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Feeding preferences of the aphidophagous hoverfly *Sphaerophoria rueppellii* affect the performance of its offspring

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Abstract Provision of additional floral resources in the crop is a successful strategy of conservation biological control for attracting several natural enemies including predatory syrphids. However, the selection of flower species is mainly based on visiting preferences, paying little attention to the link between preference and performance. In this study, we assess the influence of feeding on flowers of two insectary plants (sweet alyssum and coriander) and flowers of a crop species (sweet pepper) on performance of the parental and first generation of the syrphid *Sphaerophoria rueppellii* (Wiedemann) (Diptera: Syrphidae). We found that floral preference of the adults was linked to developmental performance of their offspring. Sweet alyssum was the flower most frequently visited by syrphid adults, enhancing adult body size and egg-to adult survival of the F1 generation.

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Introduction

Habitat management through the addition of flowering plants in and around crops is a strategy of conservation biological control that enhances the performance of natural enemies (Landis et al. 2000). The importance of floral resources for a large number of natural enemies such as many parasitoid species as well as predators like Coccinellidae, Chrysopidae and Syrphidae have been widely reported (Jervis et al. 1993; Al-Doghairi and Cranshaw 1999). Predatory hoverflies (Diptera: Syrphidae) have a high potential as biocontrol agents against aphids (Tenhumberg and Poehling 1995; Brewer and Elliott 2004; Freier et al. 2007; Haenke et al. 2009). Several studies have shown that this family of Diptera responds positively to the addition of flowering plants to the crop, which can increase their residence time and their efficiency as biocontrol agents, resulting in a lower aphid density and crop damage (Hickman and Wratten 1996; Pineda and Marcos-García 2008b; Haenke et al. 2009).

Floral resources may have a significant effect on egg production of females and other fitness-related parameters of syrphids (Scholz and Poehling 2000), since adults rely on proteins from pollen and saccharides from nectar to mature their ovaries and sustain egg production and to obtain energy, respectively (Chambers 1988; Gilbert 1993). Therefore, understanding the effect that different species of flowers have on syrphids is crucial when applying habitat management strategies for aphid control (Macleod 1992; Cowgill et al. 1993). When evaluating floral resources for habitat management in outdoor crops, traits that enhance attractiveness are desired. However, when introducing flowering plants in greenhouses, enhancing the performance and fitness of natural enemies can be as desirable as improving their attraction. Surprisingly, very little work has paid attention to the effects of flowering plants on syrphid performance (Laubertie et al. 2012; Pinheiro et al. 2013), and even fewer studies have been performed on the link between performance and syrphid foraging behaviour (Laubertie et al. 2012). Due to this fact, criteria for selecting flower resources to enhance syrphid populations have been based mainly on the floral preferences of syrphid adults. In addition, these preferences may differ between syrphid species (Haslett 1989), highlighting that for the success of habitat management implementation it is crucial to understand the effects of floral resources for the targeted natural enemy.

The hypotheses of the present study are that syrphids use their floral resources selectively (1), feeding on different flowers has a differential effect on performance of these insects (2) and there is a relation between the attractiveness of these floral foods and their effect on performance of hoverfly adults but also on that of their offspring (3). To address these questions, we compared two of the most commonly used species of flowers that have been successfully applied in habitat management strategies to enhance the populations of natural enemies: sweet alyssum [*Lobularia maritima* (L.) Desv. (Brassicaceae)] and coriander [*Coriandrum sativum* L. (Umbelliferae)]. Furthermore, we included sweet pepper [*Capsicum annuum* L. (Solanaceae)] as an additional non-host resource, to evaluate the importance that its flowers, regularly exploited by syrphids that visit this horticultural crop (Pineda and Marcos-García 2008d), may have on conservation biological control. The syrphid species we chose to conduct this work was *Sphaerophoria rueppellii* (Wiedemann) (Diptera: Syrphidae) the most abundant predatory hoverfly in Mediterranean greenhouse crops (Pineda and Marcos-García 2008c). This species is well adapted to the extreme climatic conditions occurring in these agricultural areas (Amorós-Jiménez et al. 2012), and it has previously shown a positive response to habitat management strategies including the provision of additional floral resources (Pineda and Marcos-García 2008c) and banker plants (Pineda and Marcos-Garcia 2008).

Materials and methods

Plant material, aphids and syrphids

Sweet pepper (cv. California Wonder), sweet alyssum and coriander plants were grown from seed in plastic pots (5 × 5 × 6 cm) in a glasshouse under controlled conditions and natural light (25 ± 2 °C, 60 ± 10 % RH, 12L:12D photoperiod). Flowering plants were sown weekly to assure there were fresh flowers throughout the experiment. Due to the fact that time to flowering varies among species, time of sowing was different for each flower species in order to synchronise their flowering. A stock colony of *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) was maintained on sweet pepper plants in mesh netting cages (30 × 30 × 60 cm) in a climate room under controlled conditions (25 ± 1 °C, 60 ± 10 % RH, 14L:10D photoperiod). *S. rueppellii* cohorts were reared in plastic cages (30 × 30 × 60 cm), with a fine mesh on their top under the same environmental conditions. The rearing cages contained bee pollen from various flowers, sucrose, water, and a sweet pepper plant infested with *M. persicae* to stimulate oviposition. Same-aged syrphid eggs were periodically removed from the adult cultures and the emerged larvae were reared until pupation on sweet pepper plants infested with *M. persicae*.

Syrphid floral preference

Relative attractiveness of the three flowering species was evaluated in a multiple-choice experiment. The arena consisted on an insect-proof cage (40 × 40 × 50 cm) located inside a rearing chamber under the same conditions as explained above. One flowering plant of each of the three species was placed in one of the corners of the cage. The relative position of each plant was randomised for every replicate to account for possible differences in light intensity caused by the structure of the chamber. A 2–4 day old adult syrphid was placed in the centre of the cage, inside a glass tube covered with black adhesive tape to help orientate the syrphid towards the tube opening. Each fly was used only once and had never experienced the test conditions before. Using the behavioural observation programme Etholog (Ottoni 2000), the time devoted to feeding on each flower species and the frequency of visits to each flower were recorded. Observations lasted for 10 min. Adults that did not exhibit any recognition behaviour (i.e. the syrphid performs a suspended flight near the plant or lands on it) during this time were discarded. Twenty replicates were performed releasing females and 20 replicates were done with males. Tests were always conducted from 9 to 11 a.m.

Performance of the parental generation

To assess the effect of feeding on different flower resources on the performance of *S. rueppellii*, one newly-emerged female and two males were placed in a plastic cage (30 × 30 × 60 cm), with a fine mesh on its top and under the same conditions as for the insect cultures. Each cage contained a non-flowering sweet pepper plant infested with approximately 300 individuals of *M. persicae* as an oviposition stimulus, water and a single flowering plant of coriander, sweet alyssum or sweet pepper.

Flowers and infested plants were replaced every few days to ensure syrphids had continuous access to fresh pollen and nectar as well as aphids. Each cage was daily checked by visual inspection for syrphid survival and oviposition. Eggs laid on the infested pepper plants were removed each day and they were counted to evaluate syrphid fecundity (i.e. number of eggs every 24 h). To quantify fertility (i.e. fraction of eggs hatching), leaves containing eggs were cut off from the plant, and placed in a Petri dish (90 × 15 mm) with a wet disk of paper inside, and sealed with Parafilm® to achieve a high relative humidity, necessary for egg hatching in this species (Amorós-Jiménez et al. 2012). Counts and collection of eggs stopped after fifteen days, as the optimal oviposition period for this species is within this range, and after this period egg-laying markedly decreases (Amorós-Jiménez pers. observ.). Ten replicates were performed for each flower species.

Adult lifespan, time to sexual maturation (e.g. number of days until the first egg is laid), total fecundity and fertility were measured as components of syrphid performance.

Performance of the F1 generation

To evaluate a possible effect of adult feeding habits on the performance of their offspring, three different rearing cages were prepared, one for each flowering plant species. Each cage contained approximately 100 mature adults, water and two to four plants of one of the tested flower species (alyssum, coriander or sweet pepper), which were periodically replaced by fresh ones. An aphid-infested sweet pepper plant was placed in each cage for two hours in order to obtain eggs of the same age. After this time, aphid-infested plants carrying eggs were removed from the cages. Syrphid eggs were reared under optimal conditions (see "Plant material, aphids and syrphids"), and checked daily for larval emergence. From each flowering plant cage, a total of 50 newly-born syrphid larvae were isolated (i.e. 50 replicates) in a Petri dish (90 × 15 mm) with a piece of a sweet pepper leaf (1 cm^2) and a wet disk of paper to provide moisture, and sealed with Parafilm®. *Ad libitum* food (*M. persicae*) was supplied throughout the larval cycle. The sweet pepper disc was replaced daily, to ensure that the aphids had access to fresh food throughout the experiment. Larval mortality and developmental time of syrphid larvae were assessed by observing each Petri dish every 24 h.

Once larvae pupated, the newly-formed pupae were weighed using a precision weighing scale (Acculab ALC-110.4 Analytical Balance) and they were kept under the same conditions as the larval stage until adult emergence. Wing length of the emerged adults was determined, which is a good indicator of body size, a parameter that is positively correlated with the fecundity of other predatory hoverfly species such as *Episyrphus balteatus* (De Geer) (Branquart and Hemptinne 2000b). Specifically, the shortest length between the junction of the costal vein (C) with the humeral crossvein (h) and the junction of R4 + 5 with the medial vein (M) was measured (Dziock 2005). Due to differences between males and females, measurements were analysed separately for each sex and always using the same wing (right or left), to avoid any effect due to asymmetry.

Statistical analysis

Data on weight and wing length were normally distributed and therefore were analysed with a one-way ANOVA and a two-way ANOVA respectively, followed by Tukey's post-hoc test for multiple pairwise comparisons. Time devoted to feed on each flower was transformed ($\log(x + 1)$) and then analysed with a linear mixed model, including 'sex' and 'flower species' as main factors and 'cage' as random grouping factor. A Kaplan–Meier survival analysis was used to evaluate the effect of 'sex' and 'flower species' on adult survival in the parental generation (Hosmer and Lemeshow 1999), and subsequently a log-rank test was used for pairwise comparisons. All other data were not normally distributed and therefore analysed with Generalized Linear Models (GLM), and an LSD post-hoc test for multiple pairwise comparisons. Estimated means and SE are presented in this paper. For visit frequencies, the model was adjusted to a Binomial distribution with logit link function with 'sex' and 'flower species' as the main factors, while 'cage' was included as a nested term to 'flower species'. Performance parameters of the parental generation (total fecundity, time to sexual maturation and adult life span) and developmental time of larvae and pupae in the F1 generation, were all analysed assuming a Poisson error structure of data and a log relationship between the response variable and the explanatory variables. A Binomial error structure of data and logit link function was used for fertility of the parental generation and adult emergence rate in the F1 generation. All data were analysed with the statistical packages SPSS V20.0 and Gen Stat 13.

Results

Syrphid floral preference

The average number of visits by syrphid adults was significantly different for the three flower species tested (df = 2; $\chi^2 = 16.25$; $P < 0.001$), with sweet alyssum being the species more frequently visited followed by coriander and sweet pepper in the last position (LSD test: $P < 0.05$) (Fig. 1a). The same pattern of preference was observed when the time feeding on each flowering plant was studied [df = 2, 102; $F = 13.28$; $P < 0.001$)] (Fig. 1b). The flies' sex did not have a significant effect on the number of visits nor on the feeding time.

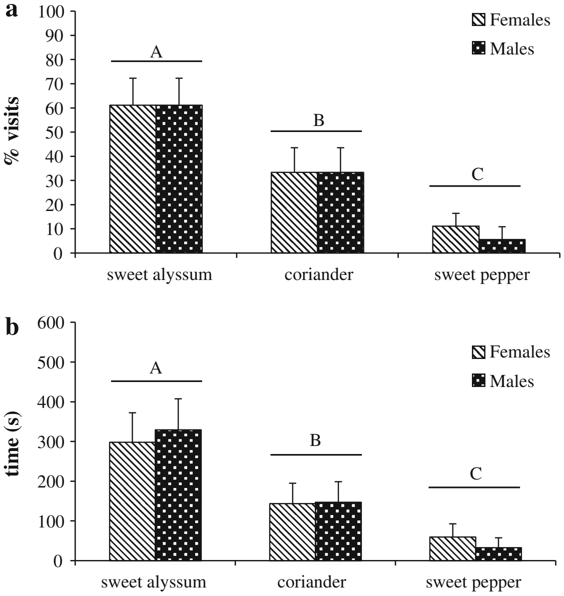

Fig. 1 Syrphid floral preference. Mean (+SE) percentage of flower visits (**a**) and feeding time (**b**) of male and female syrphid adults on each flower species. Different letters above bars indicate significant differences (LSD, $p < 0.05$)

Performance of the parental generation

Feeding on different flower resources had a strong impact on the number of eggs laid by *S. rueppellii* females. Total fecundity over 15 days was significantly higher for syrphids that had access to fresh coriander flowers (df = 2; Wald $\chi^2 = 30.7$; $P < 0.001$) (Fig. 2) whilst there were no statistical differences between sweet alyssum and sweet pepper (LSD test: $P > 0.05$). The GLM did not show a significant effect of flower species on total fertility (df = 2; Wald $\chi^2 = 3.06$; $P = 0.235$), and time to sexual maturation (df = 2; Wald $\chi^2 = 0.98$; $P = 0.616$) (Table 1). After observing that sex did not influence adult life span (data not shown), the effect of flower species was analysed using the Kaplan–Meier survival analysis, showing that they do not affect syrphid survival (log-rank; $\chi^2 = 0.66$, df = 2, $P = 0.717$).

Performance of the F1 generation

Flower species had a differential effect on the developmental time of *S. rueppellii* larvae (df = 2;

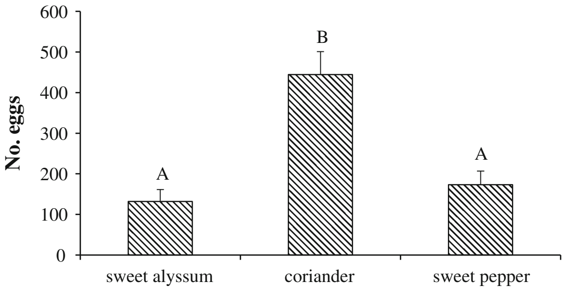

Fig. 2 Performance of the parental generation. Mean (+SE) total fecundity within 15 days (GLM, LSD) of female syrphid adults feeding on each flowering plant. Different letters above bars indicate significant differences ($p < 0.05$)

$\chi^2 = 140.9$; $P < 0.001$), which showed a faster development when the parental adults fed on flowers of sweet pepper plants, followed by those fed on sweet alyssum, and finally coriander (LSD test: $P < 0.05$) (Table 1). Contrary to what we expected, newly-formed pupae from the sweet pepper treatment weighed significantly more than those from the sweet alyssum and coriander treatments (df = 2, 104; $F = 36.01$, $P < 0.001$) (Table 1). In contrast, pupal developmental time was not affected by flower species (df = 2; $\chi^2 = 4.08$; $P = 0.135$). Interestingly, the flowering plant species on which the parents had fed had a significant effect on the survival of the next generation. The percentage of syrphids that became adults was significantly higher in the sweet alyssum treatment compared to the other flowers (df = 2; $\chi^2 = 6.91$; $P = 0.034$, LSD test: $P < 0.05$) (Fig. 3a). In the same way, flower species influenced the body size of these emerging adults (df = 2, 101; $F = 3.85$; $P = 0.025$), since feeding on sweet alyssum increased wing length of both sexes compared to coriander and sweet pepper, although statistical differences could only be found between sweet alyssum and coriander treatments (Fig. 3b). Females showed a greater wing length than males regardless of the flower species (df = 1, 101; $F = 117.56$; $P < 0.001$), a pattern that has already been shown in previous studies with the same species (Amorós-Jiménez et al. 2012).

Discussion

The present work reports for the first time on the preference towards three flowering plants of the predatory syrphid fly *S. rueppellii*. Sweet alyssum was the flower most frequently visited by *S. rueppellii* adults of both sexes, coriander was intermediate while sweet pepper flowers were visited to a lesser extent. Both sweet alyssum and coriander have been previously pointed out as two of the most attractive plant species for syrphids (Colley and Luna 2000; Ambrosino et al. 2006; Hogg et al. 2011), since both have flowers with a short corolla, facilitating the access to nectar and pollen, and white flowers which stimulate feeding in hoverflies (Branquart and Hemptinne 2000a; Colley and Luna 2000; Vattala et al. 2006). While differences in preferring either of these two species may vary among syrphid species, Tompkins et al. (2010) found a significant difference in the nectar sucrose:hexose ratio with a higher value in sweet alyssum flowers. Since the relative amounts of these sugars may be important for the attraction and fitness of flower visitors (Baker and Baker 1983; Fonta et al. 1985; Wäckers et al. 2006) these differences might also have influenced sweet alyssum's higher attractiveness to *S. rueppellii* adults. Sweet pepper flowers, on the other hand, provide large pollen and nectar

Table 1 Effect of each flowering plant on various fitness components of the parental and F1 generation (Mean ± SE)

	Sweet alyssum	Coriander	Sweet pepper
Parental generation			
Total fertility (%)	71.64 ± 6.91a	58.53 ± 4.35a	54.89 ± 6.66a
Sexual maturation time (days)	3.80 ± 0.31a	3.50 ± 0.29a	3.40 ± 0.29a
F1 generation			
Development time larva (days)	8.20 ± 0.09a	9.47 ± 0.11b	7.69 ± 0.11c
Development time pupa (days)	5.11 ± 0.07a	5.18 ± 0.07a	5.31 ± 0.08a
Pupal weight (mg)	9.63 ± 0.14a	9.86 ± 0.15a	11.40 ± 0.17b

Treatments within a row labelled with different letters are significantly different ($p < 0.05$)

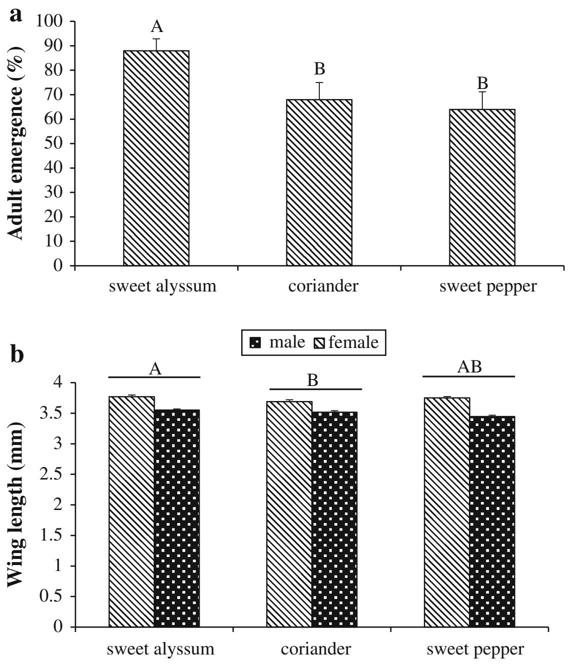

Fig. 3 Performance of the F1 generation. Mean (+SE) adult emergence rate (%) (GLM, LSD) (**a**) and wing length (mm) of male and female syrphid adults (two-way ANOVA, Tukey test) (**b**) fed with each flowering plant. Different letters above bars indicate significant differences ($p < 0.05$)

volumes, and floral rewards are also within easy access to pollinators (Rabinowitch et al. 1993). However, previous works have also reported a low attractiveness of sweet pepper flowers to honeybees and other Apoidea, presumably due to the poor sugar concentrations found in the flower nectar (McGregor 1976; Baker and Baker 1983) which could also explain the low attractiveness towards the syrphid fly found in this work.

Nevertheless, the most interesting result is the evidence that parental adult diet has an effect on offspring performance in syrphids. Several studies have already demonstrated that dietary conditions and other cues regarding the quality of the environment experienced by parents can be transmitted to the next generation's phenotype over and above the direct effect of transmitted genes, an influence known as transgenerational effects (Wolf and Wade 2009). Such adjustment may have maternal or paternal origin, although due to our experimental design, we are not able to distinguish between both effects and therefore we refer to them as parental effects. *S. rueppellii* parents fed with coriander flowers markedly laid more eggs that those fed with sweet alyssum or sweet pepper flowers. However, larvae whose parents collected pollen and nectar on coriander needed a longer time to complete their development, and produced smaller adults (although differences were only significant compared to the sweet alyssum treatment) pointing out that coriander might provide a relatively low nutritive floral resource compared to the other flowers tested. Insects can alter egg provisioning on the basis of maternal host plant experience and provide their progeny with resources accordingly (Awmack and Leather 2002). A possible outcome of parents experiencing low-quality food environments is that they invest less in offspring growth and more into maximising their own fitness (Marshall and Uller 2007) or into offspring traits that increase the chances of migrating into a high-quality habitat (Franzke and Reinhold 2013). According to this, we hypothesise that *S. rueppellii* adults increased the number of eggs laid as a way to offset negative effects of the non-optimal dietary conditions provided by coriander flowers, possibly resulting in more adults in the next generation with the potential to disperse to new areas. Yet, in exchange for this enhanced fecundity, possibly less resources were invested per egg, resulting in a longer developmental period and smaller body size of the next generation.

Prolonged larval duration is an indicator of reduced larval performance, as it may increase the exposure to predators, parasites or the risk of starvation (Cahenzli and Erhardt 2013), while a smaller body size is an indicator of poor performance due to a hampered foraging, reproductive rate, resource use or predator avoidance, among other factors (Harvey and Pagel 1991; Blackburn and Gaston 1994; Berwaerts et al. 2002). As a result, variation in body size due to parental effects may potentially affect the fitness of individuals across multiple generations (Steiger 2013). Feeding on sweet alyssum flowers, in turn, had a positive effect on the offspring's survival to adulthood, increasing this parameter with a minimum of 20 % compared to the other flowers. Furthermore, these adults had a larger body size. According to Mousseau and Fox (1998) and Qvarnstrom and Price (2001), individuals that experience high quality environments may be selected to transfer their good condition to enhance offspring performance. Consequently, offspring of parents from a resource-rich environment will perform best in both rich and poor environments. We believe that this could be the case for syrphids that fed on sweet alyssum flowers, as an enhanced survival and body size in the next generation may constitute a fitness benefit regardless of whether they exploit the same or different host plants as their parents.

Finally, *S. rueppellii* adults reared on sweet pepper flowers produced larvae with a reduced time of development in the next generation. Contrary to intuition and to our previous results (Amorós-Jiménez et al. 2012), these larvae also achieved a greater pupal weight than those whose parents were fed with sweet alyssum or coriander, which had a longer development. Because the sweet pepper treatment provides the only case in this work where both the parental and the F1 generation shared the same host plant (parentals used sweet pepper flowers as a trophic resource and produced immatures that developed on infested pepper plants), these results suggest that *S. rueppellii* parents might have acclimatised their offspring to the anticipated environment. Previous studies (e.g. Cahenzli and Erhardt 2013) have proven in insects that mothers may adjust the ability of their progeny's food intake according to their own experienced environment, which may explain the greater pupal weight achieved by syrphid larvae in the sweet pepper treatment. However, we did not measure aphid consumption rates of the F1 generation, so we lack data to confirm if these larvae had indeed an enhanced feeding rate or higher efficiency in the use of nutrients. Moreover, these results should be considered carefully, as this positive effect on performance was only apparent during the pupal stage, but it did not have ultimate positive effects on adult size nor on survival to adulthood. Adaptive parental effects have been proven for several phytophagous insects (e.g. Rotem et al. 2003; Cahenzli and Erhardt 2013) but this is the first time to our knowledge that such a phenomenon has been reported in a carnivorous insect.

The present work provides the first data on the specific way that performance of a predator syrphid is affected by two flowering plants, the suitability of which for attracting hoverflies and other natural enemies is already firmly accepted. By doing this, it gives valuable information about their usefulness as insectary plants in a context-dependent approach. Sweet alyssum seems to be the species that most positively affects performance of the next generation, increasing survival to adulthood and body size to the greatest extent. Such enhancements might potentially lead to a successful long-term establishment of syrphid populations in the field and thus it should be the flowering plant to preferably use in combination with inoculative releases of this agent. Moreover, its high attractiveness towards *S. rueppellii* adults of both sexes may ensure a high residence time on the crop, which is crucial for the effectiveness of preventive control of aphid pests with these predators (Pineda and Marcos-García 2008b). Based on our results, coriander does not arise as an optimal insectary plant when combined with inoculative releases of syrphids, due to the fact that performance parameters in the F1 are lowered as a result of feeding on its flowers. However, it also markedly boosted *S. rueppellii*'s egg-laying, which highly supports its use in combination with inundative releases. Finally, this work has shown that the provision of floral resources for natural enemies by the crop plants should be also taken in consideration. Despite the fact that some performance parameters (i.e. fecundity, survival) were higher when syrphids fed on non-harvestable plants, it is clear that pollen and nectar from sweet pepper flowers is suitable for the development and reproductive success of *S. rueppellii* even if no additional floral resources are available. Pineda and Marcos-García (2008d) showed that sweet pepper pollen was always present in the gut of predator syrphids that naturally entered greenhouses even if other flowering plants were present, and in some cases its presence in the syrphid's diet was more important than that of the introduced flowers. This indicates that syrphids that come from the outside or are released in the greenhouse regularly consume pepper pollen which in fact, according to our results, may enhance their performance in the coming generations through parental acclimatisation.

The fact that each flower species enhances different components of the syrphid's performance highlights the interest of combining several flowering plants in order to optimise the effect of habitat management strategies (Colley and Luna 2000). Further studies on the effect of different combinations of flowers on the performance of syrphids as well as on other biocontrol agents that depend on floral foods should be conducted. Also, disentangling transgenerational effects arises as a new and important dimension of research in habitat management through the addition of floral resources. Many more aspects of this phenomenon should be addressed, including the importance of temporal scale at which parental effects are observed, which seems to be central to interpreting their outcome (Marshall and Uller 2007).

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