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Aphid honeydew in intraguild interactions: enhancing predator mobility, foraging, and dynamics between *Adalia bipunctata* and *Episyrphus balteatus*

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Abstract
Honeydew is a nutrient rich excretion of aphids. This substance also emits kairomones, serving as a signal that attracts aphid predators and thereby influences the interaction among plants, aphids, and other predators. The overall aim of this study was to investigate the role of honeydew from two aphids species, *Aphis fabae* Scopoli, 1763 and *Acyrthosiphon pisum* (Harris 1776) in the predatory behavior of *Adalia bipunctata* (Linnaeus 1758) and *Episyrphus balteatus* (De Geer 1776). Specifically, we aimed to (1) evaluate the impact of honeydew on *A. bipunctata* and (2) *E. balteatus* and on intraguild interactions (IGI) among them. Our results showed that the presence of honeydew enhanced the mobility of predators by stimulating foraging behavior. In addition, the number of aphids consumed was significantly higher in the presence of honeydew. Interestingly, the predators were more attracted to *A. fabae* in the presence of *A. pisum* honeydew. These findings highlight the key role of honeydew in intraguild relationships, altering the prey's perception from being less preferred to becoming more appealing to predators, akin to their favored prey. These results provide interesting perspectives to improve aphid biological control.

Keywords Aphidophagous · Biological control · Honeydew · Intraguild interaction · Foraging · Predator mobility

Introduction

Aphids (Hemiptera: Aphididae) are agro-economically important pests globally (Blackman and Eastop 2017). They cause direct damage as phloem feeders and indirect by transmitting phytoviruses and producing honeydew, a substance known to hinder photosynthetic activity and negatively impact crop quality (Dedryver et al. 2010). In aphid control, using sustainable methods like biological control helps to deal with the environmental risks and resistances that are associated with reliance on pesticides (Hart et al. 2003; Barratt et al. 2018). Many studies have investigated how to improve biological control services by manipulating external factors such as the habitat, host plants, and natural enemies (Bischoff et al. 2023; Donner et al. 2023; Nikolova 2024).

Natural enemies such as predators are generalist species—targeting a wide host range—making them having a great potential as biological control agents against insect pests than the specialist ones like parasitoids which exhibit a narrow host range (Snyder and Ives 2003; Stiling and Cornelissen 2005). Moreover, when generalist predators occupy different spatio-temporal feeding niches, they are likely to support each other (Taylor and Snyder 2021). Although the aphid population growth initially declined, the control exerted by generalist predators might result in a continued increase in aphid population. If properly managed, they can complement the effects of specialist predators (Snyder and Ives 2003). However, parasitoids, still dominate about 80% of biocontrol programs due to their lower food requirement and ability to maintain balance at lower host densities (Singh and Singh 2016). To enhance the use of predators as generalist biological control actors, the use of "ecological engineering" as suggested by Snyder (2019) is one of the disciplines that can promote their use in applied biological control practice.

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Understanding the dynamics within these natural enemies is crucial since species and particularly generalist species may engage in various competitive interactions, such as cannibalism, hyperpredation or intraguild predation (IGP) (Rasekh and Osawa 2020; Wang et al. 2022; Labrie et al. 2023). These competitive interactions can jeopardize biological control, especially at small spatio-temporal scales, where alternative prey may divert generalists' attacks away from target pests (Snyder 2019). However, Kindlmann and Dixon (2003) demonstrated a significant decrease in aphid abundance related to IGP between hoverflies and ladybirds due to a complementary selection of oviposition sites. Moreover, predators avoided aphid colonies already exploited by their IGP competitor or those with limited larvae's development (Hemptinne et al. 1993).

While this is not the most frequent impact of IGP, some findings raised many questions about the effectiveness of predators in controlling aphids when predators had to interact and compete for same resources (Chailleux et al. 2017; Zarei et al. 2020; Dib et al. 2020). Both biotic and abiotic ecological factors influence the direction, symmetry, and intensity of cannibalism and IGP among generalists species, including those that prey on aphids (Cabrera et al. 2022; Wang et al. 2022; Labrie et al. 2023). Despite this, no information is available regarding the role of aphid honeydew in intraguild interactions (IGI)—where predation is not a necessary outcome—between aphidophagous predators.

Previous studies report that hoverflies and ladybirds larvae coexist on the same aphid-infested plants. When prey becomes scarce, their close proximity promote their interaction (Agarwala and Yasuda 2001). Various factors such as the predator mobility can influences IGI, but in most cases of IGP, the direction is determined by the relative size of opponents, with larger individuals attacking smaller ones (Lucas 2012). In this relationship, the predators do not exhibit the same foraging behavior. Ladybird larvae have an active-searching feeding strategy, looking mostly for immobile aphid prey (Lucas 2005) while hoverfly larvae have low predation rates on immobile prey (Hindayana et al. 2001). Beyond these factors, the relative stages of the predators and the timing of establishment during the season can also impact the outcome of IGI (Rasmussen et al. 2014; Labrie et al. 2023).

Moreover, aphid honeydew is naturally present in areas colonized by ladybirds and hoverflies and is recognized as a kairomone (Leroy et al. 2014; Liu et al. 2023) and as an alternative food source (van Neerbos et al. 2020; Luquet et al. 2021). However, little is known about its role in determining specific factors in IGI, such as mobility and foraging strategy. In the present study, we underline the potential of aphid honeydew on the individual and relative behavior of two aphidophagous larvae, namely the hoverfly *Episyrphus balteatus* (DeGeer 1776) and the ladybird *Adalia bipunctata* (Linnaeus 1758). We hypothesized that (1) honeydew is an indicator of aphids as prey, thereby leading to increased predator efficiency (mobility and consumption) and that (2) the increased mobility could also lead to more frequent encounters between predators, potentially resulting in increased IGI which may escalate into IGP. Therefore, we investigated whether the presence of honeydew would impact the predation behavior including the IGI of the two aphidophagous larvae, the hoverfly *E. balteatus* and the ladybird *A. bipunctata*. To comprehensively investigate the predation behavior of these predators, we conducted two primary experiments including the (1) evaluation of the impact of honeydew on predators and (2) assessment of the influence of honeydew on IGI between these two predators.

Materials and methods

Aphids rearing

Both aphid species, pea aphids *Acyrthosiphon pisum* and black bean aphids *Aphis fabae* were reared in a growth chamber at 21 ± 2 °C under 16-h light cycle on *Vicia faba* L. var. major plants, which were sown in 32 × 22 × 6 cm pots filled with universal soil (TERS50, La Plaine Chassart, Fleurus, Belgium).

Predators rearing

The two-spotted ladybird *A. bipunctata* (BioGrowi, Louvain, Belgique) and the marmalade hoverfly *E. balteatus* (maintained for years at Functional and Evolutionary Entomology, Gembloux Agro-Bio Tech) were reared in a growth chamber at 22 ± 2 °C under 16-h light cycle.

Organically produced pollen grains (Bee Care, Nectar & Co, Fernelmont, Belgium) were crushed and mixed with sugar (Tirlemont, Raffinerie Tirlemontoise s.a., Belgium) to feed adult ladybirds. To this mix we have added wildflower honey (De Traay, Lelystad, Netherlands) to ensure the feeding of adult hoverflies. Before reproduction period, adult ladybirds and hoverflies were exclusively given pollen and honey for 15 days post-pupal stage. After this period, *A. pisum* aphids were introduced to the pollen diet for 4 days to initiate reproduction. Subsequently, a non-aphid diet was maintained until the next reproductive cycles.

For *A. bipunctata* larvae, a diet based on both pollen and aphids was provided to support overall development, survival, fecundity, and longevity, following Lundgren (2009). Concerning *E. balteatus*, the eggs' incubation and larval development were carried out on *V. faba* L. var. major infested with *A. pisum*, as described by Leroy et al. (2010).

Honeydew collection

Aluminum foil discs of 6 cm diameter were prepared and initially weighted to be used for honeydew collection based on protocols by Sabri et al. (2013) and Pringle et al. (2014). Plants of *V. faba* infested with either *A. pisum* or *A. fabae* were placed over 12 of those discs cut from aluminum foil (Fig. 1). By tilting the plants at an angle of over 60°, honeydew naturally accumulates on aluminum discs beneath, by gravity, while aphids feed on the plants; this setup is maintained for 24 h before collecting and reweighing each aluminum disc, aiming for an approximate amount of 4 mg ± 1 mg of honeydew. A honeydew-covered disc was then placed, unaltered, in the corresponding Petri dish arena for the experiment.

Experimental design

Arena tests were carried out to investigate the effect of honeydew from both aphid species (honeydew aluminum disks) on (1) the aphid predation, (2) the mobility of the predators, and (3) the IGI between both predators based on the work of Zarei et al. (2020) and Dib et al. (2020). The different tested arenas with the various aphids-predators associations were conducted in sterile plastic Petri dishes (9 cm of diameter).

For the following experiments, 168 larvae of each predator species were individually isolated and starved for 24 h prior to the experiment. Furthermore, to avoid influencing the direction of IGI, the experiments were performed with similar-sized predatory larvae (Lucas and Alomar 2001). A size of 7 mm ± 0.2 mm long was set in preliminary tests, matching the size of L3 stages for both predator larvae. Finally, a fresh leaf of *V. faba* was placed in each arena and these were installed in the controlled chamber set at a temperature of 23 ± 1 °C and a light photoperiod of 16 h. For each arena a total of 12 repetitions were performed.

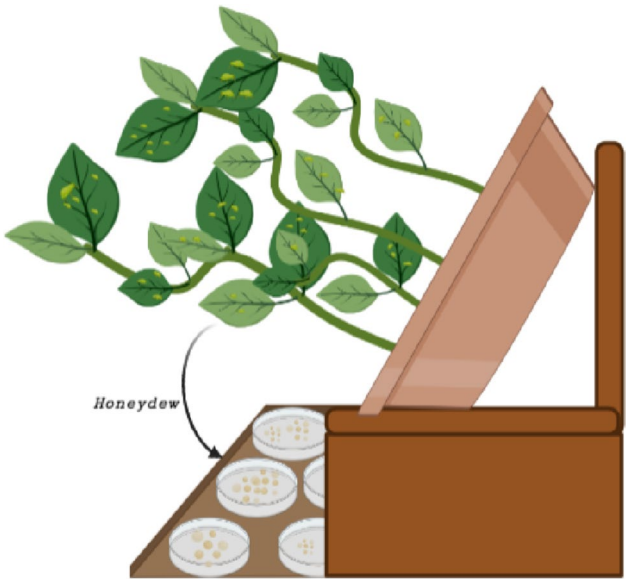

Fig. 1 Experimental setup for passive honeydew collection on aluminum foil

Aphid predation

Aphid consumption was determined by assessing the number of aphids consumed after 240 min in 12 arenas containing 50 aphids (*A. fabae*/*A. pisum*), honeydew (none/*A. fabae*/*A. pisum*), and predator larva alone or together (Fig. 2).

Predator larvae mobility

In this section we define mobility as the state of movement exhibited by the predator larva at a specific moment during the observation period. The predator mobility was described through binary responses as they were moving around (1) or at rest (0) after 15, 30, 45, 60, 90, 120, and 240 min. We individually recorded the mobility of each predator in

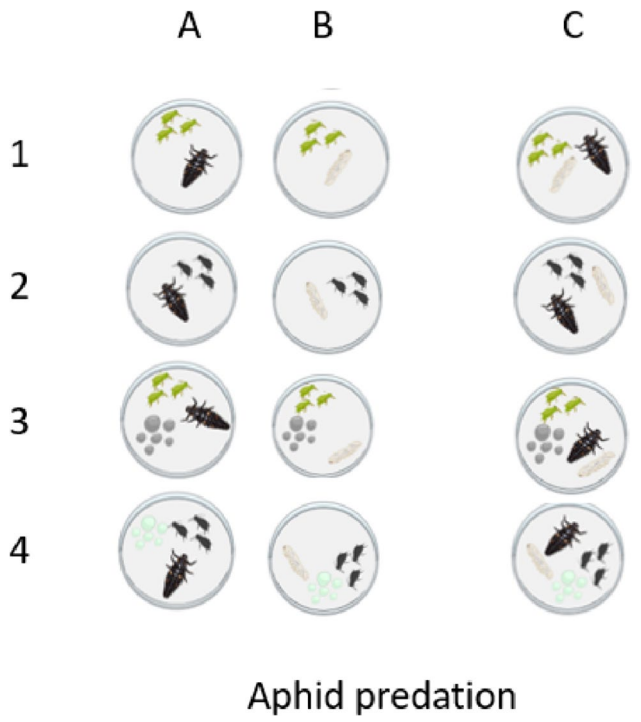

Fig. 2 Experimental arenas in which aphid predation was assessed. For aphids and honeydew, green color refers to *A. pisum* species and the black color to *A. fabae* species. Columns (A) and (B) correspond to arenas containing ladybird and hoverfly larvae, respectively. (C) Refers to arenas containing both predators' larvae. Lines (1) and (2) refer to arenas where predators larvae exclusively encounter aphids. Lines (3) and (4) correspond to arenas where predators larvae share space with one aphid species along with the honeydew from another aphid species

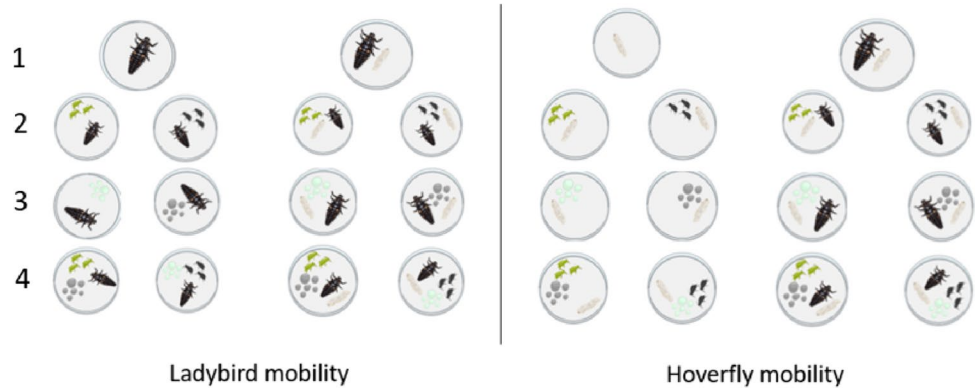

Fig. 3 Experimental arenas adopted to record predators mobility. For aphids and honeydew, green color refers to *A. pisum* and the black color to *A. fabae*. Line (1) refers to the control with only larvae in the arena. Line (2) presents arenas where predators larvae exclusively encounter aphids, while line (3) refers to arenas where predator coexists solely with aphid honeydew. Line (4) presents arenas where predators' larvae share space with one aphid species along with the honeydew from another aphid species

14 arenas (Fig. 3). These arenas present various combinations of aphid species (none/50 *A. fabae* aphids/50 *A. pisum* aphids), honeydew presence (none/*A. pisum* honeydew/*A. fabae* honeydew), and predator larvae (a single predator larva/both predator larvae).

IGI assessment

IGI events were characterized as binary responses as one predator is biting, attacking, or consuming the other one (1) or none of these behaviors is observed (0) and were recorded after 15, 30, 45, 60, 90, 120, 240 min. IGI were observed in seven arenas (Fig. 4) containing 50 aphids (none/50 *A. fabae* aphids/50 *A. pisum* aphids) with or without honeydew (none/*A. pisum* honeydew/*A. fabae* honeydew).

Statistical analysis

All statistical analyses were conducted using the statistical software R version 4.3.3. For the analysis of aphid predation (counting data), a Generalized Linear Mixed Model (GLMM) following Poisson distribution for the residuals was applied. This analysis considered the influence of aphid species, honeydew-producing aphid species, predators, and their interactions as fixed effects. To account for random variability, we included arenas and experimental days as random factors. Overdispersion in the GLMM was assessed using the DHARMA package. Analysis of deviance was conducted using a type II Wald Chi-squared test for GLMM-Poisson models, employing the *Anova* function from the CAR package. Pairwise comparisons for each combinations of aphid species/honeydew-producing aphid species/predators on the GLMMs were conducted using the *lsmeans* function from the EMMEANS package.

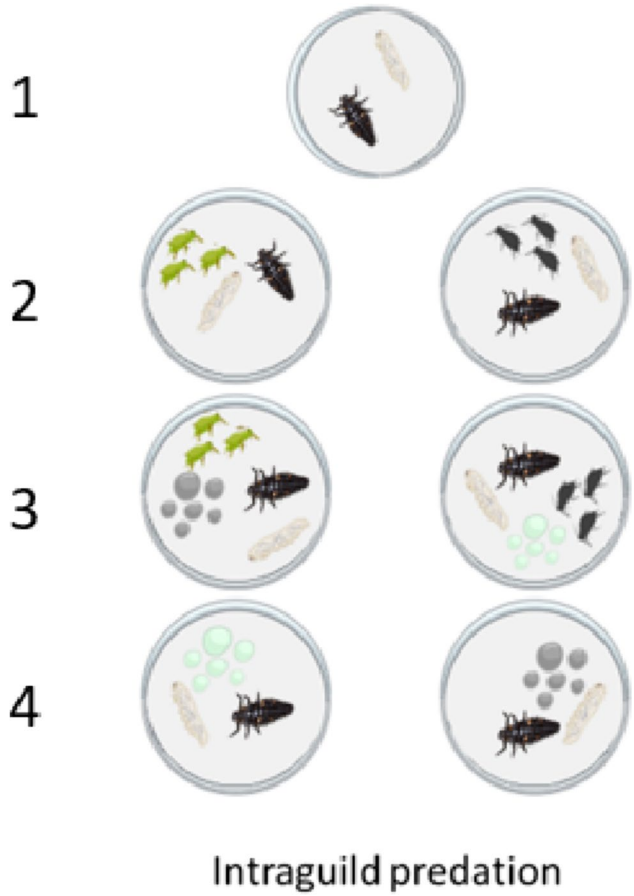

Fig. 4 Experimental arenas in which each intraguild predation events were observed. For aphids and honeydew, green color refers to *A. pisum* species and the black color to *A. fabae* species. The line (1) refers to the control with only both predator larvae in the arena. Line (2) refers to arenas where one larva from each predator coexists solely with aphids. Line (3) presents arenas where predators' larvae share space with one aphid species along with the honeydew from another aphid species. Line (4) concerns arenas where both predators' larvae coexists solely with honeydew from one aphid species

For the analysis of ladybirds' and hoverflies' mobility data (binomial events), separate GLMMs following binomial distribution of residuals were fitted. This analysis explored the effects of aphid species, honeydew-producing aphid species, predators, and their interactions as fixed effects. As with the aphid predation analysis, we included observation times, arenas, and experimental days as random factors. Analysis of deviance was performed using a type II Wald Chi-squared test for GLMM-Poisson models, employing the *Anova* function from the CAR package. Pairwise comparisons were conducted using the *lsmeans* function from the EMMEANS package.

To determine the variables influencing the IGP (binomial events), we formulated a GLMM following binomial distribution of residuals. This model incorporated aphid species, honeydew-producing aphid species, and their interaction as fixed factors, while also considering observation times, arenas, and experimental days as random factors.

Results

Aphid predation

When predator larvae are alone in the arena, aphid predation is significantly influenced by the aphid species ($\chi^2 = 6.24$, df = 1, p-value = 0.012), the species of the predator ($\chi^2 = 25.5$, df = 1, p-value < 0.001), and the interaction between the honeydew-producing aphid species and the predator ($\chi^2 = 12.93$, df = 2, p-value = 0.0015). When the predator larvae share the same arena, aphid predation is significantly influenced by both aphid species ($\chi^2 = 8.75$, df = 1, p-value < 0.001) and honeydew-producing from each aphid species ($\chi^2 = 8.86$, df = 2, p-value = 0.012).

In the absence of honeydew in the arena, aphid predators, whether alone or together, consume more *A. pisum* than *A. fabae* (Fig. 5). In the arenas where predator larvae coexist and where *A. pisum* honeydew is introduced to *A. fabae* aphids, the consumption of *A. fabae* aphids reaches a level similar to that observed when only *A. pisum* aphids are present. When the hoverfly larva is alone, we observe a similar rise in the consumption of aphids which was not the case when we are dealing only with ladybird larva. The addition of *A. fabae* honeydew to *A. pisum* aphids significantly impacts hoverfly larva aphid consumption in the absence of ladybird. Conversely, aphid consumption slightly decreases when the ladybird larva is alone with *A. fabae* honeydew and *A. pisum* aphids.

Predator larvae mobility

The mobility of the ladybird is highly significantly influenced by the aphid species ($\chi^2 = 12.89$, df = 2, p-value = 0.0049), the honeydew-aphid species related ($\chi^2 = 65.77$, df = 2, p-value < 0.001), the predators present in the arena ($\chi^2 = 97.94$, df = 1, p-value < 0.001), the time ($\chi^2 = 18.44$, df = 6, p-value = 0.0052), the interaction between aphids and predators ($\chi^2 = 10.62$, df = 2, p-value = 0.0049), and the interaction between honeydew and predators ($\chi^2 = 31.38$, df = 2, p-value > 0.001).

The highest mobility is observed when both predators are present in the arenas, and only honeydew is present without any aphids (Fig. 6). In the absence of honeydew, ladybird mobility is greater in the presence of *A. pisum* aphids compared to *A. fabae* aphids. Notably, the addition of honeydew to aphids leads to a significant increase in ladybird mobility but only when one hoverfly larva is present in the arena too.

For the hoverfly, the aphid species ($\chi^2 = 36.52$, df = 2, p-value > 0.001), the honeydew-producing aphid species ($\chi^2 = 69.79$, df = 2, p-value < 0.001), the predators present ($\chi^2 = 66.68$, df = 1, p-value < 0.001), and the interaction between honeydew and predators ($\chi^2 = 19.69$, df = 2, p-value < 0.001) exert a very highly significant influence on hoverfly mobility. According to the GLMM, both types of honeydew have a positive impact on hoverfly mobility.

Similar to ladybirds, the highest level of hoverfly mobility is observed when both predators are present in the arenas with honeydew and absence of aphids (Fig. 7). Additionally, the presence of *A. pisum* honeydew with *A. fabae* and the *A. fabae* honeydew with *A. pisum* significantly increase the hoverfly mobility in the arenas where one ladybird larva is present.

IGI assessment

The analysis of the GLMM for IGI did not reveal any significant influences from any of the examined factors. However, it's worth noting that no IGI were observed in two specific arena scenarios: one where *A. pisum* aphids were present without honeydew with both predators and the other where *A. fabae* aphids coexisted with *A. pisum* honeydew. Following some IGI, we observed IGP cases. Six ladybird larvae died out of 336 larvae. Two deaths occurred in arenas where predators were alone, while the remaining four deaths occurred in situations where the ladybird larvae were only in the presence of honeydew. In this case, the seldom dead predator larvae data are not sufficient to correlate with the presence of honeydew.

Discussion

Aphid honeydew was initially considered as a metabolic waste product until recent studies providing evidence of its complexity in terms of composition and potential role in multitrophic relationships (Nguyen et al. 2020; Tun et al.

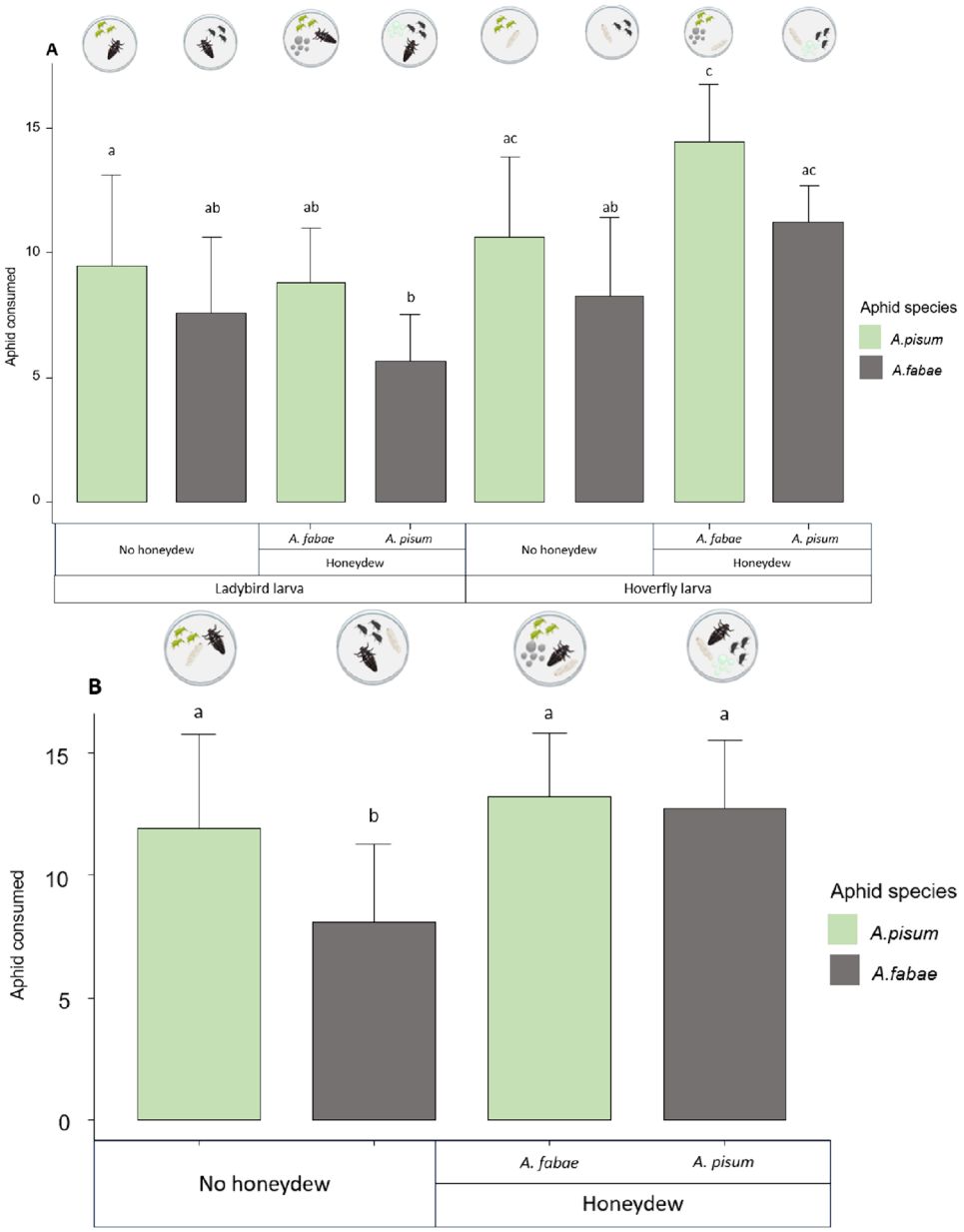

Fig. 5 Aphid predation by **A** predator larva alone and **B** predator larvae together. The predation is depicted both in the absence of honeydew and in the presence of honeydew sourced from two different aphid species (light gray to *A. fabae* and dark gray to *A. pisum*)

2020; Luquet et al. 2021). To gain a deeper understanding of honeydew's role in these complex interactions, we selected two aphid species *A. pisum*, which is typically favored by predators, and *A. fabae*, a prey often overlooked by predators but consumed when the primary prey, *A. pisum*, is scarce (Blackman 1965; Kalushkov 1998). These aphid species were studied in various trophic interaction scenarios. Although the experiments reported here were carried out only on two aphid species, our results provide new insights into the importance of this aphid excretion in multitrophic interactions.

Through our observation of mobility, we aimed to assess whether honeydew stimulates foraging behavior. Our analysis provides three main conclusions regarding mobility. Firstly, when a predator larva is alone in the arena, regardless the predator species, the presence or absence of honeydew did not result in a significant difference in mobility. This is not in accordance with Leroy et al. (2014) who demonstrated that *A. pisum* honeydew induces foraging behavior in both adults and larvae of the marmalade hoverfly. Secondly, when predator larvae coexist in the arena, both larvae demonstrate an increase in foraging behavior. Interestingly, ladybirds exhibited significantly increased mobility in the presence of the hoverfly larva in the arena, even without honeydew. This mobility was further enhanced in the presence of honeydew. Conversely, hoverfly larvae showed no difference in mobility when ladybird larva was present without honeydew. This suggests that honeydew is the key factor that increased

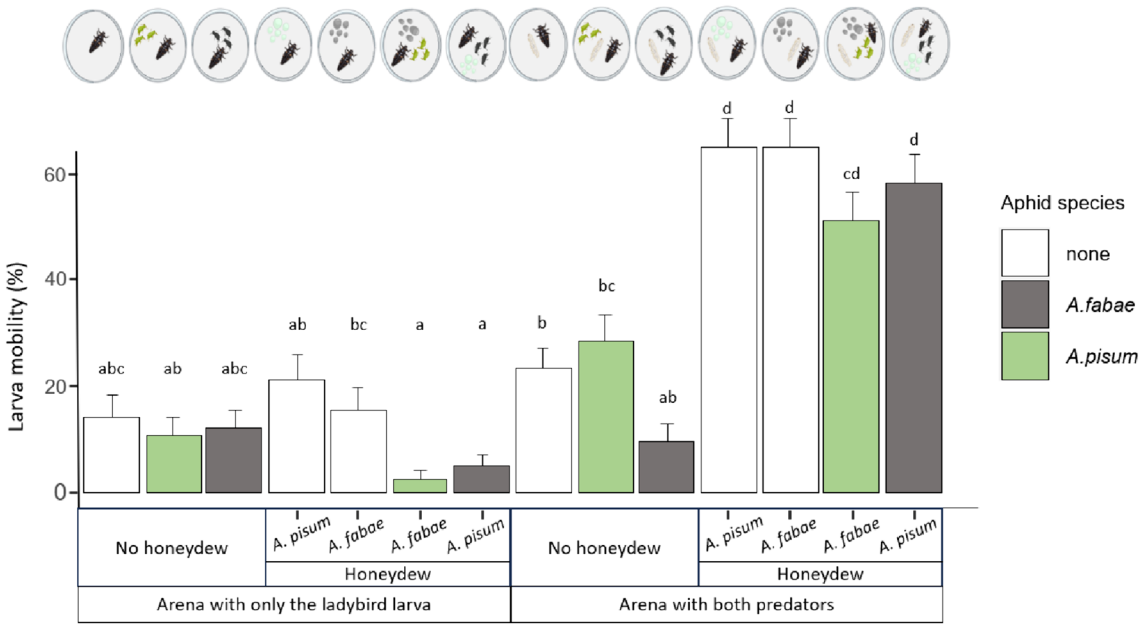

Fig. 6 Percentage of mobility of ladybird larvae. The first seven barplots present arenas containing only one ladybird larva, while the others seven show scenarios with both ladybird and hoverfly larvae. The colors in the barplots indicate the aphid species, and the letters correspond to different levels of significance (p-value < 0.05)

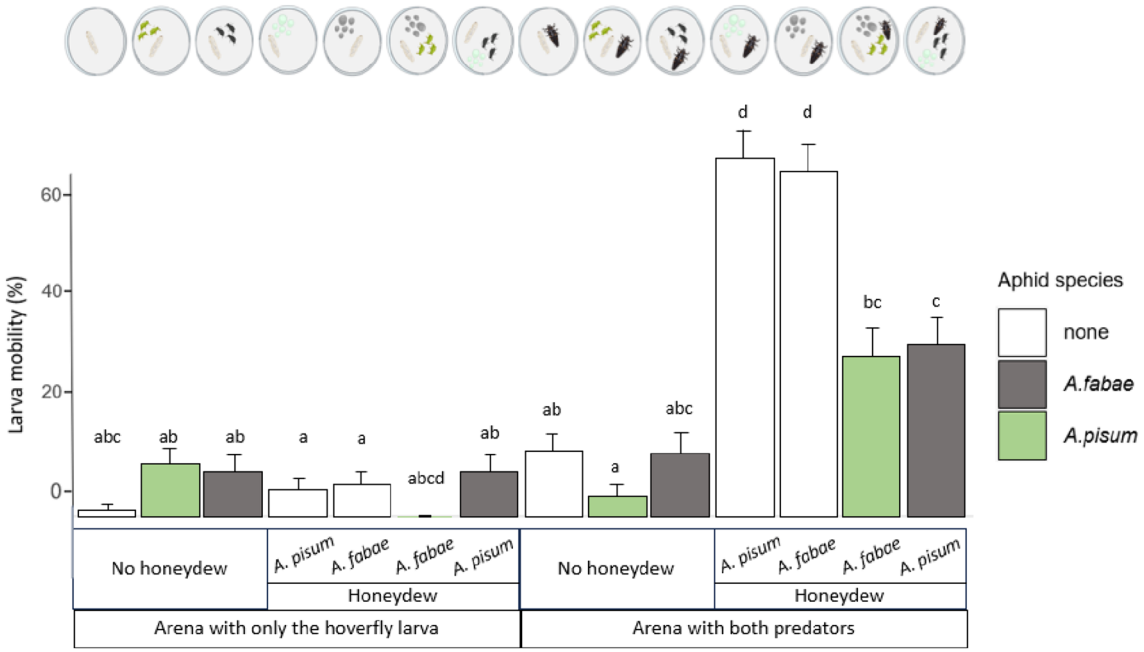

Fig. 7 Percentage of mobility of hoverfly larvae. The first seven barplots present arenas containing only one hoverfly larva, while the others seven show scenarios with both ladybird and hoverfly larvae. The colors in the barplots indicate the aphid species, and the letters correspond to different levels of significance (p-value < 0.05)

hoverfly larvae mobility. Thirdly, although both predators exhibited increased mobility in the presence of aphids and honeydew from another aphid, their responsiveness differed. Hoverfly larvae showed a significant increase in mobility regardless of the aphid species or honeydew-producing aphid species. Conversely, the difference in mobility for ladybirds was more pronounced when *A. pisum* honeydew was added to *A. fabae*. This suggests that *A. bipunctata* is

more stimulated by *A. pisum*, whereas *E. balteatus* showed no difference in behavior toward both honeydew-producing aphid species.

Regarding aphid consumption, when honeydew is absent, predators displayed a clear preference for *A. pisum*, given that *A. fabae* is recognized as a less desirable prey compared to *A. pisum*. Indeed, previous research has indicated that when offered as the sole prey, *A. fabae* leads to lower survival rates and extended development durations for the predators (Blackman 1967). Conversely, Hinkelman and Tenhumberg (2013) showed by using an artificial laboratory setting that *A. fabae* represented a lower nutritional intake for the ladybird *Hippodamia convergens*, but when given a choice, the ladybird preferred *A. fabae* rather than *A. pisum* (Hinkelman and Tenhumberg 2013). The same study suggested that the ease of grasping of *A. fabae* and the escape behavior adopted by *A. pisum* was an explanation for such preference. In our study, we used Petri dishes to perform the different bioassays. Such circular environment might alter the behavioral escape of *A. pisum*. Moreover, by omitting this behavior, the chance to be selected by predators would be equal and therefore the preference of both predators toward both prey will be directly assessed. This selection can also be biased by the specialization of predator larvae fed from their first larval stage with *A. pisum*. Indeed, it was found that specialization on one aphid species has led to poorer performance on another aphid species (Rana et al. 2002).

The experiments also showed higher consumption of aphids from both predators (once sharing the same arena) when they were with honeydew from another species. Previous studies reported that alternative prey generally increased predation of aphids for two generalist predators (Krey et al. 2021). In addition, the aphid consumption was even better when *A. fabae* aphids were in presence of *A. pisum* honeydew. This might be explained by the composition of *A. pisum* honeydew that reflects the nutritional suitability of this aphid species. It would be interesting to determine the specific compounds of each honeydew-producing aphid species and highlight their respective roles in biological control. On the other hand, when the predators are alone, the addition of *A. pisum* honeydew slightly increased hoverfly larva consumption but significantly reduced ladybird larva consumption.

By positively affecting predator's mobility and prey consumption, honeydew would have an impact on their fitness. This observation was also previously reported in Leroy et al. (2014) when ladybird oviposition was more stimulated in presence of both honeydew and aphids. Moreover, Evans and Richards (1997) demonstrated that the application of honeydew in the presence of aphids reduced the dispersion of *Coccinella septempunctata* (Linneaus 1758). Indeed, honeydew is an efficient prey-associated cue for *E. balteatus* as it is for some ladybird species, such as *A. bipunctata*, *H. convergens* (Guérin-Méneville 1842) and *C. septempunctata*.

In this study, we were unable to demonstrate that the presence of honeydew directly influences IGI and, consequently, IGP. Although the consumption and the mobility of larvae are influenced by the presence of honeydew, we did not observe a direct effect on interactions between predator larvae. Based on our findings, it would be interesting to investigate more on honeydew non-volatile compounds in correlation with aphid species and the observed predators' behavior.

Conclusion

In this study, we highlighted the role of honeydew in stimulating the foraging behavior of aphid predators, including the acceptance of a less preferred prey and acting as an alternative food source. Whatever the aphid species, honeydew acted as an active foraging cue. Moreover, we underscored the specificity of aphid honeydew and its differential impact on predator species. Whether acting upon ladybird or hoverfly larvae, and whether derived from *A. pisum* or *A. fabae*, honeydew elicited distinct responses, reporting the complex interaction between aphids and their predators. This highlights the importance of considering aphid honeydew as a key mediator of multitrophic interactions, offering promising avenues for practical applications in pest management. Based on predator–prey relationships it is, therefore, of great interest to dig into the chemical composition of honeydew and its specific effects on predators' behavior opens avenues for targeted interventions in agricultural systems.

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Data availability Not applicable.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article in any aspect, including financial and non-financial issues.

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