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Effects of pollen, sugars and honeydew on lifespan and nutrient levels of *Episyrphus balteatus*

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Abstract Hoverflies require pollen, nectar and honeydew during their adult stage, but little is known about the suitability and nutrient provision of each of those resources. Thus, in this study we assessed the effect of different types of food, such as carbohydrates (glucose, fructose, sucrose and honey), pollen, a mixture of honey and pollen, and honeydew on longevity and nutrient levels of *Episyrphus balteatus* (De Geer) (Diptera: Syrphidae). Glucose and the mixture of pollen and honey were the food sources that gave the highest longevities. Considering nutrient levels in the body of hoverflies, sucrose generated high levels of fructose, total sugars and glycogen while glucose generated high levels of lipids. This suggests that carbohydrates are important food components for the survival and energy supply of hoverflies, with glucose being the most effective. Honeydew can also be used by hoverflies, representing a significant sugar source that may replace nectar when suitable flowers are scarce in agroecosystems.

Keywords Syrphidae · Survival · Glucose · Honeydew · Nutrient levels

Introduction

Hoverflies (Diptera: Syrphidae) are important insects in agroecosystems, providing essential services to the farmers such as biological control and pollination (Gilbert 1981). The larvae of predaceous hoverflies are potential biological control agents of a range of Sternorrhyncha pests, mainly aphids and psyllids (Bugg et al. 2008; Ksantini 2003; Rojo et al. 2003). On the other hand, adult hoverflies are highly dependent on nectar and honeydew, basically sources of carbohydrates for energy, to sustain flight and metabolism, and pollen, basically proteins, for sexual maturation (Gilbert 1981; Haslett 1989a; Laubertie et al. 2012). Thus, the availability of plant resources in agricultural fields has been considered as an essential requirement for enhancing survival and reproduction of hoverflies (Langoya and van Rijn 2008; Laubertie et al. 2012; Pinheiro et al. 2013a, 2013b; van Rijn et al. 2013). However, agricultural intensification resulted

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in the simplification of the landscape and a consequent scarcity of flowering plants that sustain these beneficial insects (Bianchi et al. 2006). Promoting the implementation of floral resources in agroecosystems may be a sustainable way to improve the abundance of hoverflies for a more effective biological control of pests (Haenke et al. 2009; Ricarte et al. 2011).

Plant species such as sweet alyssum (*Lobularia maritima* L. Desv.), coriander (*Coriandrum sativum* L.), phacelia (*Phacelia tanacetifolia* Benth.), fennel (*Foeniculum vulgare* Mill.), buckwheat (*Fagopyrum esculentum* Moench) and common mallow (*Malva sylvestris* L.) have been referred to as useful non-crop plants that enhance longevity and fecundity of adult hoverflies (Ambrosino et al. 2006; Colley and Luna 2000; Laubertie et al. 2012; Nicholls et al. 2001; Pineda and Marcos-García 2008; Pinheiro et al. 2013b; White et al. 1995), mainly gravid females (Irvin et al. 1999). The amount and accessibility of pollen and nectar produced by these plants can have a significant effect on the performance of hoverflies. Pollen is the main source of amino acids and according to Haslett (1989b), hoverflies can take nutrients from pollen even if they cannot digest the exine. Nectar is a source of energy mainly composed of sucrose, glucose and fructose as well as of other sugars and several amino acids represented in low concentrations (Nicolson and Thornburg 2007; Petanidou et al. 2006).

At sufficient Sternorrhyncha densities, either on infested crop or non-crop plants, the honeydew produced by these sap-sucking insects may even be used by hoverflies as a supplementary source of sugars (van Rijn et al. 2013). Although the composition of the honeydew depends on the insect and host plant interaction, sucrose, fructose and glucose are among the most abundant sugars commonly found in honeydew. Besides, honeydew also contains other oligosaccharides which are less common or inexistent in floral nectar (Wäckers 2001). Previous studies showed that survival and oviposition rate were favoured in *Episyrphus balteatus* (De Geer) in the presence of aphid honeydew (Scholz and Poehling 2000; van Rijn et al. 2013).

Despite the relative contribution of each naturally occurring food source (pollen, nectar and honeydew) to adult lifespan, little is known about the suitability of each of these foods and individual carbohydrates for hoverflies. It is expected that each food source influences longevity and also nutrient levels (sugars, glycogen and lipids) of hoverflies in different ways. Accordingly, the objective of this study was to obtain an overview of the nutrient utilization by *E. balteatus* of pollen, honeydew and different carbohydrates and compare their effects on longevity. The honeydew tested was obtained from the black scale, *Saissetia oleae* (Olivier) (Hemiptera: Coccidae), and was chosen because (i) scale honeydew was never tested on *E. balteatus*, (ii) the black-scale is a cosmopolitan pest hosted by several plant species including citrus, olives as well as ornamental trees and shrubs (e.g. *Nerium oleander* L.) (Noguera et al. 2003; Panis 1977; Santos et al. 2010) and (iii) throughout the year, the black scale honeydew can be the main resource in intensive crops in the Mediterranean region, helping to maintain hoverflies in agroecosystems or even supporting their migratory flights when searching for oviposition sites.

Materials and methods

Hoverflies

Episyrphus balteatus were purchased from Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands) and were supplied in the pupal stage. In the laboratory, *E. balteatus* pupae were held in plastic cages (4.5 × 7.5 cm) with a moistened filter paper and a perforated lid. Plastic cages were placed in a climate chamber at 21 ± 1 °C, 70 ± 5 % relative humidity (RH), and a photoperiod of 16:8 (L:D) h till emergence of adults. Newly emerged hoverflies were paired and 50 individuals of *E. balteatus* (25 males and 25 females) were used for each diet. In addition and as a reference of initial nutrient levels before feeding, a second group of 50 unfed newly emerged (<24 h) individuals of *E. balteatus* (25 males and 25 females) was immediately frozen and stored at −20 °C for further assays.

Food sources

The food sources tested were: bee-collected pollen obtained from an organic beekeeper, commercial organic honey (as mimic for nectar), two monosaccharides (D-(−)-fructose ≥ 99 % and D-(+)-glucose ≥ 99 %, purchased from Acros Organics, Geel, Belgium), a disaccharide (D-(+)-sucrose ≥ 99 %, purchased from Fisher Scientific, Leicestershire, UK and *S. oleae* honeydew. *Saissetia oleae* (not a prey item for hoverflies) was reared on small olive trees in a climate chamber at 24 ± 1 °C, 70 ± 5 % RH and a photoperiod of 16:8 h (L:D).

Longevity

For the longevity experiment, cylindrical cages of 21 cm height and 9 cm in diameter were used. The wall was made from a colourless acetate sheet, a plastic Petri dish formed the top and another plastic cup formed the basis of the cage. The ventilation inside the cage was assured by multiple perforations in the acetate sheet. Female and male *E. balteatus* were kept with one of the following diets: (1) water only (starved – negative control), (2) honey at a solution of 10 % (v/v), (3) fructose, (4) glucose and (5) sucrose at solutions of 1 M, (6) moist powdered pollen (0.5 g), (7) honey at a solution of 10 % and moist powdered pollen (0.5 g), and (8) *S. oleae* honeydew. Water was also provided in all diet treatments.

Pairs of newly emerged individuals were placed in each cylindrical plastic cage and presented with one of the diets mentioned above. Fifty individuals of *E. balteatus* (25 males and 25 females) were used for each treatment. Water and the solutions of honey, fructose, glucose and sucrose were provided by filling a 3 ml glass vial fitted with a strip of an absorbent cloth through a hole in the cap of the vial. Moist powdered pollen was placed on a strip of cloth. Each diet was changed every two days. *Saissetia oleae* honeydew was collected by placing overnight a Parafilm© strip under infested leaves and this diet was changed every day. Cages were kept in a climate chamber at 21 ± 1 °C, 70 ± 5 % RH, and a photoperiod of 16:8 (L:D) h and checked for insect survival on a daily basis. Dead hoverflies were promptly removed, labeled and stored at −20 °C for further analyses.

Nutrient levels analysis

Nutrient levels (fructose, total sugars, lipids and glycogen) in hoverflies were quantified in adult females and males of *E. balteatus* derived from the longevity experiments and in newly emerged specimens. Levels of fructose, total sugars, lipids and glycogen were quantified in individual hoverflies using a series of biochemical tests adapted from van Handel (1985a, b) and Fadamiro et al. (2005). Fructose levels were quantified in order to assess the amount of this monosaccharide in the gut, while total sugars, glycogen and lipids were quantified to assess energy reserves. Each hoverfly was crushed with a plastic pestle in a 1.5 ml microcentrifuge tube containing 100 µl of 2 % sodium sulphate solution and 900 µl of chloroform–methanol (1:1), after which the tube was vortexed and placed on ice. The mixture was centrifuged at 13,200 rpm for 4 min at 4 °C and 50 µl of the resulting supernatant was transferred to a 1.5 ml microcentrifuge tube for further analyses of fructose and total sugars and 50 µl from the lower layers of the mixture were transferred to another 1.5 ml microcentrifuge tube for lipid analysis. The remaining supernatant was discarded and the precipitate was kept in the 1.5 ml microcentrifuge tube for glycogen analysis. For each of the nutrients described below, a blank tube was run alongside, following the same procedure of the samples.

Fructose analysis

950 µl of anthrone reagent was added to the 50 µl solution in the 1.5 ml microcentrifuge tube, vortexed and left to react at room temperature for 1 h 30 min (cold anthrone test). After the reaction time had elapsed, the solution was poured into a 1.5 ml methacrylate cuvette and the absorbance measured at 625 nm using a spectrophotometer. Absorbance readings were converted to absolute fructose amounts (µg), using fructose standard curves generated by determining the cold anthrone absorbance (at 625 nm) of different amounts of fructose ranging from 0 to 50 µg, in triplicate per dose. This amount was then multiplied by a factor of 20 because only 50 µl of the original 1 ml was used for the fructose assay.

Total sugars analysis

The same solution used for the cold anthrone test was poured back into the previous 1.5 ml microcentrifuge tube, heated at 90 °C for 10 min and cooled on ice. The absorbance was read at 625 nm to give an estimate of total sugars (hot anthrone test). Absorbance readings were converted to absolute amounts (µg), using sucrose standard curves generated by determining the hot anthrone absorbance (at 625 nm) of different amounts of sucrose ranging from 0 to

50 µg, in triplicate. The absolute amount of total sugars present in each hoverfly was estimated by multiplying the amount of sugars from the hot anthrone test by 20 because only 50 µl of the original 1 ml was used.

Glycogen analysis

The amount of glycogen was estimated by adding 1 ml of anthrone reagent to the 1.5 ml microcentrifuge tube containing the precipitate. After vortexing, tubes were heated at 90 °C for 10 min and then cooled on ice and the absorbance read at 625 nm. Absorbance readings were converted to absolute glycogen amounts (µg) using glycogen standard curves generated by determining the absorbance (at 625 nm) of different amounts of glycogen from oyster (Sigma-Aldrich, Steinheim, Germany), ranging from 0 to 125 ml, in triplicate. The amount of glycogen estimated above was considered to be representative of the whole hoverfly because all glycogen in the sample is presumed to precipitate to the bottom of the tube.

Lipid analysis

The different batches of 1.5 ml microcentrifuge tubes with 50 µl of solution for the lipid analysis were heated at 90 °C for complete evaporation of the solution. 40 µl of sulfuric acid was added and heated at 90 °C for 2 min followed by ice cooling of the samples. 960 µl of vanillin phosphoric acid was added to the new solution, vortexed and left to react at room temperature for 30 min. After the reaction time had elapsed, the solution was poured into a 1.5 ml methacrylate cuvette and the absorbance was measured at 525 nm using a spectrophotometer. Absorbance readings were converted to absolute lipid amounts (µg), using lipid standard curves generated by determining the vanillin absorbance (at 525 nm) of different amounts of soybean oil (Sigma-Aldrich, Steinheim, Germany) ranging from 0 to 200 µl, in triplicate. This amount was then multiplied by a factor of 20 because only 50 µl of the original 1 ml was used for the lipid assay.

When the nutrient levels measures in *E. balteatus* were very high it was necessary to dilute the initial 50 µl of the original 1 ml in 5–9 ml of each solution for fructose, total sugars, glycogen and lipid analyses in order to enable reading of absorbance.

Data analysis

Statistical analyses were performed with IBM-SPSS statistics, version 19.0.0 (SPSS Inc. IBM Company 2010). The normal distribution of the residuals and the homogeneity of variances were evaluated by means of the Kolmogorov–Smirnov and Levene's tests, respectively. Longevity and nutrient analyses were conducted for comparison among treatments and sex by using general linear models to test the effects of treatment, sex and treatment × sex, followed by the Tukey–Kramer HSD test.

Survival curves were generated and compared using Kaplan–Meier estimates of the function "Survdiff" from the "survival" package in R (R Core Team 2014). A log-rank or Mantel–Haenszel test was used to account for each of the pair-wise comparisons. In this case, the Bonferroni correction was applied in order to avoid false significant effects by random chance.

All statistical tests were performed at 5 % significance level. Data are presented as mean values ± 1 standard error (SE).

Results

Longevity

The different treatments had a significant effect on the longevity of *E. balteatus* but neither the sex nor the treatment × sex interaction were significant (Table 1). There was a highly significant effect of the different food sources on longevity, compared to the water only treatment (Table 2). The food sources that gave higher values of female longevity were glucose (1 M) with 14.08 days, honey 10 % + pollen with 13.60 days, honey (10 %) and pollen, both with 11.96 days. Different results were obtained for male hoverflies that showed higher longevities when fed on honey (10 %) with 13.96 days, glucose (1 M) with 13.76 days, honey 10 % + pollen with 12.08 days and sucrose (1 M) with 11.00 days (Table 2). The mean longevity of *E. balteatus* fed on glucose was 7.64 times greater in males and 7.65 times in females than the mean longevity of individuals fed on water only (Table 2). *E. balteatus* fed on black scale honeydew and fructose had significantly lower longevities (4.32 and 7.42 days, respectively) when compared with the other food sources. However, these

Table 1 Results of ANOVA for longevity, and levels of fructose, other sugars, glycogen and lipids in *Episyrphus balteatus*, n = 50

	df	F	P
Longevity			
Treatment	7, 384	123.758	< 0.001
Sex	1, 384	0.132	0.716
Treatment × Sex	7, 384	1.863	0.074
Fructose			
Treatment	4, 240	19.990	< 0.001
Sex	1, 240	0.823	0.365
Treatment × Sex	4, 240	0.127	0.972
Other Sugars			
Treatment	7, 384	85.321	< 0.001
Sex	1, 384	1.017	0.314
Treatment × Sex	7, 384	1.177	0.315
Glycogen			
Treatment	8, 432	58.219	< 0.001
Sex	1, 432	0.874	0.350
Treatment × Sex	8, 432	0.856	0.554
Lipids			
Treatment	8, 432	51.604	< 0.001
Sex	1, 432	2.015	0.156
Treatment × Sex	8, 432	0.501	0.855

two treatments yielded significant differences when compared with individuals fed on water only (Table 2). Sucrose was the only treatment with significant differences between sexes in terms of longevity, resulting in significantly higher longevities for males than for females.

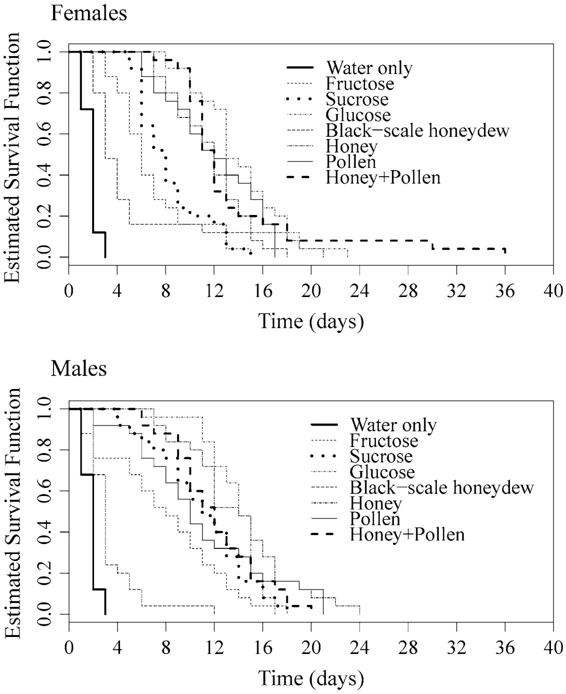

Fig. 1 Kaplan-Meier estimates of the survival functions of females and males of *Episyrphus balteatus* provided with water only, fructose, glucose, sucrose, black-scale honeydew, honey, pollen or honey + pollen

Survival curves for both sexes differed significantly among treatments (females: $\chi^2 = 254$; d.f. = 7, $P < 0.001$; males: $\chi^2 = 186$, d.f. = 7, $P < 0.001$; Fig. 1). Females survived significantly longer when fed on honey + pollen, glucose, honey and pollen when compared with the other four treatments and no

Table 2 Longevity (mean ± SE) of *Episyrphus balteatus* adults on each food source tested and water only, n = 25 for females and males, n = 50 for total

Treatments	Longevity (days)		
	Male	Female	Total
Water only	1.80 ± 0.13^{d}	1.84 ± 0.12^{d}	1.82 ± 0.09^{f}
Fructose	7.92 ± 0.97^{b}	6.92 ± 0.67^{b}	7.42 ± 0.59^{d}
Glucose	13.76 ± 0.48^{a}	14.08 ± 0.73^{a}	13.92 ± 0.44^{a}
Sucrose	11.00 ± 0.79^{a}	8.32 ± 0.57^{b}	9.66 ± 0.52^{c*}
Black-scale honeydew	3.48 ± 0.43^{c}	5.16 ± 0.92^{c}	4.32 ± 0.52^{e}
Honey 10 %	13.96 ± 0.90^{a}	11.96 ± 0.75^{a}	12.96 ± 0.60^{ab}
Pollen	10.96 ± 1.12^{a}	11.96 ± 0.78^{a}	11.46 ± 0.68^{cb}
Honey 10 % + Pollen	12.08 ± 0.75^{a}	13.60 ± 1.28^{a}	12.84 ± 0.74^{ab}

Means within a column with the same letter are not significantly different at $p < 0.05$

The asterisk indicates that females and males had significantly different longevities for the same food source at $p < 0.05$

Table 3 Fructose contents (mean ± SE) in *Episyrphus balteatus* for adults fed on each food source tested, water only and for newly emerged individuals; n = 25 per treatment for females and males, n = 50 per treatment for total

Treatments	Fructose ($\mu g\ ml^{-1}$)		
	Male	Female	Total
Newly emerged	0	0	0
Water only	0	0	0
Fructose	307.29 ± 62.01^{a}	493.61 ± 100.53^{a}	400.45 ± 59.95^{a}
Glucose	0	0	0
Sucrose	695.00 ± 152.95^{a}	698.25 ± 116.94^{a}	696.62 ± 95.28^{a}
Honeydew black scale	0	0	0
Honey 10 %	99.65 ± 39.34^{b}	96.53 ± 29.29^{b}	98.09 ± 24.28^{b}
Pollen	65.04 ± 18.03^{b}	60.31 ± 17.91^{b}	62.68 ± 12.58^{b}
Honey 10 % + Pollen	68.91 ± 29.05^{b}	89.75 ± 24.84^{b}	79.33 ± 19.97^{b}

Means within a column followed by the same letter are not significantly different at $p < 0.05$

significant differences were found among those treatments. Males survived longer when fed on honey, but no significant differences were found between that treatment and pollen or honey + pollen. When offered black scale honeydew, some individual hoverflies survived up to 18 days (for females) and 12 days (for males). Survival was significantly higher than that recorded in the water only treatment (females: $\chi^2 = 28$, d.f. = 1, $P < 0.001$; males: $\chi^2 = 20.5$, d.f. = 1, $P < 0.001$) (Fig. 1) and no significant differences were found, for females, between black scale honeydew and fructose treatments ($\chi^2 = 2.6$, d.f. = 1, $P = 0.106$).

Body nutrient analysis

Episyrphus balteatus showed a variable distribution of nutrient levels resulting from the different treatments. Fructose was detected only in individuals fed on fructose, sucrose, honey, pollen and honey + pollen (Table 3). The highest levels of fructose were detected in females and males fed on sucrose followed by fructose (696.62 and 400.45 $\mu g\ ml^{-1}$, respectively), although no statistically significant differences were found between these two treatments (Table 3).

In relation to the levels of other sugars in the body of hoverflies, only individuals fed on pollen and black scale honeydew presented statistically significant lower values than the newly emerged ones (Table 4). In the case of the water only treatment, the levels of other sugars were detected only in three individuals out of 50 analyzed (two females with 14.80 and 56.28 $\mu g\ ml^{-1}$ and one male with 155.84 $\mu g\ ml^{-1}$). The highest levels were obtained in males and females fed on sucrose, fructose and glucose (Table 4). Females fed on fructose contained significantly higher levels of other sugars than males (Table 4). The levels of fructose and other sugars were not significantly influenced by sex and treatment × sex interaction (Table 1).

Glycogen levels were higher in individuals fed on sucrose and fructose (700.76, 503.80 $\mu g\ ml^{-1}$, respectively) and the differences between sexes were not statistically significant (Table 5). On the other hand, the lowest levels of glycogen were registered in individuals fed on pollen, black scale honeydew, water only and honey + pollen. Glycogen levels were influenced by treatment but not by sex and treatment × sex interaction (Table 1).

The highest lipid levels were measured in individuals fed on glucose (703.44 $\mu g\ ml^{-1}$ for males and 636.21 $\mu g\ ml^{-1}$ for females), although no statistically significant differences were found between adults offered this food source and the newly emerged individuals. The lipid levels were significantly higher in males than in females fed on sucrose (Table 6).

Discussion

The results show that female and male *E. balteatus* are able to feed on all the food sources provided in this study, since their lifespan significantly increased when compared with individuals fed on water only. At the nutritional level, hoverflies emerged with high capital reserves (nutrients that are acquired during the larval stage and used during the adult stage) of sugars, lipids and glycogen. However, after two or three days

Table 4 Total sugar contents (mean ± SE) in *Episyrphus balteatus* for adults fed on each food source tested, water only and for newly emerged individuals; n = 25 per treatment for females and males, n = 50 per treatment for total

Treatments	Other sugars (μg ml^{-1})		
	Male	Female	Total
Newly emerged	206.90 ± 37.62^{d}	277.71 ± 68.86^{c}	242.30 ± 39.16^{b}
Water only	–	–	–
Fructose	573.86 ± 80.98^{abc}	954.95 ± 109.51^{ab}	$764.40 \pm 72.69^{a*}$
Glucose	740.12 ± 82.92^{ab}	706.28 ± 89.31^{ab}	723.20 ± 60.36^{a}
Sucrose	$1{,}573.60 \pm 330.30^{a}$	$1{,}472.37 \pm 194.13^{a}$	$1{,}522.98 \pm 189.74^{a}$
Honeydew black scale	27.27 ± 9.69^{e}	13.04 ± 5.92^{d}	20.15 ± 5.71^{d}
Honey 10 %	$244.33 \pm 42.47\ ^{cd}$	315.52 ± 62.22^{c}	279.92 ± 37.63^{b}
Pollen	85.30 ± 20.93^{e}	69.73 ± 24.22^{d}	77.52 ± 15.88^{c}
Honey 10 % + Pollen	261.83 ± 36.76^{bcd}	376.16 ± 70.39^{bc}	319.00 ± 40.14^{b}

Means within a column followed by the same letter are not significantly different at $p < 0.05$

The asterisk indicates that nutrient levels in females and males were significantly different for the same food source at $p < 0.05$

Table 5 Glycogen contents (mean ± SE) in *Episyrphus balteatus* for adults fed on each food source tested, water only and for newly emerged individuals; n = 25 per treatment for females and males, n = 50 per treatment for total

Treatments	Glycogen (μg ml^{-1})		
	Male	Female	Total
Newly emerged	55.21 ± 4.64^{bc}	$54.21 \pm 3.93\ ^{cd}$	$54.71 \pm 3.01\ ^{cd}$
Water only	28.54 ± 5.48^{d}	26.37 ± 4.74^{e}	27.45 ± 3.59^{e}
Fructose	464.71 ± 86.49^{ab}	542.88 ± 90.70^{b}	503.80 ± 62.27^{ab}
Glucose	278.24 ± 31.17^{a}	265.52 ± 33.58^{b}	271.88 ± 22.69^{b}
Sucrose	625.30 ± 115.09^{a}	776.21 ± 94.47^{a}	700.76 ± 74.47^{a}
Honeydew black scale	$28.46 \pm 1.02\ ^{cd}$	26.99 ± 1.85^{de}	27.71 ± 1.05^{de}
Honey 10 %	137.12 ± 21.28^{b}	126.92 ± 21.11^{c}	132.02 ± 14.85^{c}
Pollen	24.77 ± 2.55^{c}	29.41 ± 5.10^{de}	27.09 ± 2.84^{e}
Honey 10 % + Pollen	33.27 ± 2.30^{d}	32.32 ± 3.20^{de}	27.25 ± 2.06^{e}

Means within a column followed by the same letter are not significantly different at $p < 0.05$

feeding on only water, capital reserves (especially sugars) declined significantly. On the other hand, hoverflies mainly benefited from the ingestion of glucose, fructose and sucrose for which sugar and glycogen levels exceeded those measured in the newly emerged and water only fed individuals. This suggests that an ad libitum provision of 1 M solutions of those carbohydrates resulted in high levels of food consumption and energy conversion. Nevertheless, glucose and sucrose (9–14 days) promoted longer lifespans than fructose (7–8 days). As Wäckers (1999) pointed out, the suitability of a sugar as food source is determined at the sensory level (it must be detectable by receptor cells and elicit a gustatory response) and at the physiological level (digestion and energy convertibility). Thus, a natural enemy will feed on a sugar source if it is able to perceive the different molecules. As found by Wacht et al. (2000), the receptor cells of the hoverfly *Eristalis tenax* (L.) (Diptera: Syrphidae) responded most strongly to sucrose and glucose, while fructose was less detectable by the fly. This probably suggests that, in our study, fructose was less consumed by *E. balteatus* than glucose and sucrose. This idea is supported by the levels of fructose measured in the gut of individuals fed on sucrose (a glucose-fructose disaccharide), which reached about twofold the levels of fructose measured in individuals fed on fructose (Table 3).

Sucrose, glucose and fructose are the dominant sugars in nectars (Petanidou et al. 1996) and are also found in honeydew (Davidson et al. 1994) and pollen (Stanley and Linskins 1974). Considering sugar

Table 6 Lipid contents (mean ± SE) in *Episyrphus balteatus* for adults fed on each food source tested, water only and for newly emerged individuals; n = 25 per treatment for females and males, n = 50 per treatment for total

Treatments	Lipids (µg ml^{-1})		
	Male	Female	Total
Newly emerged	517.63 ± 45.88^{a}	465.65 ± 41.05^{ab}	491.64 ± 30.69^{a}
Water only	117.27 ± 61.55^{c}	84.74 ± 30.57^{hf}	101.01 ± 34.09^{ce}
Fructose	184.10 ± 30.76^{b}	151.28 ± 28.69^{ef}	167.69 ± 20.95^{be}
Glucose	703.44 ± 48.60^{a}	636.21 ± 51.59^{a}	669.82 ± 35.40^{a}
Sucrose	635.84 ± 62.75^{a}	348.16 ± 43.40^{abc}	$492.00 \pm 42.99^{a*}$
Honeydew black scale	63.79 ± 5.62^{c}	142.73 ± 55.12^{cef}	103.26 ± 27.99^{c}
Honey 10 %	64.56 ± 33.83^{c}	35.39 ± 19.13^{h}	49.97 ± 19.34^{e}
Pollen	198.15 ± 28.45^{b}	227.18 ± 49.25^{de}	212.66 ± 28.22^{b}
Honey 10 % + Pollen	102.86 ± 23.00^{c}	260.19 ± 172.47^{bd}	181.53 ± 86.84^{bc}

Means within a column followed by the same letter are not significantly different at $p < 0.05$

The asterisk indicates that nutrient levels in females and males were significantly different for the same food source at $p < 0.05$

composition in nectars, measured as sucrose/hexose (glucose + fructose) ratio, Petanidou (2005) found that hoverflies prefer high hexose-nectars. These types of nectars are produced in larger amounts, are more common, more diluted and easily absorbed in the gut of insects than sucrose-rich nectars (Nicolson 1998). Hexose-rich nectars are commonly found in open flowers that can be more easily explored by insects with a short proboscis, such as hoverflies (Petanidou 2005). In addition, nectars can be the only source of water in many agroecosystems (Petanidou 2007). Honey was used in this study as a mimic of a hexose-rich nectar. Although honey can include trace amounts of proteins, enzymes or amino acids, mainly due to the presence of pollen, it is composed of high levels of glucose and fructose (that can account for 85–99 % of honey dry matter) and low levels of sucrose (Ball 2007; Krell 1996). Longevity of individuals fed on honey was similar to that fed on glucose only which shows the importance of this monosaccharide for the lifespan of hoverflies. However, nutrient levels determined in individuals fed on honey were significantly lower than on glucose, probably because the concentration of this sugar in honey (10 %) was about 3.8 times below its concentration in the glucose solution 1 M (considering that the concentration of glucose in honey is, on average, 35 % -w/w- and density is about 1.36 kg l^{-1}) (Krell 1996).

Honeydew is another important source of energy for hoverflies. The black scale honeydew favored the survival of *E. balteatus*, mainly in the case of females, when compared with the water only treatment, but longevity was significantly lower than on the other food sources. Honeydew has a greater diversity of sugars and other nutrients when compared with nectars and can be the main carbohydrate source in many agroecosystems (Wäckers and Swaans 1993). The black scale honeydew is mainly composed of the sugars trehalose (193.3 mg g^{-1}), sucrose (25.0 mg g^{-1}), glucose and melibiose (24.9 mg g^{-1}) (L. Torres, data not published). However, in comparison to nectar, honeydew has often an inferior nutritional suitability for natural enemies (Wäckers 2001), which can be based on the action of secondary metabolites produced by plants against herbivorous insects (Kos et al. 2011) or on pest synthesized compounds (Wäckers 2000). Both sugar composition and the occurrence of plant-derived defensive chemicals can explain the results obtained with *E. balteatus* fed on black scale honeydew. Nevertheless, honeydew can be an alternative or supplementary resource as it was already reported for *E. balteatus* (Langoya and van Rijn 2008; van Rijn et al. 2006) and for males of *Syrphus ribesii* (L.) (Diptera: Syrphidae) fed on nectar and honeydew from *Acer* (Gilbert 1984). Moreover, when hoverflies are unable to exploit the nectar, i.e., when the proboscis length is not adequate to the flower anatomy, honeydew may easily be explored. Besides, the black scale honeydew may represent a source of sugars helping to support hoverflies in agricultural areas where vegetation has been removed.

Consumption of pollen resulted in high longevity, similar to that obtained by individuals fed on glucose and honey. Moreover, results obtained for nutrient levels showed that pollen was a source of fructose and other sugars, probably because bee-collected pollen used in this study has small amounts of honey that bees use to aggregate pollen grains. In the field, pollen is the main source of proteins for hoverflies and, usually, females consume larger amounts of pollen grains than males (Irvin et al. 1999; Haslett 1989a; Hickman et al. 1995; Wratten et al. 1995). Pollen is considered an essential resource for *E. balteatus* females that are unable to produce eggs when fed on sucrose and honeydew, but promptly begin oviposition when pollen is provided (Lundgren 2009). Moreover, Haslett (1989a) showed that the amount of pollen consumed by hoverflies depends on the stage of reproduction. Males need an initial amount of pollen for spermatogenesis while females need greater amounts, and for a longer period, for ovary maturation and egg production (Branquart and Hemptinne 2000; Gilbert 1981, 1985). Hoverflies were able to convert sugars into lipids, contrarily to many species of parasitoids (Fadamiro et al. 2005; Giron and Casas 2003). Apparently, pollen, honey and honeydew did not contribute to replace capital lipids. But, for hoverflies fed on pollen and honey + pollen, differences found in lipid levels could be influenced by the activation of gametogenesis in those individuals (this should be clarified in further studies).

In conclusion, hoverflies mainly benefited from the consumption of sugars and pollen that significantly increased longevity and contributed to the maintenance of the nutrient levels. Honeydew was a less suitable food source when compared with the other types of food tested, although it improved the longevity of hoverflies when compared with water fed individuals. The occurrence of these resources in agroecosystems is crucial to satisfy the specific needs of hoverflies and maintain them in the crop.

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