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ORIGINAL ARTICLE

Larval development and voracity of *Eupeodes americanus* (Diptera: Syrphidae): comparison of the focal prey *Aphis gossypii* (Hemiptera: Aphididae) and the banker prey *Rhopalosiphum padi* (Hemiptera: Aphididae)

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Abstract Unlike European species, the potential of Nearctic syrphids as biological control agents is still poorly studied. However, the American hoverfly, *Eupeodes americanus* (Wiedemann), has recently demonstrated promising traits as a biocontrol agent, notably against the foxglove aphid, *Aulacorthum solani* Kaltenbach, on pepper. The present study aims to extend our knowledge of the American hoverfly by evaluating its potential as a biocontrol agent in a banker plant system against the melon aphid, *Aphis gossypii* Glover, in a greenhouse cucumber crop. The preimaginal development and voracity of *E. americanus* were compared when preying upon the focal prey/pest (*A. gossypii*) or the banker prey (bird cherry-oat aphid, *Rhopalosiphum padi* L.) by daily observations of larvae from egg to adult. Preimaginal development time, survival rate, and occurrence of deformation were similar on both prey species. The weight of third instar and pupae, however, was higher for larvae that fed on the banker prey. The *ad libitum* voracity of the syrphid larvae was generally very high and did not significantly differ between prey species, except for the third-instar larvae which consumed more focal prey. Results suggest that a banker plant system involving the bird cherry-oat aphid may be a promising tactic for utilizing *E. americanus* for melon aphid biocontrol.

Key words american hoverfly; banker plant system; biological control; bird cherry-oat aphid; greenhouse cucumber; melon aphid

Introduction

Infestations by the melon aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae), in cucumber greenhouses are a major problem in organic and conventional crops (Capinera, 2000; Prado *et al*., 2015; Messelink *et al*., 2020). This pest has a high growth rate on cucurbits and is a vector for many phytopathogens (Capinera, 2000; Messelink *et al*., 2020). Chemical control is rarely effective because the pest rapidly develops resistance to pesticides and the products may not reach individuals feeding within protected plant structures (Capinera, 2000). To control the melon aphid in organic crops, most Canadian growers use a combination of the parasitoid wasps *Aphidius colemani* Viereck (Hymenoptera: Braconidae) or *Aphidius matricariae* Haliday (Hymenoptera: Braconidae) and the predatory midge, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae)

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(Messelink *et al*., 2020). There are issues utilizing these species, however, as the parasitoid wasps can be hyperparasitized (Vacante & Kreiter, 2018) and the midges can be victims of intraguild predation (Messelink *et al*., 2020) in mid-summer. Thus, to control this pest, particularly in cucurbit crops, it is imperative to find new agents to complement existing ones.

The American hoverfly, *Eupeodes americanus* (Wiedemann) (Diptera: Syrphidae), a Nearctic species with a generalist aphidophagous larval stage and a pollinating adult stage (Rojo *et al*., 2003; Skevington *et al*., 2019), is a candidate for controlling the melon aphid in North American cucurbit crops. Predatory species in the Syrphidae family generally exhibit characteristics that predispose individuals to be successful biocontrol agents, including high voracity, ability to function at low temperatures, good flight ability, rapid finding of aphid colonies, and high voracity and fecundity (Almohamad *et al*., 2009; Pekas *et al*., 2020; Rodríguez-Gasol *et al*., 2020; Bellefeuille *et al*., 2021; Van Oystaeyen *et al*., 2022). Notably, the American hoverfly has demonstrated good potential as a biocontrol agent against the foxglove aphid, *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae) (Bellefeuille *et al*., 2019, 2021).

An important limitation for the successful control of aphids, which have high population growth rates, is the delay in the action of the natural enemies (Fischer & Leger, 1997; Miller & Rebek, 2018). Even when aphid colonies are discovered early, the delay of introduction and action of biological control agents frequently allows pest population to surpass the economic threshold of damage (Fischer & Leger, 1997). The use of a banker plant system can reduce this delay by ensuring the enduring presence of biocontrol agents in the crop prior to the arrival of the pests, thus improving their effectiveness (Huang *et al*., 2011). The system utilizes noncrop plants placed near or within a target crop, providing biocontrol agents with alternative resources such as food (often prey that does not feed on the crop) or a more suitable environment for their reproduction and population growth (Frank, 2010; Huang *et al*., 2011; Miller & Rebek, 2018; Yano, 2019).

The success of a banker plant system is determined by an array of different factors, including compatibility of the system with the greenhouse environment and with the other biological control methods used by growers. One of the key points is the oviposition preference of the natural enemy for the focal versus the banker plant/banker prey systems. As proven by Gonzalez *et al*. (2023), the American hoverfly has a strong preference for the melon aphid on cucumber when given the choice between that crop and a banker plant of finger millet, *Eleusine coracana* Gaert (Poaceae), with the bird cherry-oat aphid, *Rhopalosiphum padi* L. (Hemiptera: Aphididae). The oviposition preference of the American hoverfly should therefore not inhibit pest control. The second point of concern is regarding the respective nutritional values of the banker prey and the focal prey (Sadeghi & Gilbert, 2000). If the focal prey is of lower nutritional quality than the banker prey for the development of the biocontrol agent, its arrival in the focal crop can both lower the predator's population growth and potentially shift its egg-laying preference toward other prey. To facilitate successful biological control, a banker prey should allow rapid development of the predator (for population growth) and generate heavy individuals (since it is generally linked to fecundity), as well as a balanced sex ratio (for reproduction) and low deformation and mortality rates (as an indicator of individual fitness and long-term population growth) (Coppel & Mertins, 1977; Tenhumberg, 1995; van Lenteren & Manzaroli, 1999; Almohamad *et al*., 2009). The voracity of a predatory biological control agent is also directly related to its predation rate, which needs to be high for the control of fast-growing pests like the melon aphid (Coppel & Mertins, 1977; Dunn *et al*., 2020). Both development and voracity must ensure that the quantity of prey consumed by the biocontrol agent population exceeds the population growth of the pest (van Lenteren & Manzaroli, 1999).

Several studies have shown that the aphid species consumed by a predator can have an impact on its growth, development, and survival in the case of generalist predators such as lacewings (Neuroptera) (Liu & Chen, 2001) and ladybirds (Coleoptera: Coccinellidae) (Hauge *et al*., 1998; El-Serafi *et al*., 2000; Omkar & Srivastava, 2003; Soares *et al*., 2005; Hodek & Evans, 2012; Sebastião *et al*., 2015; Rosagro *et al*., 2020). This also appears to be true for some hoverfly (Diptera: Syrphidae) species such as *Eupeodes corollae* (Fabricius), *Episyrphus balteatus* (De Geer), and *Heringia calcarata* (Loew) (Rüzička, 1975; Short & Berg, 2004; Putra & Yasuda, 2006; Rosagro *et al*., 2020; Jiang *et al*., 2022). In some cases, certain aphid species can be considered unsuitable for the development of the hoverfly. For instance, Rüzička *et al*. (1975) and Jiang *et al*. (2022) showed that the majority (or close) of *E. corollae* larvae died when fed with *Aphis sambuci* L. or *Megoura crassicauda* Mordvilko, respectively. The voracity of a biocontrol agent also differs between prey species (Short & Berg, 2004; Putra & Yasuda, 2006; Rodríguez-Gasol *et al*., 2020). For example, *E. balteatus* has a higher predation rate on *Microlophium carnosum* Buckton (Hemiptera: Aphididae) compared to *Acyrthosiphon*

pisum Harris (Hemiptera: Aphididae) and *Sitobion avenae* Fabricius (Hemiptera: Aphididae) (Alhmedi *et al*., 2008).

The aim of the present study was to determine if the American hoverfly can be a suitable biological control agent for the melon aphid if used in a banker plant system. More specifically, the first objective was to assess if the focal prey (melon aphid = pest) was as adequate as the banker prey (bird cherry-oat aphid = rearing prey) for the development of the American hoverfly. The second objective was to determine if the voracity of the hoverfly was as high when feeding on the focal prey than on the banker prey. For both objectives, the banker prey was considered as the reference prey since it is the rearing prey of the syrphid since 2014 and because syrphid larvae demonstrated a high voracity on this aphid. Anecdotal observations in the field showed that bird cherry-oat aphids on barley banker plants had been almost completely consumed in 1–2 weeks by 10 American hoverfly larvae (Fournier M, pers. comm.). Furthermore, the bird cherry-oat aphid is often used in banker plants and is suitable for an array of biocontrol agents, including other syrphid species (Pineda & Marcos-García, 2008; Huang *et al*., 2011).

We predicted that (1) since the hoverfly is a generalist aphidophagous species, both focal and banker prey will allow the predator to complete its development; (2) since the banker prey is also the rearing prey and has proven to be high-quality food for the predator, the development will be optimal when larvae are fed on the banker prey; and (3) the voracity of the predator will be superior on the banker prey.

Materials and methods

Plant material and insect rearing

Plants were grown in greenhouses located at the University of Quebec in Montreal (UQAM), under the following conditions: 23 °C average temperature, 16 L : 8 D photoperiod with natural and artificial light (high-pressure sodium), and 50% R.H. Barley, *Hordeum vulgare* L. (Poaceae), seeds were sown directly into 13 × 13 × 15 cm pots at a density of approximately 50 seeds per pot. The broad bean, *Vicia faba* L. (Fabaceae) was sown by groups of two seeds in 8 × 8 × 10 cm pots. Cucumber, *Cucumis sativus* L. (Cucurbitaceae), was sown in seed trays and transplanted individually after approximately 2 weeks in 13 × 13 × 15 cm or 8 × 8 × 10 cm pots. Plants were watered two to three times a week and fertilized with water-soluble fertilizer (N-P-K, 20-20-20) once a week.

Insect rearing was done at the UQAM Biological Control Laboratory. Melon aphids (focal prey) were reared on cucumber and bird cherry-oat aphids (banker prey) on barley plants (18 °C, 16 L : 8 D photoperiod, and 60% R.H). American hoverfly rearing followed that described by Bellefeuille *et al*. (2019). Adults were fed with artificial flowers (cotton soaked in sugar water and covered in bee pollen, hung on a wooden stick) and small jars of sugar water (20 g/L approximately). Broad bean plants were provided as an ovipositional substrate. Posteclosion, larvae were transferred from the broad bean plants onto 2-week-old barley plants inoculated with *R. padi*.

Effect of prey species on the development of the American hoverfly

Experimental trials took place under controlled conditions of 25 °C and 50% R.H. Hoverfly eggs were allowed to hatch in Petri dishes containing broad bean leaves placed on damp cotton, which originated from laboratory colonies. Less than 24 h postlarval eclosion, larvae were placed individually in Petri dishes (5 cm ø) that were filled with Agar (*bacteriological grade I-tech*, 55.7 g/L) and the underside of either cucumber or oat leaves on top with respectively melon aphids or bird cherry-oat aphids. Larvae were fed daily *ad libitum* for the total length of their development. The stage and weight of the larvae as well as the presence of deformities and mortality were recorded daily until pupation. Duration of pupal stage and sex of adults after emergence were also recorded. A total of 24–27 independent replicates were performed for each treatment (and 34 to 40 replicates when accounting for mortality).

Effect of prey species on the voracity of the American hoverfly

Experiment trials examining larval voracity were conducted in two temporal blocks under the conditions described above. The first temporal block addressed the voracity of larvae from less than 24 h old to the end of second instar (less than 24 h after the beginning of stage three). The second temporal block addressed the voracity of larvae less than 24 h after the beginning of third instar to the beginning of pupal stage. For the first and second blocks, 150–600 aphids and 900–1100 aphids were provided daily, respectively. Aphids provided to larvae were between first and third instar to make sure they could not reproduce and to standardize the size of individuals

within the species. To control for natural aphid mortality, two control Petri dishes were set every day under the same conditions, except for the presence of hoverfly larvae. The number of aphids supplied daily to hoverfly larvae was adjusted to the consumption of the larvae by assuming if at least 15% of the aphids provided daily were not consumed after 24 h, the larvae were feeding at maximum capacity. Given this criterion, more *A. gossypii* than *R. padi* were provided to the larvae (because the prey is smaller, and pretests showed that more were needed to ensure *ad libitum* consumption). Three replicates were discarded due to larvae getting insufficient food for development, which could have otherwise biased results toward less voracious larvae. For the first temporal block, 14 and 13 independent replicates were performed for larvae fed with *R. padi* and *A. gossypii*, respectively. For the second temporal block, 10 independent replicates were performed for each prey.

The biomass of individuals was calculated for each of the two aphid species. For each species, five samples of 200 aphids of stages one to three, representative of the aphids supplied to the larvae, were weighed to 0.00001 g. The individual biomasses of the two aphid species were then estimated by dividing the average weight of the five samples by 200.

Statistical analysis

All statistical analyses were performed using R statistical software version 4.0.3. (R Core Team, 2020). The packages lme4 (Bates *et al*., 2015) (for linear and logistic mixed models) and emmeans (Lenth, 2022) (for post hoc analysis of mixed models and for estimation of the marginal means presented in the figures) were used. For all models, the choice of inclusion of the fixed effects and interaction terms was based on the biological pertinence of the terms as well as on the comparison of the AIC of the different models. The validation of the models was done with Shapiro tests and Q–Q plots for the normality of residuals. Plots of Pearson residuals against explanatory variables as well as Cooks distance plots were performed to verify homoscedasticity of variance and leverage of the data. Developmental time and maximal weight of each instar (or initial weight for the pupal stage, which was only weighted less than 24 h after pupation) were extracted from the data. Global survival rate and deformity occurrence of the larvae for its entire development were also extracted. All were used as dependent variables for statistical analysis.

Developmental time and larval weight (after log transformation of developmental time) were evaluated by two distinct linear mixed models with the prey species and the stage of development as fixed effects and the identity of individuals (ID) as random effect. The interaction between stage of development and prey species was included only in the larval weight model for the reasons mentioned above.

Survival rate was evaluated by a mixed effects logistic regression with the prey species and the stage of development (larva or pupa) as fixed effects and ID as random effect. The larval instar could not be included as an explanatory variable due to the low mortality rate. Logistic regressions assume that less than 20% of the contingency table groups have a frequency of less than five (Josephat & Ame, 2018) and including the larval instar in the model would have generated that problem.

For the same reason, deformities occurred too rarely (2.70%) to be interpreted statistically.

The effect of the prey consumed by the larvae on the differential mortality between males and females was analyzed by looking at the sex ratio of the emerged adults. It was tested by a logistic regression with the prey species as the explanatory variable.

Statistical analyses of the voracity at first and second instars were done separately from those at third instar since the data for first and second instars were taken from the same individuals, but not those for third instar. Number of aphids eaten by the larva was extracted from the data by subtracting the number of live aphids remaining in the Petri dishes from the number of aphids supplied to the larvae (calculated by the number of aphids supplied minus the average natural mortality of the two controls). The daily voracity of larvae was calculated by dividing the larval voracity at each instar by the duration of each instar (number of days) for every replicate. The biomass consumed for each larval instar was also extracted from that data by multiplying the voracity for each larval instar by the average individual biomass of the aphid species concerned.

The effect of the prey species on the voracity, the daily voracity, and the biomass consumed by first and second instars larvae were evaluated by linear mixed models with the prey species and the stage of development as fixed effects and the identity of the larva as random effect. Interaction between prey species and stage was kept in the model only when significant, and in that case, a post hoc analysis, using emmeans package, was performed to look at the contrasts of interest. Effect of prey species on voracity and daily voracity of third-instar larvae was tested with Student's *t*-tests. Effect of prey species on the aphid biomass consumed by third-instar larvae was tested with a nonparametric Wilcoxon test.

Biomass difference between the two aphid species was tested with a nonparametric Wilcoxon test due to the low number of replicates.

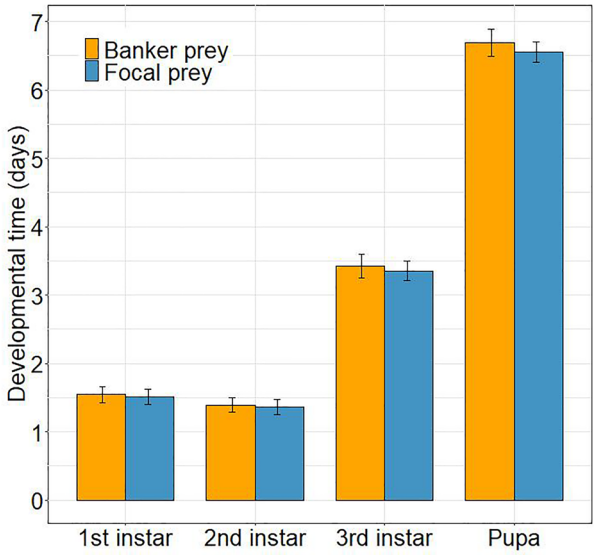

Fig. 1 Preimaginal developmental time of the American hoverfly depending on a diet composed of the banker prey (bird cherry-oat aphid) or the focal prey (melon aphid). Statistical significance of the effect of the prey species on the larval development time was determined using a mixed effects linear model with the prey species and the stage of development as fixed effects and the ID as random effect. Means displayed are estimated marginal means derived from the model.

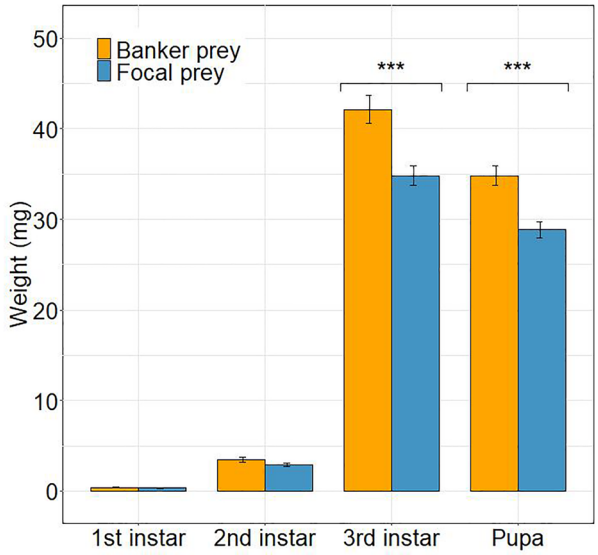

Fig. 2 Preimaginal weight of the American hoverfly depending on a diet composed of the banker prey (bird cherry-oat aphid) or the focal prey (melon aphid). Statistical significance of the effect of the prey species on preimaginal weight was determined using a mixed effects linear model with the prey species, the stage of development, and the interaction between the two factors as fixed effects and the ID as random effect. Means displayed are estimated marginal means derived from the model. Significance: ***$P < 0.001$.

Results

Development

Developmental time Larval mean (± standard error) developmental time (from first instar to the end of third instar) was 6.57 ± 0.15 d, all diets combined, ranging from a minimum of 5 d to a maximum of 10 d. Pupal mean (± standard error) developmental time (from third instar to adult emergence) was 6.64 ± 0.13 d, all diets combined, ranging from a minimum of 6 d to a maximum of 8 d.

Mean larval developmental time was 6.50 ± 0.22 d when the larvae fed on the banker prey and 6.63 ± 0.20 d when larvae fed on the focal prey. When larvae fed on the banker prey, first instar accounted for 25.08% ± 1.68% of the total larval development time, second instar accounted for 22.16% ± 1.72%, and third instar duration represented the majority, that is 52.76% ± 1.45% (Fig. 1). Proportions were similar with larvae fed on the focal prey, that is, 24.53% ± 1.41% for first instar, 22.86% ± 1.47% for second instar, and 52.60% ± 1.40% for third instar. The effect of aphid prey species on hoverfly development time was not significant (Fig. 1) ($n = 181$, df = 49, t-value = –0.466, $P = 0.643$) and was similar for all stages (no main effect or interaction term was significant and model without interaction between stage and diet best fitted with an AIC of 108.52 versus 121.61 with the interaction).

Weight Mean (± standard error) global weight for first, second, and third instars and pupa were, respectively, 0.37 ± 0.03 mg, 3.16 ± 0.17 mg, 38.26 ± 1.06 mg, and 31.67 ± 0.80 mg. The weight increased exponentially from first to third instar and slightly decreased during pupal stage (Fig. 2). Mean larval weight, when fed on the banker prey, was 0.40 ± 0.04 mg at the end of the first instar, 3.43 ± 0.28 mg at the end of the second instar (7.57 times heavier than first instar), 42.12 ± 1.56 mg at the end of the third instar (11.29 times heavier than second instar), and 34.84 ± 1.07 mg at the beginning of pupal stage (17% lighter than third instar). When fed on the focal prey, mean larval weight was 0.35 ± 0.03 mg at the end of the first instar, 2.93 ± 0.20 mg at the end of the second instar (7.47 times heavier than first instar), 34.83 ± 1.09 mg at the end of the third instar (10.89 times heavier than second instar), and 28.84 ± 0.87 mg

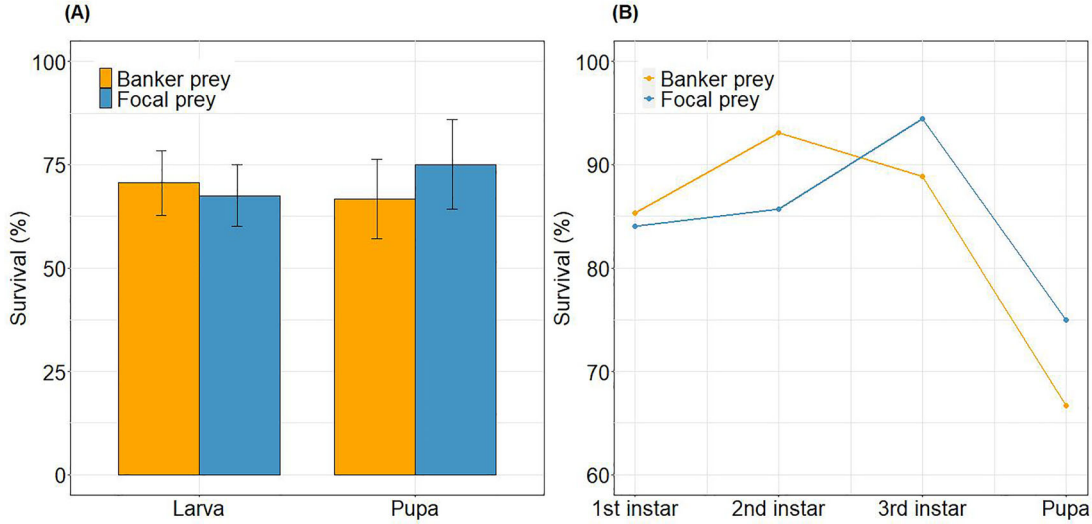

Fig. 3 Overall survival (A) and survival trajectory (B) depending on the prey species: the banker prey (bird cherry-oat aphid) or the focal prey (melon aphid). Statistical significance of the overall survival was determined using a mixed effects logistic regression with the prey species and the stage of development (larva or pupa) as fixed effects and ID as random effect. Overall survival means (A) displayed are estimated marginal means derived from the model. Survival trajectory (B) displayed are raw data.

at the beginning of pupal stage (17% lighter than third instar).

Larval weight of third-instar larva and pupa was significantly higher when the larvae had been fed on the banker prey than when fed on the focal prey (Fig. 2) ($n = 204$, df $= 49$, $t = –6.222$, $P < 0.001$ for third instar and $n = 204$, df $= 49$, t-value $= –5.095$, $P < 0.001$ for pupa). When larvae were fed on the banker prey, average third-instar larval weight was 20.95% higher, and average pupal weight was 20.81% higher than when fed on focal prey. First- and second-instar larval weight did not differ significantly with a diet composed of the focal or the banker prey ($n = 204$, df $= 49$, $t = –0.048$, $P = 0.962$ and $n = 204$, df $= 49$, $t = –0.429$, $P = 0.667$ for first and second instars, respectively).

Survival Global larval survival rate was 68.89% ± 5.42% and global pupal survival rate was 68.63% ± 6.56%. Survival was not significantly different between diets, neither for the larval nor the pupal stage (Fig. 3A) (respectively, $n = 114$, $Z = –0.286$, $P = 0.7749$ and $n = 114$, $Z = 0.562$, $P = 0.5742$). Larval survival rate was 70.59% ± 7.81% when larvae were fed with the banker prey and 67.50% ± 7.41% when larvae were fed with the focal prey (Fig. 3A). Pupal survival (emergence) rate was 66.67% ± 9.62% when larvae were fed on the banker prey and 75.00% ± 10.83% when fed on the focal prey. Although not evaluated statistically due to the low occurrence of mortality, when larvae were fed on the banker prey, the survival rate was slightly higher at second instar, and when larvae were fed on the focal prey, the highest survival rate occurred at the third instar (Fig. 3B). Lowest survival rate occurred at pupal stage with both preys.

Deformities Deformities occurred only with larvae fed on the focal prey, but it happened in only 2.70% (2/74) of all replicates, so no statistical analysis was performed. Both deformities took the form of a growth located on the head of the larvae and only one of the two larvae survived for its entire development.

Sex ratio Adult sex ratio (number of males/number of females emerged) was 1.00 when larvae fed on the banker prey and 1.40 when larvae fed on the focal prey (Fig. 4). Proportion of females emerged was not significantly related to the prey species consumed by the larvae (Fig. 4) ($n = 28$, $Z = 0.437$, $P = 0.662$).

Voracity

Total voracity Total larval voracity (mean number of aphids consumed during the entire larval stage) was 1780 banker aphids and 2266 focal aphids. Average third-instar voracity represented 78.32% and 82.39% of the total voracity with larvae fed on the banker prey and the focal prey, respectively (Fig. 5A).

At third instar, larval voracity (mean number of aphids eaten at each instar) was 33.22% higher when fed on the

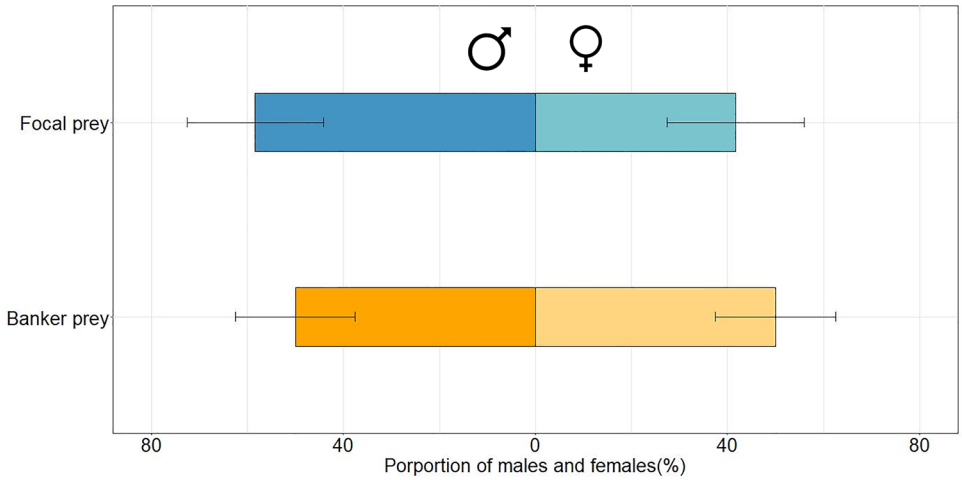

Fig. 4 Proportion of females emerging from *Eupeodes americanus* pupae depending on the prey consumed by the larvae: the banker prey (bird cherry-oat aphid) or the focal prey (melon aphid). Statistical significance of the proportion of females emerged was determined using a logistic regression with the prey species as the explanatory variable. Means displayed are estimated marginal means derived from the model.

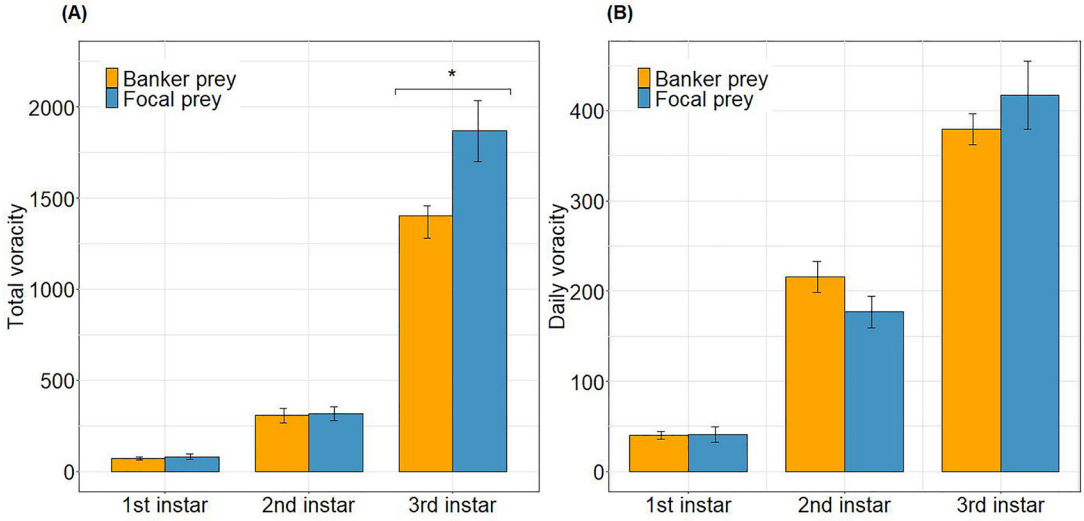

Fig. 5 Total instar voracity (number of prey consumed by instar) (A) and daily voracity (B) of *E. americanus* depending on the prey species. Statistical significance of the effect of the prey species on the total instar voracity and the daily voracity of first- and second-instar larvae was determined with a mixed effects linear model with the prey species and larval developmental stage as fixed effects and the ID as random effect. Interaction between prey species and larval developmental stage was also included as a fixed effect for the daily voracity only. Statistical significance of the effect of the prey species on the total instar voracity and daily voracity of third-instar larvae was determined with Student's *t*-tests. Means displayed are estimated marginal means derived from the models. Significance: $*P < 0.05$.

focal prey than on the banker prey (Fig. 5A) ($n = 20$, t-value $= 2.440$, df $= 14$, $P = 0.029$). Voracity of the first and second instars did not significantly differ between prey types ($n = 54$, t-value $= -0.354$, df $= 51$, $P = 0.725$).

Daily voracity As in the case of total voracity of each instar, daily voracity increased during the development (Fig. 5B). When larvae fed on the banker prey, third-instar daily voracity was 8.43 times higher than first-instar daily voracity and 0.76 times higher than

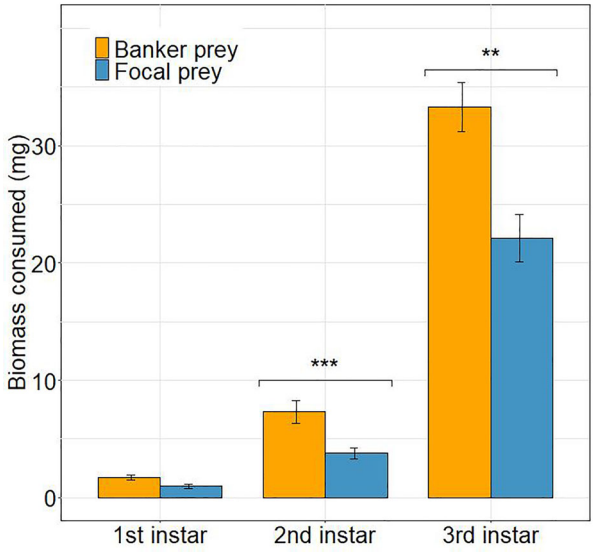

Fig. 6 Biomass consumed by *E. americanus* depending on the prey species. Statistical significance of the effect of the prey species on the biomass consumed by first- and second-instar larvae was determined with a mixed effects linear model with the prey species, the larval developmental stage, and the interaction between prey species and larval developmental stage as fixed effects and the ID as random effect. Statistical significance of the effect of the prey species on the voracity of third-instar larvae was determined with a nonparametric Wilcoxon test. Means displayed are estimated marginal means derived from the model. Significance: $^{**}P < 0.01$ $^{***}P < 0.001$.

second-instar daily voracity. When larvae fed on the focal prey, third-instar daily voracity was 9.15 times higher than first-instar daily voracity and 1.35 times higher than second-instar daily voracity. The daily voracity was similar for both preys at all larval instars (Fig. 5B) ($n = 54$, t-value $= 0.065$, df $= 47$, $P = 0.948$; $n = 54$, t-value $= -2.113$, df $= 47$, $P = 0.040$ and $n = 20$, t-value $= 0.910$, df $= 12$, $P = 0.380$ for first, second, and third instars, respectively).

Biomass consumed by instars Aphid individual mean biomass was significantly different between the banker and focal species ($W = 0$, $P = 0.008$). Banker prey's biomass was approximately 2.01 times that of the focal prey. For this reason, voracity was expressed and then also analyzed in terms of biomass consumed.

The total biomass consumed by larvae during their entire development was higher when fed on the banker prey (42.34 mg) than on focal prey (26.88 mg).

At second and third instars, biomass consumed was significantly higher for larvae fed on the banker prey than on the focal prey (Fig. 6) ($n = 54$, t-value $= -4.468$, df $= 50$, $P < 0.001$ and $n = 20$, W $= 11$, $P = 0.002$ for second instar and third instar, respectively). Biomass of banker prey consumed was approximately 0.94 times higher at second instar and 0.50 times higher at third instar than that of focal prey. Biomass consumed at first instar was not different depending on the prey species consumed ($n = 27$, t-value $= -0.922$, df $= 50$, $P = 0.361$).

Discussion

Aligned with our first prediction, both focal and banker prey allowed for complete preimaginal development of the syrphid predator. Contrary to the second prediction, the focal prey engendered a similar development to the banker prey for most of the parameters studied. Finally, in contrast with the third prediction, the third-instar voracity, expressed in number of preys eaten, was higher on the focal prey than on the banker prey and the daily voracity was similar for both preys. Nonetheless, consistently with the third prediction, the biomass consumed was higher on the banker prey.

Considering that the high-quality banker prey *R. padi* sustains a viable colony of *E. americanus* at the Biological Control Laboratory since 2014, this suggests that *A. gossypii* could also be adequate for the development of the predator. Except for larval weight, this prediction is supported by the fact that focal prey quality was similar to banker prey with respect to preimaginal development time, mortality, deformation rate, and sex ratio. Results from this study, showing *E. americanus* development was similar between individuals feeding on the banker and focal prey, differ from findings of other studies that have demonstrated the influence of prey species on different aspects of predator development, such as developmental time, mortality, and fecundity (Hodek, 1993; Sadeghi & Gilbert, 2000; Liu & Chen, 2001; Putra & Yasuda, 2006; Hodek & Evans, 2012). However, findings of these studies are not always consistent. For example, Rüzička (1975) and Du and Chen (1993) found contradictory results concerning the quality of *Brevicoryne brassicae* L. (Hemiptera: Aphididae) for *E. corollae*. While Rüzička (1975) found that the prey caused a longer development time, Du and Chen (1993) concluded that *E. corollae* was unable to develop on *B. brassicae*. Despite these contradictions, both studies conclude on the good quality of other common prey species studied, such as *A. pisum* and *Aphis craccivora* Koch (Hemiptera: Aphididae). Discrepancy in the results cited in the literature could be explained by the fact that density of aphids and host plant species can modulate the impact of the prey species

on the predators (Hodek, 1993; Vanhaelen *et al*., 2002; Putra & Yasuda, 2006). Considering this, investigation of the effect of prey at low density on the present system would be interesting since focal preys tend to be at very low densities on the field.

Contrary to the other aspects of development, focal prey was of lower quality for the predator regarding its larval weight; with third instar and pupae being 20.81% and 20.95%, lighter, respectively, when feeding on it. This result is not surprising since smaller prey (like the focal prey) can cause greater capture costs on larvae (Sadeghi & Gilbert, 2000). Considering that generally, within the same insect species, lighter individuals tend to have lower fecundity (Honěk, 1993), it is possible that the larvae that are fed with the focal prey would have lower fecundity than larvae fed on banker prey. This phenomenon has been demonstrated with *E. balteatus* whose lifetime fecundity and egg production rate were linked to female body size, which was directly related to their somatic dry mass (Branquart & Hemptinne, 2000). Nonetheless, it is possible that this relation does not apply to all hoverfly species. Indeed, Scott and Barlow (1984) demonstrated that females of *E. corollae* could compensate for low body weight by overproducing eggs. They showed that total number of eggs produced was the same independently of the number of aphids consumed by the larvae, and therefore, independently of the pupal weight as well, which derives from voracity.

However, two other studies found contradictory results, that is, that total fecundity of *E. corollae* was positively linked with pupal weight (Cornelius & Barlow, 1980; Whittingham, 1991). Nonetheless, both studies suggest that pupal weight has a stronger effect on fecundity when longevity of adults is higher, potentially because compensation takes a lot of resources and shortens the longevity of individuals utilizing this strategy (Cornelius & Barlow, 1980; Whittingham, 1991). If this compensatory effect applies to the American hoverfly, even if it concerns only short-lived individuals, it could lessen the effect of the weight on the fecundity. Considering this and the fact that the effect size is relatively small, we can still conclude that the quality of the focal prey for *E. americanus* is not drastically lower than that of the banker prey, which sustains a viable colony of hoverflies at the Biological Control Laboratory since 2014.

The results concerning voracity are also partly divergent from what the literature suggests. Indeed, contrary to our expectations, the number of prey consumed by each larval instar was similar, or higher (at third instar), when larvae fed on the focal prey than on the banker prey. Those results are surprising since syrphid larvae tend to move with more difficulty on surfaces containing trichomes like cucumber (Verheggen *et al*., 2009; Vosteen *et al*., 2018), which could have made the predation more difficult and therefore reduce voracity. Nonetheless, as stated earlier, smaller prey can engender higher capture costs, meaning that the lighter weight of the focal prey probably generated a higher predation rate since more prey were needed to complete development. It could also explain why the difference in voracity only appeared at third instar, where the voracity represented 78.32%–82.39% of the total number of aphids consumed by a larva so the impact of prey size was emphasized. However, since the biomass consumed by larvae on the focal prey diet was lower at second and third instars—even though the number of aphids consumed was higher at third instar—it seems that the higher predation rate on the focal prey diet did not totally compensate for the smaller weight of the melon aphids. This result is consistent with the fact that *E. americanus* tends to be lighter when feeding on the focal prey.

Overall, our results emphasize the potential of the American hoverfly to control the melon aphid in a banker plant system involving the bird cherry-oat aphid. Indeed, the fact that, at least at high aphid densities, the focal prey engenders similar results to the banker prey concerning hoverfly development time, survival, deformations, and sex ratio suggests that melon aphids could sustain a viable population of American hoverflies given that the banker prey has been successfully used as a rearing prey at the Biological Control Laboratory since 2014. It also implies that the population growth of the American hoverfly would not be altered by longer development, higher mortality, and unbalanced sex ratio with the arrival of the focal prey in the crop. Moreover, even though the focal prey produced lighter individuals, considering that the difference was only about 20% and that hoverfly reproductive performance is also strongly dependent on other factors like available floral resources (Laubertie *et al*., 2012; van Rijn *et al*., 2013), arrival of the focal prey in the system would probably not significantly reduce the reproductive performance of individuals.

However, more research is needed to properly assess the impact of the arrival of the focal prey on the population dynamics of the American hoverfly in a banker plant system in the field. Among other things, if the predator does not tend to lay eggs in populations of aphids parasitized or predated by other natural enemies, it could lead to control failure. Apart from the necessity to develop well on its prey, the capacity of biocontrol agents to be effective against pest populations also relies on intrinsic characteristics such as their voracity (Dunn *et al*., 2020). Results suggest that the huge voracity of the American hoverfly on both the focal and banker preys

should generate a high killing rate, which is essential, particularly in the case of fast-growing aphids like the melon aphid.

Conclusion

In conclusion, based on our preliminary laboratory results, the American hoverfly may be well suited as a melon aphid biocontrol agent. Hoverfly larvae developed rapidly and had low mortality rates on a melon aphid diet. In addition, the higher voracity of the predator on the smaller focal prey should maximize its predation impact on the melon aphid population. Moreover, as tested by Gonzalez *et al*. (2023), the American hoverflies should readily oviposit in melon aphid colonies on cucumber in a greenhouse context if it is presented with the right banker plant species. Nonetheless, future studies should also examine how other factors such as interactions with other natural enemies, the presence of additional alternative prey species, and variable weather conditions in the field may alter the effectiveness of the American hoverfly as a biocontrol agent for *A. gossypii*. Due to the small sample sizes utilized in this study, we suggest that these results be interpreted with caution. Nevertheless, this study provides novel evidence to suggest that *E. americanus* can be successfully reared on melon aphids in the laboratory, and thus American hoverflies may well be a suitable candidate for development as a biocontrol agent against *A. gossypii* in the future.

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Disclosure

We declare that the authors have no conflict of interest.

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