



## Biological and Microbial Control

# Reproductive parameters of a new biocontrol agent, *Eupeodes americanus* (Diptera: Syrphidae) and comparison with the commercialized *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae)

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The American hoverfly *Eupeodes americanus* (Wiedemann) (Diptera: Syrphidae) is an aphidophagous predator during its larval stage and is currently being evaluated for inclusion in biocontrol programs as a new biocontrol agent. However, little is known about its reproductive aptitudes. The objective of the present study was to determine the reproductive parameters of *E. americanus* and to compare them with those of a commercialized and widely used biological control agent for aphids, the aphid midge *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae). The preoviposition period, oviposition period, adult longevity, lifetime and daily fecundity, egg hatching rate, and fertility were determined for *E. americanus* females and compared to those of *A. aphidimyza*. Trials were conducted under laboratory conditions in rearing cages on the broad bean plant *Vicia faba* L. (Fabaceae), infested with pea aphids *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae). The results revealed that the preoviposition period, oviposition period, and adult longevity were significantly longer in *E. americanus* than in *A. aphidimyza*. The daily fecundity and egg-hatching rate were similar in both species. However, lifetime fecundity and fertility were considerably higher in *E. americanus* than in *A. aphidimyza*. This study demonstrates that the reproductive capacity of *E. americanus* is clearly superior to that of *A. aphidimyza* and therefore supports its inclusion in the aphid pest management program as a new biocontrol agent.

**Key words:** preoviposition period, oviposition period, longevity, fecundity, fertility

## Introduction

Aphids (Hemiptera: Aphididae) are among the most harmful pests of numerous crops around the world, including greenhouse-grown sweet pepper and cucumber (Ramakers 2004, Sanchez et al. 2007, Messelink et al. 2020) or cotton and soybeans among field crops (Blackman and Eastop 2007). Over the past decades, the intensive use of insecticides has favored not only the emergence of resistant populations of several aphid species (Herron et al. 2001, Kift et al. 2004, Bass et al. 2015), but has also led to the emergence of health and environmental issues (Cabrerá 2017). With increased awareness linked to these problems, concepts such as sustainable agriculture and environmental conservation have been championed in recent

times, which promote biological control as a better alternative to chemical control (van Lenteren et al. 2018).

Within aphidophagous guilds of natural enemies, many studies demonstrate that the predatory larvae of several species of Syrphidae can play important roles as natural control agents (Chambers 1986, Belliure and Michaud 2001, Putra and Yasuda 2006, Amorós-Jiménez et al. 2012, Arcaya et al. 2017, Dunn et al. 2020). In Europe, several species have been studied and 3 of them, namely *Episyrphus balteatus* (De Geer) (Diptera: Syrphidae), *Sphaerophoria rueppellii* (Wiedemann), and *Eupeodes corollae* (Fabricius) (Diptera: Syrphidae) are already commercialized (Almohamad et al. 2006, van Lenteren et al. 2018, Pekas et al. 2020). Recently, the American

hoverfly, *Eupeodes americanus* (Wiedemann) has been commercialized in Canada and represents the first hoverfly species available to growers in North America. It is a generalist Nearctic aphid predator (Skevington 2019), feeding on more than 40 different aphid species (Rojo et al. 2003). Among their aphid hosts, are numerous crop pests such as the foxglove aphid *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae) on pepper (Bellefeuille et al. 2021), the melon aphid *Aphis gossypii* Glover on melon and cucumber (Heiss 1938, Fauteux et al. 2024), the soybean aphid *Aphis glycines* Matsumura on soya (Kaiser et al. 2007, Noma et al. 2010), and the green peach aphid *Myzus persicae* (Sulzer) on potatoes and pepper (Vockeroth 1992, Gonzalez et al., 2023a).

In a previous study, Bellefeuille et al. (2019) examined the efficacy of *E. americanus*, and highlighted its ability to fly, lay eggs and feed on aphids even at low temperatures (from 12 °C to 18 °C), which is not the case for most commercialized aphidophagous natural enemies such as parasitoids, coccinellids or the aphid midge *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) (Langer et al. 2004, Alotaibi 2008, Sørensen et al. 2013). Moreover, the larva of the American hoverfly is a furtive predator, as is the aphid midge (Lucas and Brodeur 2001) and can feed on aphids without triggering a defensive response (Meseguer et al. 2021).

In order to resolve aphid problems in greenhouses, it is important for biological control agents to become established within growing environments before pest aphids invade. To facilitate this, it is possible to establish a banker plant system within greenhouses (Frank 2010, Huang et al. 2011, Gonzalez et al. 2023b). The efficacy of *E. americanus* associated with a banker plant system was demonstrated in experimental and commercial greenhouses in spring production by Bellefeuille et al. (2021). *Eupeodes americanus* has been able to use the banker plant system to feed and reproduce on it. Furthermore, adults that emerged from banker plant systems were able to locate and lay eggs on infested plants in the focal crop and finally control aphid populations (Bellefeuille et al. 2021). This demonstrates that *E. americanus* has several attributes to be an efficient biological control agent. However, basic information on the biology and ecology of this species is still missing.

Among the most fundamental aspects of the bioecology of potential biocontrol agents to describe are their life cycle, reproductive potential, and voracity (Coppel and Mertins 1977, Soleyman-Nezhadiyan and Laughlin 1998, Stiling and Cornelissen 2005, Hoddle and Van Driesche 2009). These characteristics are essential for the development of an effective biological control program and for the development of productive mass-rearing systems (Soleyman-Nezhadiyan and Laughlin 1998, Stiling and Cornelissen 2005). To this end, prior work helped to define the life cycle of *E. americanus* and compared it to *A. aphidimyza*, a commercially available biocontrol agent. The aphid midge, *A. aphidimyza*, is one of the most important predators used for aphid control, making it a good reference in comparative studies (Boulanger et al. 2019). Results demonstrated that *E. americanus* larval developmental time and adult longevity are clearly longer than *A. aphidimyza* and consequently have a higher potential for biological control (Ouattara et al. 2022). The voracity of *E. americanus* was found to be very high as 1 larva can consume around 2,000 aphids (Fauteux et al. 2024). This great voracity should generate a high killing rate which makes *E. americanus* a good predator, however, crucial information regarding its reproductive potential remains unavailable.

The objective of the present study was to determine the length of the preoviposition and oviposition periods, the fecundity, the egg-hatching rate, the fertility, and the adult longevity. These different factors were determined in *E. americanus* and compared with those

of a commercially available biological control agent, *A. aphidimyza*. Our first hypothesis is that the longevity, lifetime fecundity, and daily fecundity of females *E. americanus* will be higher than that of females *A. aphidimyza*, since these parameters are usually correlated with body size (Elgar and Pierce 1988, Jikumaru et al. 1994, Branquart and Hemptinne 2000, García-Barros 2000, Šešlija and Tucić 2003). Our second hypothesis is that the oviposition and preoviposition periods of female *E. americanus* will be longer than those of female *A. aphidimyza* because these parameters are correlated positively with adult longevity in predators (Scott and Barlow 1984, Jikumaru et al. 1994, Coll 1996).

## Materials and methods

### Insects Rearing

*Eupeodes americanus* specimens came from an experimental colony held at the biocontrol laboratory of the Université du Québec à Montréal since 2014. These individuals were originally collected as wild adults on *Phlox* sp. L. (Polemoniaceae) flowers in Sainte-Agathe-de-Lotbinière (N 46°23'726", W 71°21'446"), Québec, Canada. The laboratory colony was refreshed yearly with new wild individuals. The Fraser methodology was used to rear multiple generations in the laboratory (Fraser 1972). A rearing cage of dimension 81 × 53 × 60 cm covered with muslin was used to keep adults in a greenhouse at 22 °C during the day, 19 °C at night, at 60% RH and 16:8 (L:D) under high-pressure sodium lamps. Adults were fed through an artificial flower and a sugar:water mixture (1:10 v/v). Artificial flowers consisted of a wooden stick inserted inside a round cotton makeup remover pad saturated with a honey:water mixture (1:3 v/v) and covered with wildflower bee pollen. These food resources were replaced twice a week. Broad bean plants *Vicia faba* L. (Fabaceae) (Norseco, Quebec, Canada) infested with pea aphid *Acyrtosiphon pisum* (Harris) were replaced in the adult rearing cage twice a week in order to allow females to oviposit after mating. Larvae were collected and transferred to two 35 cm<sup>3</sup> rearing cages covered with muslin maintained in a growth chamber (Convicon, Model E15, Canada) set at 24 °C, 70% RH and 16:8 (L:D) once each week. These larval cages contained barley plants *Hordeum vulgare* L. (Poaceae) (Sollio Agriculture, Quebec, Canada), infested with cereal aphids *Rhopalosiphum padi* (L.). When the larvae became adults, they were introduced into the adult rearing cage described previously.

*Aphidoletes aphidimyza* specimens were obtained from a commercial supplier, Anatis Bioprotection (Saint-André, Quebec, Canada) as pupae. They were reared in 35 × 35 × 35 cm rearing cages covered with muslin and put in the same growth chamber as hoverfly larvae. All life stages of *A. aphidimyza* were reared on green peach aphid *M. persicae* on potato plants *Solanum tuberosum* L. (Solanaceae) (var. Norland, Propur, Quebec, Canada). A sugar:water mixture (1:10 v/v) was used to feed adults.

### Experiment on Preoviposition Period

Tests were done under controlled conditions of 24 °C, 70% RH and 16:8 (L:D). The temperature of 24 °C was chosen as it is in the optimal range of temperatures for our reference, *A. aphidimyza* (Havelka and Zemek 1999, Boulanger et al. 2019) but also for *E. americanus*. In this study, the reproduction parameters of 20 females in *E. americanus* and 15 females in *A. aphidimyza* were determined. After emergence, each female (less than 24 h old) was immediately placed with 2 males in rearing cages covered with muslin of 71 × 71 × 31 cm for *E. americanus* and 14.5 × 11 × 11 cm for *A.*

*aphidimyza* and were reared as described above. Each rearing cage contained about one 10 cm high broad bean plant *Vicia faba* L. (Fabaceae) infested with about 85 *A. pisum* nymphs of the second and third stages. Females were observed daily until the first oviposition. The oviposition date was recorded, and the preoviposition period was determined as the period between female emergence and its first egg-laying (Dje et al. 2011).

### Experiment on Fecundity, Fertility, Oviposition Period, Egg Hatching Rate, and Longevity of Females

As soon as the first egg was observed, the broad bean plant infested with aphids was removed and replaced by another one every 24 h in each cage. The number of eggs deposited by the female on the broad bean plant was noted daily. The experiment continued until the death of the female. Males were replaced if they died before the female. The longevity of males was not monitored in this study. Lifetime fecundity was determined as the sum of eggs laid per female. The egg hatching rate was determined for 258 eggs in *E. americanus* and for 165 eggs in *A. aphidimyza* randomly chosen among the eggs laid (number of offspring (L1) produced/total number of incubated fertile eggs  $\times$  100). The fertility of females or viability of eggs laid (Leather 1995) was assessed by taking into account both lifetime fecundity (number of eggs laid) and egg hatch rate. The date of the last oviposition was noted, and the oviposition period (the period between the first and the last oviposition) was determined in days. Then, the daily fecundity was determined by dividing the lifetime fecundity by the length of the oviposition period. Finally, female longevity was determined as the period between adult emergence and death (Dje et al. 2011).

### Statistical Analysis

All statistical analyses were performed within the R statistical environment (v. 3.4.2, R Foundation for Statistical Computing 2017). For each test, the significance level was set at  $\alpha = 0.05$ .

Prior to any subsequent analysis, assumptions for parametric analyses were fulfilled following a Shapiro–Wilk test of normality ( $P > 0.05$ ) and with the inspection of diagnostic plots (residuals vs fitted, normal QQ plot, scale location, and constant leverage). The mean preoviposition period, oviposition period, longevity, lifetime fecundity, fertility, and daily fecundity did not follow a normal distribution. No transformation is allowed to meet a normal distribution. Then, those data were compared between predator's species using a nonparametric Wilcoxon rank-sum test. A generalized linear mixed model (GLMM) was employed to investigate the oviposition across the 2 aphid predator species over time ('lme4' package in R) (Bates et al. 2015). The GLMM was specified with the number of eggs laid as the response variable. Fixed effects included time (in days), species (*E. americanus* or *A. aphidimyza*), and their interaction. A random factor was included to account for random variability in oviposition among individuals within species. Given the non-normal distribution and typical right-skewness of the count data, Poisson distribution was used, with a log link function. The validation of the model was assessed through residual diagnostics including Q–Q plots for the normality of residuals and plots of Pearson residuals against explanatory variables as well as Cooks distance plots to verify homoscedasticity of variance. The Spearman rank correlation test was conducted to measure the degree of relatedness between the oviposition period and longevity and between the oviposition period and fecundity for each predator. Finally, egg hatch rates were compared between predators using a Pearson  $\chi^2$  analysis.

## Results

### Preoviposition Period, Oviposition Period, and Longevity of Females

The preoviposition period varied from 3 to 6 days in length for *E. americanus* and from 1 to 2 days for *A. aphidimyza*. The mean preoviposition period of *E. americanus* was significantly longer than of *A. aphidimyza* with  $4.1 \pm 0.2$  and  $1.1 \pm 0.1$  days, respectively (Wilcoxon,  $W = 0$ ;  $df = 1$ ;  $P < 0.001$ ; Fig. 1).

The mean longevity of adult *E. americanus* and *A. aphidimyza* females were  $20.6 \pm 1.6$  and  $3.1 \pm 0.2$  days, respectively, which were significantly different from one another (Wilcoxon,  $W = 0$ ;  $df = 1$ ;  $P < 0.001$ ; Fig. 1). The oviposition period varied from 5 to 31 days for *E. americanus* and from 1 to 3 days for *A. aphidimyza* (Fig. 3). The mean oviposition period,  $15.9 \pm 1.6$  days for *E. americanus* was drastically longer (9.5 times more) than for *A. aphidimyza* at only  $1.7 \pm 0.2$  days long (Wilcoxon,  $W = 0$ ;  $df = 1$ ;  $P < 0.001$ ; Fig. 1). The oviposition period in females was positively correlated with their longevity in both species (Spearman,  $S = 27.75$ ;  $R_s = 0.98$ ;  $P < 0.001$  for *E. americanus*,  $S = 99.79$ ;  $R_s = 0.82$ ;  $P < 0.001$  for *A. aphidimyza*).

### Lifetime Fecundity, Daily Fecundity, Egg Hatching Rate, and Fertility

Among both species assessed, the highest overall number of eggs laid per individual was of 693 for *E. americanus* with a mean lifetime fecundity of  $295.7 \pm 40.4$  eggs. The highest total number of eggs laid per *A. aphidimyza* female was 89 eggs with a mean lifetime fecundity of  $39 \pm 7.6$  eggs. *Eupeodes americanus* had a lifetime fecundity 7.6 times higher than that of *A. aphidimyza* (Wilcoxon,  $W = 0$ ;  $df = 1$ ;  $P < 0.001$ ; Fig. 2). Logically, females who had a longer oviposition period laid more eggs than those with shorter oviposition period in both species (Spearman,  $S = 456.38$ ;  $R_s = 0.66$ ;  $P = 0.002$  for *E. americanus*,  $S = 103.38$ ;  $R_s = 0.82$ ;  $P < 0.001$  for *A. aphidimyza*). The number of eggs laid daily per female varied from 0 to 105 in *E. americanus* and from 0 to 39 in *A. aphidimyza*. The mean daily fecundity was not significantly different between *E. americanus* and *A. aphidimyza* with respectively  $19.4 \pm 2.0$  and  $21.7 \pm 2.3$  eggs (Wilcoxon,  $W = 170$ ;  $df = 1$ ;  $P = 0.52$ ; Fig. 2).

The GLMM analysis revealed significant effects of time and the interaction between time and species on the oviposition activity. Specifically, time had a notable negative impact on the number of eggs laid (Estimate =  $-0.27833$ , SE =  $0.05838$ ,  $z = -4.768$ ,  $P < 0.001$ ),

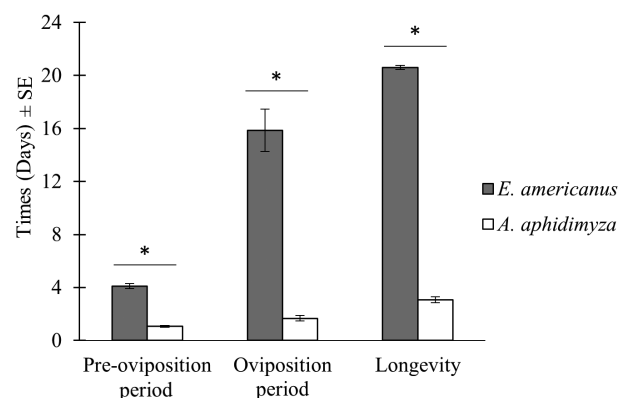


Fig. 1. Mean preoviposition period; oviposition period and female adult longevity ( $\pm$ SE) for *E. americanus* ( $n = 20$ ) and *A. aphidimyza* ( $n = 15$ ). An asterisk (\*) indicates a significant difference between species ( $P < 0.05$ ).

indicating a decrease in egg-laying as time progressed (Fig. 3). The species effect, represented by the comparison between *E. americanus* and *A. aphidimyza*, was not statistically significant (estimate = -0.01659, SE = 0.10371,  $z = -0.160$ ,  $P = 0.87$ ), suggesting no initial difference in oviposition rates between the 2 species. However, the interaction between time and species was significant (estimate = 0.21616, SE = 0.05844,  $z = 3.699$ ,  $P < 0.001$ ), demonstrating that *E. americanus* experienced a less pronounced decline in egg-laying over time compared to *A. aphidimyza*. There was no difference in egg hatch rate between *E. americanus* (68.2%) and *A. aphidimyza* (76.4%) (Pearson,  $\chi^2 = 2.88$ ;  $df = 1$ ;  $P = 0.09$ ; Fig. 4a). The mean fertility was significantly superior in *E. americanus* than in *A. aphidimyza*, with respectively 201.7 and 29.8 larvae (Wilcoxon,  $W = 2$ ;  $df = 1$ ;  $P < 0.001$ ; Fig. 4b).

## Discussion

The reproductive aptitudes of potential predators may constitute key factors for deciding to apply agents within biocontrol programs. The objective of the present study was to determine the

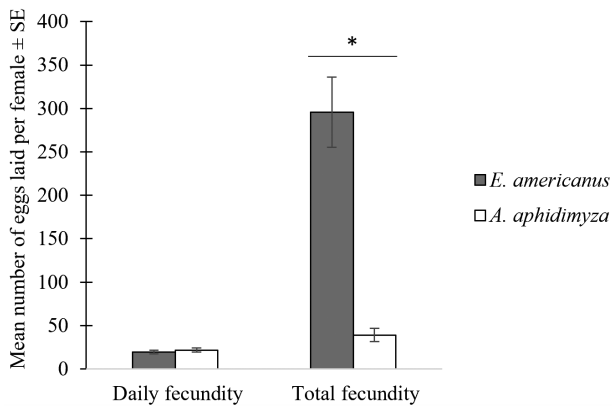


Fig. 2. Mean daily fecundity and total fecundity ( $\pm$ SE) for female *E. americanus* ( $n = 20$ ) and female *A. aphidimyza* ( $n = 15$ ). An asterisk (\*) indicates a significant difference between species ( $P < 0.05$ ).

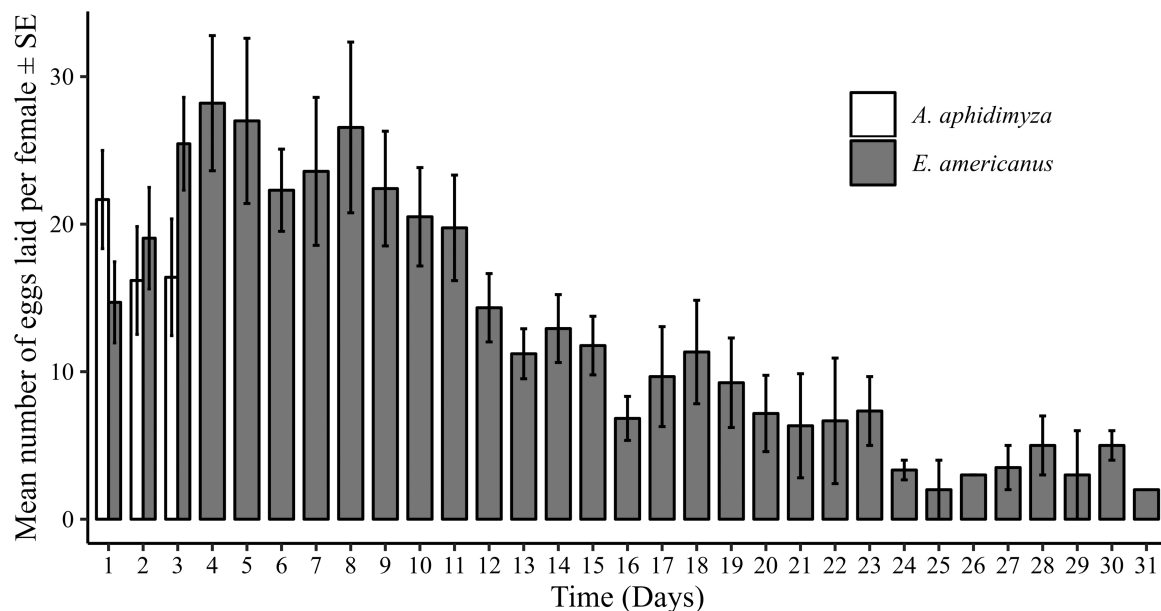
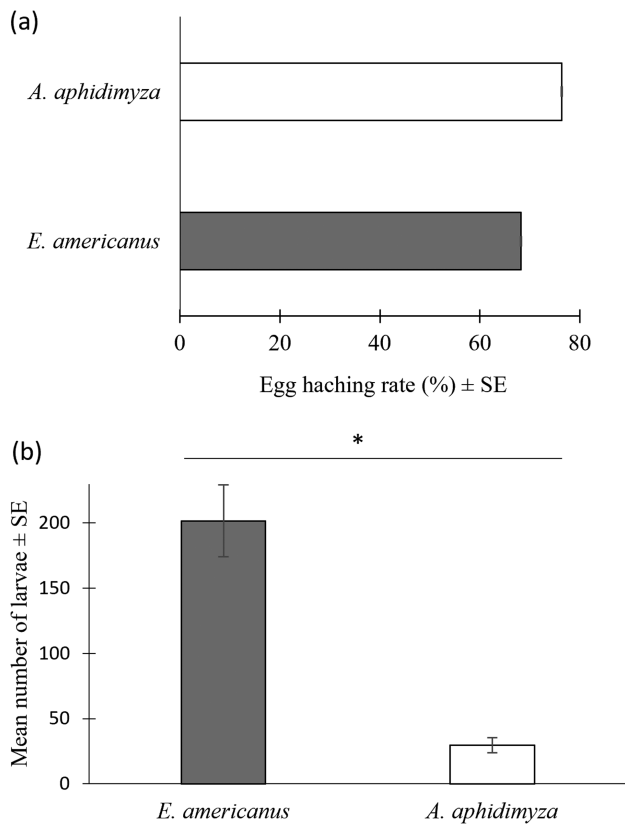


Fig. 3. Evolution of the mean number of eggs laid per female ( $\pm$ SE) over time (in days) for *E. americanus* ( $n = 20$ ) and *A. aphidimyza* ( $n = 15$ ).

reproductive capacity of *E. americanus* and to compare it with that of a commercially available agent, *A. aphidimyza*, in order to evaluate its potential as a new aphidophagous biological control agent. Globally, considering the reproductive aspects of both species, our results demonstrate a high potential for biocontrol in the American hoverfly. Indeed, the results of this study showed that the longevity, the preoviposition period and the oviposition period of *E. americanus* females were significantly longer than those of *A. aphidimyza*. The fecundity and fertility of *E. americanus* were also higher than those of *A. aphidimyza*. These results therefore confirm our alternate hypotheses, which posited that adult longevity, oviposition, and preoviposition periods, as well as lifetime fecundity and daily fecundity of *E. americanus* will be higher than that of *A. aphidimyza*. Building on these findings, it is essential to consider them in conjunction with the body sizes of the 2 predators with *E. americanus* being considerably larger than *A. aphidimyza*. Indeed, literature has shown that female body size is correlated with higher fecundity, indicating that body size is a primary constraint on an insect's potential fecundity (Honěk 1993).

The preoviposition period of *E. americanus* (4.1 days) was shorter or similar to those observed in other syrphid species. Indeed, the egg-laying period for *Dioprosopa clavata* (Fabricius) lasts an average of 6.6 days at 23 °C (Belliere and Michaud 2001), 8.8 days for *E. balteatus* at 20 °C (Guest 1984), 6.8 days for *Melangyna viridiceps* (Macquart), 5.6 days for *Symosyrphus grandicornis* (Macquart) at 20 °C (Soleyman-Nezhadiyan 1996) and 3.8 days for *E. corollae* at 20 °C (Lillo et al. 2021). Several factors can influence oviposition times in predators such as larval foraging, temperature, and food quantity and quality (Zheng et al. 1993, Gotoh et al. 2004, Jandricic et al. 2013). A longer preoviposition period may be detrimental for a biocontrol agent since it delays the time when the larvae will start consuming the pest.

Female longevity was approximately 7 times longer for *E. americanus* than for *A. aphidimyza* (20.6 and 3.1 days, respectively). Female longevity is a crucial factor in biological control that influences the dynamics of predator-prey populations (Laubertie 2007). Indeed, a longer adult stage can allow females to multiply their mating occasions and thus increase their oviposition rates and



**Fig. 4.** (a) Egg hatching rate ( $\pm$ SE) (*E. americanus*  $n = 258$ ; *A. aphidimyza*  $n = 165$ ) and (b) mean total fertility ( $\pm$ SE) for *E. americanus* ( $n = 20$ ) and *A. aphidimyza* ( $n = 15$ ). An asterisk (\*) indicates a significant difference ( $P < 0.05$ ) between species.

consequently the length of their reproductive period (Arnqvist and Nilsson 2000). Among syrphids, most species also have a longer female longevity than *A. aphidimyza*, lasting for example 11.6 days for *Allograpta exotica* (Wiedemann) at 25 °C (Arcaya et al. 2017), but was shorter than in *E. americanus* (20.6 days). The longevity of *E. americanus* was comparable to that reported for *S. grandicornis* at 20 °C (Soleyman-Nezhadiyan 1996) but was shorter than that for *E. balteatus* which is around 40 days at 21 °C (Branquart and Hemptinne 2000). However, adult syrphid nutrition, as indicated by pollen from different plant species, also influences their longevity (Laubertie et al. 2012, Pinheiro et al. 2013, 2015). Another study suggests that *A. aphidimyza* has an average longevity of 2.5 days on *R. padi* but 4 days on *M. persicae* at 20 °C (Higashida et al. 2016) which is close to our results (3.1 days). Of course, in a real situation, the longevity of biocontrol agents must be evaluated in combination with a careful consideration of realized mortality in the greenhouse environments.

The oviposition period of *E. americanus* was also drastically longer than in *A. aphidimyza* (15.9 and 1.7 days, respectively). This long oviposition period is a clear advantage in biological control because the overall oviposition is more spread out over time (Borges et al. 2013). This would keep the population of *E. americanus* in a greenhouse longer than *A. aphidimyza* which has a short oviposition period. This is of real interest for biological control since *E. americanus* could have a medium- or long-term biocontrol effect, while *A. aphidimyza* will rather have a short-term biocontrol effect. The oviposition period in *E. americanus* obtained in this study (15.9 days) is relatively shorter than that reported in *E. corollae* (18 days)

at 28 °C (Benestad 1970), *E. balteatus* (19 days) at 20 °C (Guest 1984) and *M. viridiceps* (19.9 days) at 20 °C (Soleyman-Nezhadiyan 1996). It was however longer than that obtained in *E. corollae* (9.8 days) at 20 °C (Lillo et al. 2021) and *S. grandicornis* (13.8 days) at 20 °C (Soleyman-Nezhadiyan 1996). Our study indicated that there was a positive correlation between oviposition period and female adult longevity. This positive correlation has been previously demonstrated in several studies in Syrphidae (Scott and Barlow 1984) and other predatory species (Jikumaru et al. 1994, Coll 1996, Borges et al. 2013).

According to the size difference, logically, the lifetime fecundity, and fertility of *E. americanus* were also drastically higher than those of *A. aphidimyza* (respectively, 295.7 vs. 89 eggs per female and 201.7 vs. 29.8 larvae). Fertility is the ultimate index of the reproductive potential of a predatory species since the overall impact is a function of larval number and larval voracity. Fecundity is also a factor in inoculative biological control because it is an important determinant of the population size for a given predator species (Coppel and Mertins 1977). Thus, the combination of a greater fecundity and a longer oviposition period in *E. americanus*, along with a favorable egg-hatching rate, results in the production of more larvae (aphidophagous stage) over time (Chambers and Adams 1986, Rojo et al. 1996). Other syrphid species also have higher fecundity than *A. aphidimyza* (Geusen-Pfister 1987, Soleyman-Nezhadiyan 1996, Fathipour et al. 2006). In our study, the fecundity of females was positively correlated with their oviposition period as reported in predatory syrphids and other predator species (Scott and Barlow 1984, Coll 1996). Furthermore, *E. americanus* has a higher lifetime fecundity than do other syrphid species such as *Scaeva albomaculata* (Macquart) (95.5 eggs) feeding on *M. persicae* at 25 °C (Fathipour et al. 2006), *S. scripta* (195.2 eggs) on *Aphis crassivora* Koch at 22 °C (Moetamedinia et al. 2004), *E. corollae* (169 eggs) on *M. persicae* at 20 °C (Lillo et al. 2021) and *M. viridiceps* (288 eggs) on *Macrosiphum rosae* (L.) at 20 °C (Soleyman-Nezhadiyan 1996). However, it was lower than that obtained in *D. clavata* (421.3 eggs) on *Aphis spiraecola* Patch (Hemiptera: Aphididae) at 23 °C (Belliure and Michaud 2001), *E. corollae* (436 eggs) on *M. persicae* at 28 °C (Benestad 1970) and *E. balteatus* (780 eggs) on *A. crassivora* and *A. pisum* at 25 °C (Geusen-Pfister 1987). For *A. aphidimyza*, the mean lifetime fecundity in this study was higher than that obtained by Higashida et al. (2016) (19.9 eggs) on *R. padi*, but was similar to those reported for this species by Watanabe et al. (2014) (39 eggs) on *A. gossypii* and by Higashida et al. (2016) (40.1 eggs) on *M. persicae* at 25 °C. Lifetime fecundity and fertility in predatory syrphids and other predators depend not only on both larval and adult nutrition (Schneider 1969, Havelka and Růžička 1984, Hickman and Wratten 1996) but also on aphid density present in the host plants (Tenhumberg 1995). Indeed, the fecundity of females in syrphid species can be influenced by their adult diet, in particular, the availability and quality of pollen (Gilbert 1981, Amorós-Jiménez et al. 2014). Pollen is a crucial resource for syrphid females because it provides the protein necessary for sexual maturation and egg development (Schneider 1969, Haslett 1989, Pinheiro et al. 2013). This means that in a greenhouse environment devoid of border vegetation, it is advisable to introduce flowering plant resources along with syrphid biocontrol agents to support predator reproduction (Hickman and Wratten 1996, Landis et al. 2000, Pineda and Marcos-García 2008, Gillespie et al. 2011, Hogg et al. 2011, Leman et al. 2023). Variation in aphid prey species and aphid density offered to larval stages can also influence the fecundity of subsequent adults (Cornelius and Barlow 1980) because an aphid species with a low nutritional value or a low density of aphids offered to larval syrphid stages may induce the emergence of smaller syrphid adults

at the next generation with lower fecundity (Jikumaru et al. 1994, Branquart and Hemptinne 2000) as well as those of other predator species (Dixon and Guo 1993, Zheng et al. 1993). However, the use of banker plants in inoculative biological control in greenhouses would reduce not only these larval nutritional problems but also the period of preoviposition in adults (Frank 2010, Huang et al. 2011). Finally, the fecundity of females is also influenced by the aphid density present in host plants. In many aphidophagous hoverfly species, an absence of aphids on host plants leads to egg resorption by adult females (Dixon 1959, Schneider 1969, Branquart and Hemptinne 2000, Orenge-Green et al. 2022). According to Gonzalez et al. (2023c), the number of eggs laid by *E. americanus* females increases with the abundance of aphids, as it does for *A. aphidimyza*. It was also shown that *E. americanus* responds to low densities of aphids early in the infestation (2–5 aphids) process and that its oviposition is better than that of *A. aphidimyza* on sweet pepper plants and similar on cucumber (Gonzalez et al. 2023c). From a practical standpoint, these findings are promising, as it is crucial that the minimum aphid density above which *E. americanus* females start to oviposit remains low in order to ensure its success in a biocontrol context. For mass-rearing purposes, it will be essential to determine the optimal aphid density above which the number of eggs laid per female decreases. For example, in *S. grandicornis*, the number of eggs laid by a female increased with densities up to 100 aphids, then decreased when the number of aphids exceeded 100 individuals (Soleyman-Nezhadiyan 1996).

In conclusion, our study has demonstrated the considerable potential of *E. americanus* as a new candidate biological control agent for combatting aphids in agroecosystems. The results also highlight, under our study condition, the superiority of the syrphid over *A. aphidimyza* with several especially important points: (1) the longer longevity and oviposition period for *E. americanus* and (2) the drastically higher lifetime fecundity and fertility in *E. americanus*. Furthermore, previous studies have also demonstrated other important characteristics of this biological control agent: (1) the great efficacy at low temperatures or short photoperiod of the syrphid (Bellefeuille et al. 2019, Gonzalez et al. 2023a), and its superiority over *Leucopis glyphiniivora* Tanasijtshuk (Diptera: Chamaemyiidae) (Barriault et al. 2019), (2) the immature development time of *E. americanus* similar to that of *A. aphidimyza* and the larval development time significantly longer than in *A. aphidimyza* representing a longer predation period (Ouattara et al. 2022). All these demonstrate that *E. americanus* has great potential to be used as a biological control agent of aphid pests.

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Tene Yacine Ouattara (Conceptualization [Equal], Formal analysis [Equal], Funding acquisition [Equal], Investigation [Lead], Methodology [Equal], Visualization [Lead], Writing – original

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