on the larvae. An observed *P. melanarius* adult grasped the cocoon with its mandibles and, using its anterior tarsi for support, opened the cocoon to feed on the larva inside. In some cases, parts of the cocoon remained intact, but the larva was fully consumed. Occasionally, *P. melanarius* bit into the cocoon, and consumed both the silk and the larva. In this case, the only material left behind was the sand from the cocoon's exterior.

After one hour, *P. melanarius* adults ate significantly ($\chi^2 = 5.77$, $df = 1$, $p = 0.016$) more free

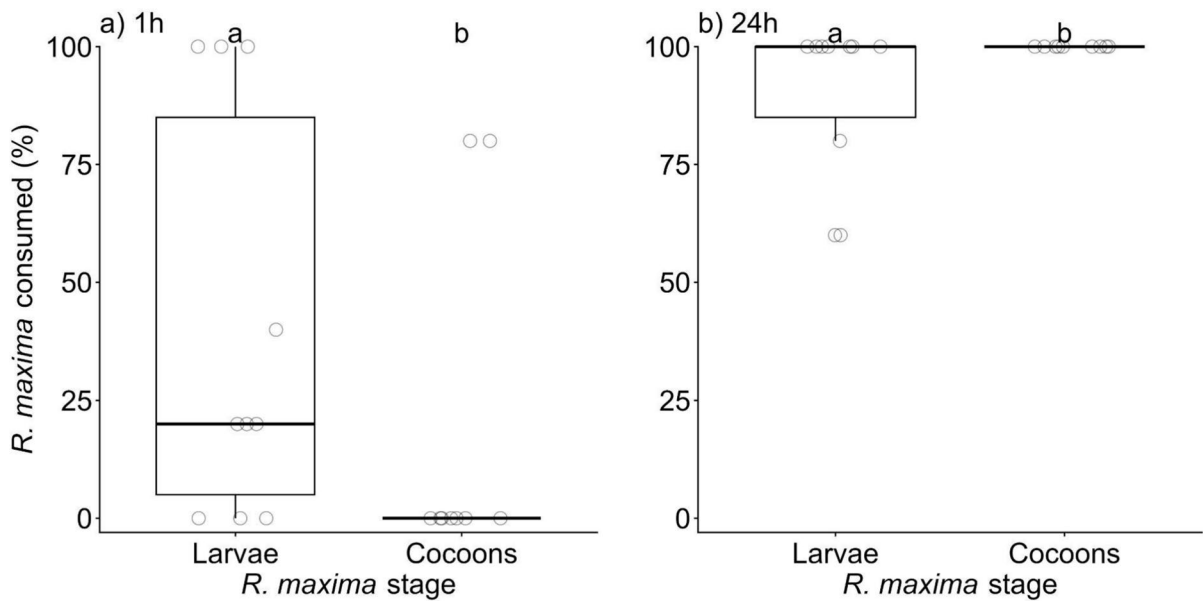


Fig. 2 Percentage of *Resseliella maxima* free larvae (“larvae”) and cocooned larvae (“cocoons”) consumed by *Pterostichus melanarius* adults in a no-choice test at 1 h (a) and 24 h (b). Boxplots show the median (horizontal line), interquartile range

(box), and minimum and maximum values (whiskers). Individual points represent replicate observations. Different lower-case letters indicate significant differences between prey stages within each time period ($p < 0.05$)

larvae ($40.00 \pm 13.66\%$) than cocooned larvae ($17.77 \pm 11.76\%$) (Fig. 2a), with seven *P. melanarius* adults eating free larvae and two eating cocooned larvae. In contrast, after 24 h, *P. melanarius* adults ate significantly ($\chi^2 = 5.65$, $df = 1$, $p = 0.017$) more cocooned larvae ($100.00 \pm 0.00\%$) than free larvae ($90.00 \pm 5.37\%$) (Fig. 2b). All *P. melanarius* adults consumed at least one prey within 24 h.

Choice test

When given the choice between free larvae and cocooned larvae of *R. maxima* as prey (Fig. 3), *P. melanarius* adults consumed both stages but ate significantly more free larvae ($78.00 \pm 7.57\%$) than cocooned larvae ($34.00 \pm 13.35\%$) after one hour (Wilcoxon signed rank test, $W = 40$, $p = 0.043$). Ten *P. melanarius* adults were used in the test, and all of them consumed free larvae, while only six ate cocooned larvae during the first hour. After 24 h, there was no significant difference in consumption between free larvae ($98.00 \pm 2.00\%$) and cocooned larvae ($70.00 \pm 13.08\%$) (Wilcoxon signed rank test, $W = 15$, $p = 0.058$). However, after 24 h, all *P. melanarius* adults consumed free larvae, and only eight of

them consumed cocooned larvae, with the data indicating a trend towards a higher consumption of free larvae.

Soil test

Pterostichus melanarius adults consumed both life stages (i.e., free larvae and cocooned pupae) of *R. maxima* within 24 h in all the treatments tested (Fig. 4). Our results showed a significant difference in consumption among treatments ($\chi^2 = 118.91$, $df = 4$, $p < 0.001$). The highest consumption occurred for free larvae without soil ($56.00 \pm 7.20\%$). The second highest consumption occurred for cocooned pupae without soil ($21.00 \pm 8.27\%$), but this did not significantly differ from the consumption of cocooned pupae on the soil surface ($7.00 \pm 2.19\%$) or free larvae with soil ($7.00 \pm 2.63\%$). The lowest consumption occurred for cocooned pupae placed 1 cm deep in the soil ($2.00 \pm 1.38\%$), but this did not differ from the consumption of cocooned pupae on the soil surface or larvae with soil. The majority of the free larvae used as prey burrowed in the soil and formed cocoons during the 24 h duration of the experiment.

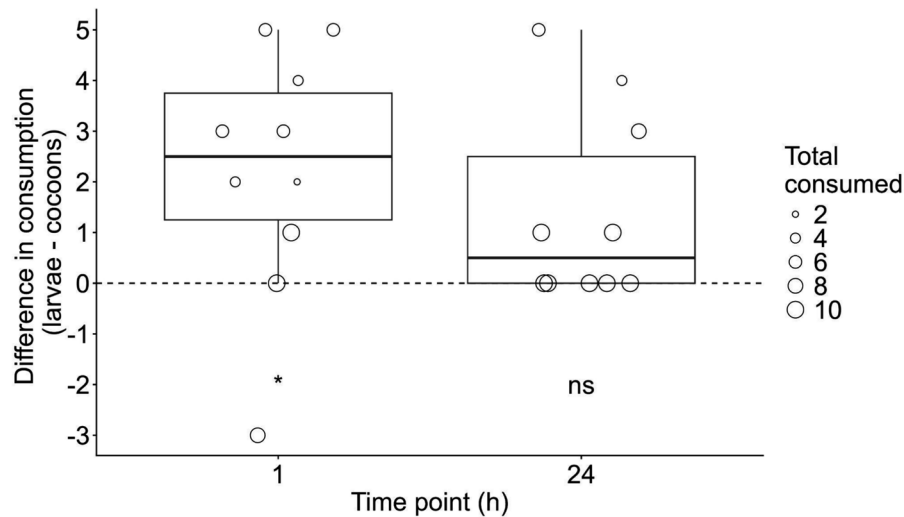


Fig. 3 Consumption of *Resseliella maxima* free larvae (“larvae”) and cocooned larvae (“cocoons”) by *Pterostichus melanarius* adults in a choice test at 1 h and 24 h. Boxplots show the median (horizontal line), interquartile range (box), and minimum and maximum values (whiskers). “ns” indicates a non-significant difference ($p > 0.05$), while an asterisk (*) indicates a significant difference ($p < 0.05$) when compar-

ing the mean difference in consumption to zero within each assessment time (1 h and 24 h). Values above zero indicate that beetles consumed more larvae, values below zero indicate that more cocoons were consumed, and zero indicates no preference. The size of each point represents the total number of prey consumed by each beetle

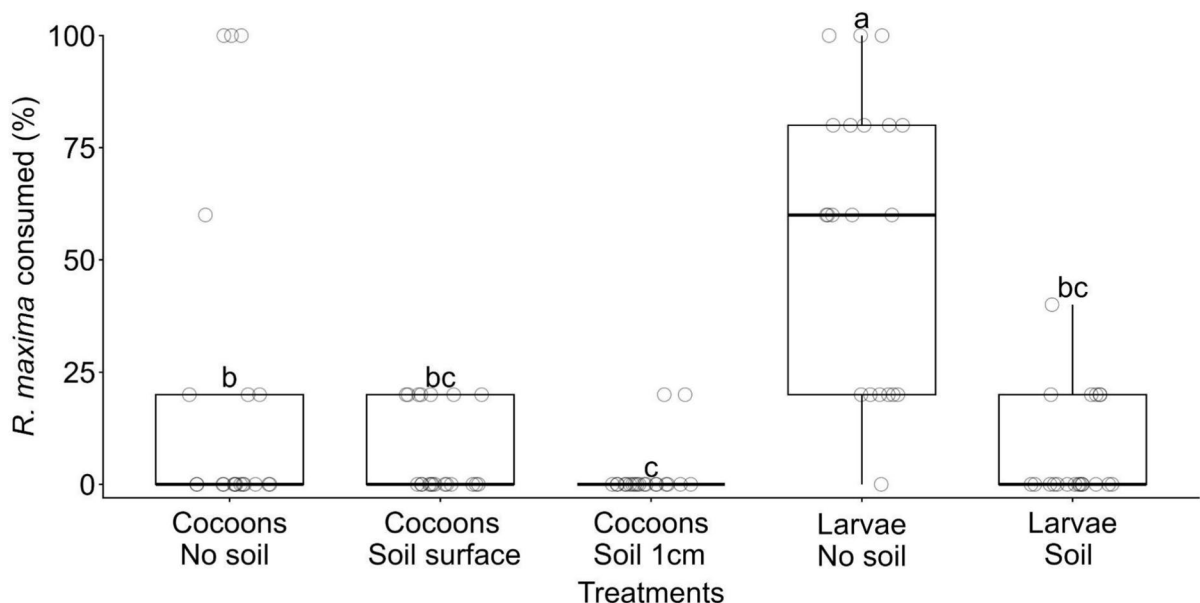


Fig. 4 Percentage of *Resseliella maxima* free larvae (“larvae”) and cocooned pupae (“cocoons”) consumed by *Pterostichus melanarius* adults with or without soil, and either on the soil surface or buried. Consumption was recorded after 24 h. Box-

plots show the median (horizontal line), interquartile range (box), and minimum and maximum values (whiskers). Different lowercase letters indicate significant differences among treatments ($p < 0.05$)

Discussion

Biological control is an important method in integrated pest management that utilizes natural enemies to control pest populations (van den Bosch et al. 1982; Waage and Greathead 1998). This method can be valuable in managing pests like *R. maxima*, where other effective practical methods for controlling the pest are limited. This study explored the potential of *P. melanarius* adults as a biological control agent for *R. maxima* by assessing their ability to prey on multiple life stages of the pest.

Previously, predation of *R. maxima* larvae by *P. melanarius* adults was examined (Melotto et al. 2023c; von Gries et al. 2025b), but it was unclear if they consumed other stages such as cocooned larvae or cocooned pupae. The results presented here confirm that *P. melanarius* adults can indeed prey on larval and cocooned stages (both larvae and pupae) of *R. maxima*, indicating a broader predatory scope. This finding aligns with the known behavior of the genus *Pterostichus*, which seems capable of consuming any prey of a size they could ingest (Hengeved 1980). The consumption of cocooned insects by *Pterostichus* spp. was previously observed by Epstein et al. (2001), where both *P. melanarius* and *Pterostichus adstrictus* E. fed on cocooned larvae of *Cydia pomonella* L. (Lepidoptera: Tortricidae).

While *P. melanarius* is capable of consuming cocooned prey, several factors may influence the likelihood and efficiency of predation. The ability of a generalist predator to attack its prey depends on multiple factors, including its capacity to detect and access the prey, and how easily the prey can be consumed (Guershon and Gerling 1999; Eubanks and Denno 2000; Desneux and O'Neil 2008). Cocoons often serve to protect larvae or pupae from predatory attacks (Censier et al. 2014). The lower consumption of cocooned larvae compared to free larvae of *R. maxima* suggests that cocoons may reduce prey accessibility or detectability. This likely explains why a significantly higher number of free larvae were consumed during the first hour in the no-choice test where beetles were offered only one prey type.

However, the significantly higher consumption of cocooned larvae after 24 h in the no-choice test may be related to learning abilities of insects (Allaway 1972; Dukas 2008; Giurfa 2015). Reznikova and Dorosheva (2013) described catalog learning in

carabids, where beetles optimize existing behaviors based on past successes. In addition, Plotkin (1979) demonstrated that *P. melanarius* uses odor cues to guide their behavior, associating specific scents with prey or resources. Similarly, if larvae or pupae of *R. maxima* emit olfactory cues, it is possible that adults of *P. melanarius* could learn to associate these signals with the prey, increasing consumption of cocooned prey over time. Furthermore, in the context of cocoons, *P. melanarius* might initially engage in various exploratory behaviors and, upon success (i.e., breaking a cocoon and finding prey), select and repeat the successful pattern more consistently over time.

In the choice test, when both stages of *R. maxima* were offered to the *P. melanarius* adults simultaneously, there was greater consumption of free larvae at both 1 and 24 h. However, the difference was not statistically significant at 24 h. In a previous food preference study, *Pterostichus globosus* F. tended to select prey items that offered higher energy intake relative to the handling time required (Dinis et al. 2016). Thus, comparing the time and effort required for *P. melanarius* to find and open a cocoon with the time needed to locate and consume free larvae, feeding on the larvae appears to be more cost-efficient which may explain why *P. melanarius* initially exhibited a preference for consuming the free larvae over the cocooned *R. maxima*.

For the soil test, *P. melanarius* consumed significantly more free larvae without soil compared to cocooned pupae without soil. When soil was present, the consumption rates were lower when compared with the treatments without soil, which suggests that *P. melanarius* could have difficulty locating or handling *R. maxima* when they are in contact with soil, even when the prey is on the soil surface. Lee and Edwards (2012) observed that carabid beetles, including *P. melanarius*, showed reduced predation when prey were buried at depths of 1.3 or 5 cm, or when the prey had burrowed into the soil of potted strawberry plants. Similarly, Kulkarni et al. (2015) demonstrated that *P. melanarius* consumed a higher number of weed seeds located on or close to the soil surface (0.5 cm deep) as compared to those located farther below the surface. These findings highlight how studies conducted without any soil or other substrate might overestimate a predator's potential for biological control. Therefore, the finding that *P. melanarius*

adults can locate and consume cocooned *R. maxima* buried in soil, even at a low rate, is important, especially considering that the cocoon provides an additional layer of protection for the prey.

Although laboratory experiments do not fully replicate field conditions, the findings of this study indicate that predation by *P. melanarius* may occur on the soil surface, and, to a lesser extent, even after the larvae enter the soil and form a cocoon. Renkema et al. (2012) showed that ground predators, including *P. melanarius*, contributed to mortality of blueberry maggot, *Rhagoletis mendax* Curran (Diptera: Tephritidae), a pest of similar size to *R. maxima*, on bare soil in a blueberry (*Vaccinium corymbosum* L.; Ericales: Ericaceae) field. A previous study observed *P. melanarius* feeding on wandering *C. pomonella* larvae searching for pupation sites in an apple (*Malus domestica* Borkh; Rosales: Rosaceae) orchard in England (Glen and Milsom 1978). In the field, *R. maxima* larvae leave the plants once they reach maturity to pupate in the soil (McMechan et al. 2021b). This is likely an important moment where *P. melanarius* could consume *R. maxima* larvae, but *R. maxima* larval behavior after leaving the plant to pupate is still not well known. Based on the results of this study, if larvae burrow rapidly into the soil, they may potentially evade predation by *P. melanarius* adults. However, it remains unknown whether *P. melanarius* larvae prey on *R. maxima* larvae or cocoons in the soil.

When comparing the results of the no-choice test to those of the soil test treatments without soil, we observed higher levels of prey consumption in the no-choice test (100% of cocooned larvae and 90% of free larvae consumed) compared to the soil test (21% of cocooned pupae and 56% of free larvae consumed), despite these treatments being similar. This difference in consumption, whether for cocooned prey or free larvae, could be explained by potential prior exposure of the predators to the prey. For the no-choice test, *P. melanarius* adults were collected later in the 2023 season (July and August), while, for the soil test, they were collected earlier in the 2024 season (early June). It is possible that *P. melanarius* adults used in the no-choice test had prior (and/or greater) exposure to *R. maxima* in the field before collection. Furthermore, the cocoons contained different life stages in the two experiments. In the no-choice test, cocooned larvae were used, whereas cocooned pupae were used in the soil test. Behavioral variation or differences in

predatory cues can occur due to different life stages of prey (Pote and Nielsen 2017), which may have influenced predation outcomes in the cocooned prey treatments across the two tests. Although the slightly higher temperature during the soil test could have influenced predation rates, beetle collection dates and the developmental stage of the prey likely had a stronger effect.

The ability of *P. melanarius* to prey on *R. maxima* cocooned larvae and pupae is a significant finding, as the cocoon stage remains exposed outside the plant and in the soil for an extended period of time, making it a potential target for biological control. However, further studies are needed to assess the duration of exposure for each *R. maxima* stage and the likelihood of *P. melanarius* adults preying on them in a more natural setting.

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Declarations

Conflict of interests The authors have no competing interests to declare that are relevant to the content of this article.

Ethical approval This work does not contain any studies with human participants or animals (vertebrates).

Consent for publication All authors gave consent to the publication of this work.

Informed consent Informed consent was not applicable to this work.

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