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ORIGINAL PAPER

Effect of different dietary resources on longevity, carbohydrate metabolism, and ovarian dynamics in two fruit fly parasitoids

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Abstract A growing body of literature reports the importance of non-prey food sources in boosting fitness of arthropod natural enemies, thus further contributing to their pest control efficacy. Although resources such as nectar, pollen, or honeydew have received a fair amount of research attention, little is known about the role of fruit juices. Under natural conditions, Tephritid fruit fly parasitoids enjoy ample access to fallen or damaged fruits and their saccharide-rich juices, and wasp fitness can potentially benefit in multiple ways from access to these resources. In this study, we compared the effect of fruit juice with other food resources on multiple fitness parameters in parasitoids that commonly forage on fallen, damaged fruits: the braconid *Diachasmimorpha longicaudata* and figitid *Aganaspis pelleranoi*. Parasitoids were subject to simple or combined diets of guava juice (*Psidium guajava*), honey and pollen, and their effect on wasp longevity, ovarian dynamics and (body) carbohydrate levels was assessed. For both species, adult longevity proved lowest on simple diets of water, guava juice, or pollen, while greatest longevity was attained on honey or combined diets. For *D. longicaudata*, egg load did not differ between the various diets, while *A. pelleranoi* egg load was higher for individuals that had access to honey or pollen, but did not differ between newly emerged wasps and those fed guava juice. In both parasitoid species, total sugars, fructose, and glycogen levels were highest in wasps fed with honey or combined diets and lowest under (simple) guava juice, pollen, or water diets. In conclusion, *D. longicaudata* and *A. pelleranoi* attained superior longevity and body nutrient levels with access to high-sucrose sugar sources, such as honey, but benefited comparatively little from access to guava juice. Our work hints the role of high-sucrose foods such as (extra-) floral nectar or artifical sugar sprays in boosting fitness of fruit fly parasitoids. We further discuss the relevance of these findings for fruit fly biological control, in crops such as guava.

Keywords Biological control · Fruit fly parasitoids · Nutritional physiology · Fitness · Longevity · Sugar levels · Egg load

Introduction

For many natural enemies, overall fitness, lifetime reproductive success, and ultimate pest control efficacy inherently depend upon their access to key resources, including non-prey foods (e.g., Tylianakis et al. 2004; Heimpel and Jervis 2005). Sugar-rich foods such as (extra-)floral nectar help satisfy energetic requirements of several parasitoids (e.g., Jervis et al. 1996; Wäckers 2005; Lundgren 2009).

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Access to nectar regularly augments longevity (Idris and Grafius 1995; Wyckhuys et al. 2008), fecundity (Baggen and Gurr 1998; Winkler et al. 2006), and overall activity of parasitic wasps (Takasu and Lewis 1994; Wäckers 1994). Similarly, resources such as pollen provide valuable nutrients for a myriad of natural enemy guilds (Majerus 1994; Canard 2001; Gilbert 1986) and benefit fitness of several parasitoid species (Hickman et al. 1995; Eijs et al. 1998). Next, honeydew is receiving growing attention as a food source for several predators and parasitoids (Wäckers et al. 2008; Dulaurent et al. 2011). However, one sugar-rich food that has received comparatively little attention is fruit pulp or juice (but see Eijs et al. 1998; Bautista et al. 2001; Sivinski et al. 2006; Hein and Dorn 2008; Yokoyama et al. 2011). Fruit juices are widely available in temperate and tropical fruit cropping systems and constitute major sources of multiple sugars (e.g., Brecht and Yahia 2009). In the meantime, countless natural enemies maintain an intimate connection with fruits, with some species even "swimming" in fruit pulp during host foraging (Ovruski 1994). Hence, fruit juices could be essential, yet under-studied, food resources for some of the natural enemies of high-profile pests, such as Tephritid fruit flies.

Fruit flies (Diptera: Tephritidae) are key pests of horticultural crops in the (sub-)tropics (White and Elson-Harris 1992; Aluja 1993). To control these pests, insect parasitoids have been used in many parts of the Americas (e.g., Ovruski et al. 2000; Montoya et al. 2009). Even though past efforts greatly promoted the mass release of exotic parasitoids, native species are increasingly incorporated in current biological control programs (Ovruski et al. 2000; Palenchar et al. 2009). The parasitoid *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) has been released in many parts of the globe for control of *Ceratitis capitata*, *Bactrocera dorsalis,* and several *Anastrepha* species (Montoya et al. 2003; Wang and Messing 2004; Cancino et al. 2009). Unlike some other fruit fly parasitoids, *D. longicaudata* forages both on infested fruit on the tree and on damaged fruit on the ground (Purcell et al. 1994). This parasitoid attacks a range of fruit fly pests in guava (*Psidium guajava*) orchards, among others (e.g., Purcell et al. 1998). On the other hand, *Aganaspis pelleranoi* (Hymenoptera: Figitidae) is a native parasitoid in the Neotropics and attacks fruit fly species, such as the tephritids *C. capitata* and *Anastrepha* spp. and the lance fly *Neosilba batesi* (Wharton et al. 1998; Ovruski et al. 2000). In many parts of Latin America, *A. pelleranoi* is a key parasitoid of fruit flies on guava (Nuñez et al. 2004). This parasitoid commonly forages for hosts in fallen fruits (Ovruski et al. 2004), with female wasps penetrating the fruit through cracks and crevices and moving within the pulp in search of host larvae (Ovruski 1994). Similar to *D. longicaudata*, this parasitoid shows a favor for fruit juices from several fruit crops.

Several researches have shown the nutritional benefits of fruit juice or pulp for a limited set of parasitoid species. For example, *Hyssopus pallidus*, an ecto-parasitoid of coddling moth, experiences increased longevity and fecundity with access to apple juice (Hein and Dorn 2008). Similarly, *D. longicaudata* increased longevity and egg load when provided access to orange and peach juice (Sivinski et al. 2006). Lastly, Eijs et al. (1998) indicated that parasitoids of Drosophilidae increased longevity and fecundity through (adult) feeding on natural host substrates or honey. In contrast, other research showed no fitness benefits of access to (ripe) coffee juice or cut olive fruits for the parasitoids *Fopius arisanus* or *Psyttalia humilis*, respectively (Bautista et al. 2001; Yokoyama et al. 2011). Not only is little known about the comparative importance of distinct food resources for fitness of fruit fly parasitoids, but the few existing research endeavors have yielded starkly contrasting results. Lastly, it has been hypothesized that parasitoids that forage for hosts on fallen or damaged fruits rely more on fruit juice to sustain their fitness.

In this study, we investigated fitness implications of access to simple and combined diets of guava juice, (bee) pollen, and honey for the parasitoids *A. pelleranoi* and *D. longicaudata*. Under laboratory conditions, we assessed effects of the different diets on the following fitness currencies: longevity, egg load, and body nutrient levels. A profound understanding of the effect of these distinct food sources on performance of fruit fly parasitoids should further contribute to biological control of pests that are of global relevance.

Materials and methods

Insects

During January–July 2009, an *A. pelleranoi* laboratory colony was established by collecting adult parasitoids and (parasitized) *Anastrepha striata* (Diptera: Tephritidae) larvae from guava orchards in the townships of Velez (6°01′N, 73°41′W) and Barbosa (05°56′N, 73°37′W) in the territorial department of Santander (Colombia). Fruit fly larvae were transported to the laboratory and incubated at 25 ± 2°C, 70 ± 10% RH and 12:12 h l:D until parasitoid emergence. Adult *D. longicaudata* wasps were obtained from colonies at the Moscafrut Program facilities (Chiapas, México) (e.g., Montoya et al. 2000). Experimental colonies were kept at the Entomology Laboratory of the Universidad Jorge Tadeo Lozano (Chía, Colombia) and at the Biological Control Department in the Moscafrut Program.

Parasitoids were maintained on third instar *Anastrepha obliqua*, obtained from laboratory colonies at the Instituto Colombiano Agropecuario (ICA) in Mosquera and Ibague (Colombia) where they were reared on artificial diet (Artiaga-López et al. 2004). Fourteen-day old *A. obliqua* larvae were separated from artificial diet through washing with sterile distilled water. Larvae were subsequently placed in 10 cm diam. ring-type oviposition devices inside 30 cm × 30 cm × 30 cm fiberglass cages and exposed to 5–15-day-old adult parasitoids. Parasitoids were allowed to oviposit *A. obliqua* larvae exposed over the course of 24 h, after which parasitized larvae were extracted from oviposition devices and transferred to plastic trays with moistened vermiculite to permit pupation. Newly emerged parasitoids were transferred to a 30 cm × 30 cm × 30 cm plexiglass cage, allowed access to water and fed ad libitum with diluted honey. Parasitoid colonies were maintained in climate-controlled growth chambers at 25 ± 2°C, 70 ± 10% RH and 12:12 h l:D. Experimental trials were conducted under identical climatic conditions.

Longevity

Newly emerged, unmated wasps of either species were individualized within 90 ml cylindrical plastic containers. Each container was equipped with a 1 cm diam. ventilation opening and either one of the following food sources was provided: (1) honey, (2) pollen, (3) guava juice, (4) pollen, honey and guava juice, or (5) nothing. All wasps were allowed ample access to water.

Honey and sterile water solution (1:1, Natural Honey, Productos El Dorado S.A, Bogotá) was applied on separate cotton wicks that were inserted within the container. Approximately 100 mg of commercially available (honeybee) pollen was pulverized and brushed on moistened filter paper at the bottom of the container. Guavas were peeled and blended with sterile water. The resulting guava juice was applied on cotton balls that were placed in a 1 cm diam. opening in the lid. On a daily basis, food was replenished and wasp mortality in each container recorded. A total of 20 replicates were done for each diet, parasitoid species, and sex.

Carbohydrate metabolism (anthrone analysis)

Newly emerged, unmated parasitoid males and females were subject to the different diets, using the above procedures. For each diet, we collected a total of ten individuals at each of the following times: 2, 4, 6, 8, and 10 days. Each wasp was gently placed within a 1.5 ml microcentrifuge tube and frozen at—20°C. Additionally, twenty newly emerged wasps (10 females and 10 males) from each species were collected and frozen at −20°C. Wasps that died during the course of the experiment were not included in the experiment.

We determined the amounts of glycogen, total sugars, and fructose in each wasp using a series of biochemical tests (Olson et al. 2000; Fadamiro and Heimpel 2001; Lee et al. 2004). Procedures are similar to the ones in Wyckhuys et al. (2008). In brief, each wasp specimen was placed within a 1.5 ml Eppendorf tube, to which 50 µl of 2% sodium sulfate was added. Wasps were not surface-sterilized, possibly causing minor contamination from wasps walking in the different diets. Wasps were crushed using a glass capillary, which was subsequently washed with 250 µl of methanol:chloroform (2:1). Next, tubes were centrifuged at 13,000 r.p.m. for 3 min. The resulting supernatant was transferred to another microcentrifuge tube for fructose analysis, while the precipitate was used for analysis of glycogen.

To assess body glycogen content, we added 1,000 µl of anthrone reagent (Product# A1631-25G, Sigma, Saint Louis, MO, USA) to the tube containing the precipitate. Next, the solution was mixed and heated to 90°C in a dry bath incubator for 15 min. After heating, tubes were placed in crushed ice for 15 min. Aliquots of 200 µl were pipetted in each of the 96-well plate, and absorbance was read at 620 nm using an ELISA reader (Sensident Scan, Merck, Germany). To determine fructose content (i.e., cold anthrone assay), we heated 200 µl of the supernatant in a dry bath incubator at 90°C for 30 min or until the liquid has evaporated. Tubes were placed in crushed ice for 15 min. Subsequently, we added 950 µl of anthrone reagent to each tube and heated them to 34°C for 1 h. The resulting solution was pipetted into 96-well plate and the absorbance was read at 620 nm. For total sugar assays (i.e., hot anthrone test), cold anthrone solutions were pippeted back into their respective Eppendorf tubes. Next, tubes were heated for 15 min at 90° C and cooled on crushed ice for 15 min. Again, samples were transferred into a 96-well plate and absorbance was read at 620 nm.

Standard curves were generated to convert absorbance readings into absolute amounts (mg) for each of the different sugars. For this purpose, we prepared glucose, fructose, and sucrose solutions at 1, 5, 10, 20, 30, 40, and 50 mg, with addition of 1 ml anthrone reagent. For glycogen (Product# G8876, Sigma, Saint Louis, MO, USA), solutions were prepared with 1, 5, 10, 25, 50, 75, and 100 mg, with addition of 1 ml anthrone reagent. Solutions were transferred to an ELISA plate and read at 620 nm. Per concentration, we ran a total of 3 replicates. Standard curves were obtained through linear regression.

Egg load

To examine the effect of food resources on parasitoid egg load, newly emerged females were individualized in a 90-ml plastic container and subjected to distinct diet regimes (as above). For each diet and species, a total of 10 females were collected at ages 2, 4, 6, 8, and 10 days. Females were dissected immediately, as such: the ovipositor was gently pulled using fine needles, until both the ovipositor and the ovaries became detached from the abdomen. The ovaries were subsequently placed on a Petri dish with a 1 ml of ringer solution (NaCl 6 g/l; $C_3H_5NaO_3$ 3.1 g/l; KCl 0.3 g/l; $CaCl_2{\cdot}2H_2O$ 0.2 g/l) and examined under a stereoscope. Ovaries were pressed with fine needles until eggs were expulsed, and fully matured eggs were counted for each of the wasps (e.g., Olson et al. 2000; Oskan 2007; Riddick 2007).

Statistical analysis

The effect of diet and sex on wasp longevity was analyzed using proportional hazard models (Lee et al. 2004; Fadamiro and Chen 2005). In the first analysis, we compared sugar levels present in newly emerged wasps (i.e., day 0) versus those at the end of their lives (or day 10), under the distinct diet regimes. Nutrient levels were compared using ANOVA, followed by a Tukey's HSD post hoc test. In the second analysis, we assessed the effects of diet, age, and diet × age interaction on fructose, glycogen, and total sugars content, using multiple linear regression. Multiple regression was also used to determine the effect of diet regime upon egg load in both parasitoid species. Regression models were included with different diet types and age, and model coefficients were reported. Prior to analysis, we assessed normality and homoscedasticity of the data set and carried out logarithmic transformations, if necessary. Statistical analysis was done using absolute values instead absorbance values. All statistics were conducted using SPSS.

Results

Longevity

For *D. longicaudata*, greatest longevity was recorded for honey and complete (i.e., honey, pollen, guava juice) diet, with wasps attaining maximum longevity of 32 days (Fig. 1). Mean longevity of *D. longicaudata* with access to pollen and guava juice did not differ from that of wasps with sole access to water (Table 1). Proportional hazard models indicated a significant effect of diet on *D. longicaudata* longevity ($X^2 = 4.966$, $df = 1$, $P = 0.026$), while no effect was registered of wasp sex ($X^2 = 1.80$, $df = 1$, $P = 0.18$). Similarly, the interaction sex × diet did not affect longevity ($X^2 = 0.007$, $df = 1$, $P = 0.934$).

Similar results were found for *A. pelleranoi,* with wasps attaining maximum longevity of 57 days for honey and complete diet (Fig. 2). Longevity of *A. pelleranoi* with

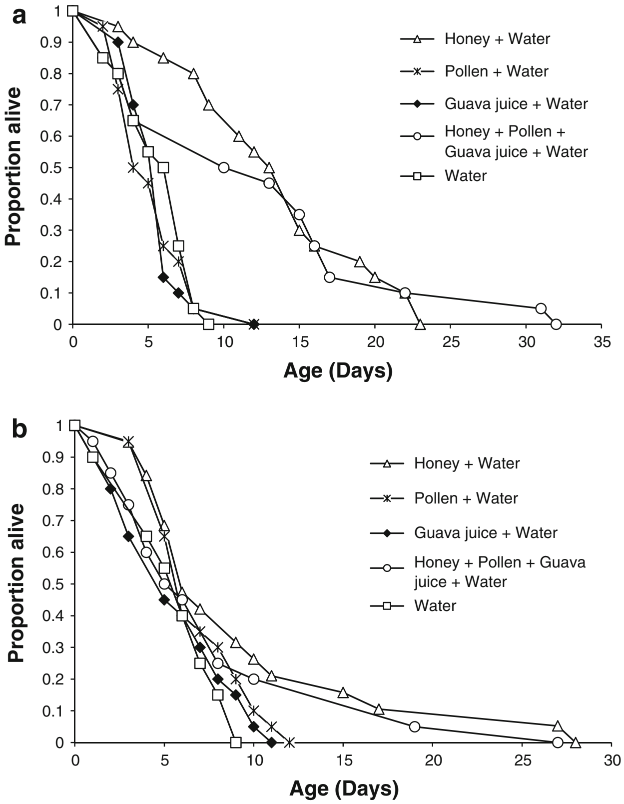

Fig. 1 Survivorship curves for female (**a**) and male (**b**) *Diachasmimorpha longicaudata* provided with different diets (females: honey $n = 20$, pollen $n = 20$, Guava juice $n = 20$; Honey + Pollen + Guava juice + water $n = 20$, water $n = 20$; males: $n = 19$, 20, 20, 20, 20, respectively)

Table 1 Average longevity (mean ± SE) in days for *Diachasmimorpha longicaudata* and *Aganaspis pelleranoi* under different diets

Longevity (mean ± SE)		
Diet	Female	Male
Diachasmimorpha longicaudata		
Honey + Water	13.4 ± 5.9a*	9.6 ± 7.2a
Pollen + Water	5.3 ± 2.4b	6.9 ± 2.4b
Guava juice +Water	5.6 ± 1.9b	5.6 ± 3.0b
Honey + Pollen + Guava juice + Water	12.2 ± 9.0a	8.2 ± 7.1a
Water	5.6 ± 2.2b	5.7 ± 2.4b
Aganaspis pelleranoi		
Honey + Water	22.2 ± 7.1a	24.5 ± 10.9a
Pollen + Water	10.2 ± 4.5b	16.5 ± 4.6b
Guava juice + Water	10.3 ± 2.4b	10.1 ± 2.7b
Honey + Pollen + Guava juice + Water	20.9 ± 5.6a	24.4 ± 14.3a
Water	8.0 ± 2.2b	9.6 ± 2.2b

* Means within the same column followed by different letters are significantly different for a given parasitoid species, at $P < 0.05$ level according to Tukey HSD test

access to guava juice and pollen did not differ from that of wasps with sole access to water (Table 1). Significant effects on *A. pelleranoi* longevity were recorded for diet ($X^2 = 14.652$, $df = 1$, $P < 0.001$), sex ($X^2 = 4.962$, $df = 1$, $P = 0.026$), and a diet × sex interaction ($X^2 = 13.401$, $df = 1$, $P < 0.001$).

Carbohydrate metabolism

Both female and male *D. longicaudata* emerged with low total sugar levels, being 10.95 ± 21.02 μg, 12.07 ± 15.95 μg (mean ± SEM); respectively. With progressing parasitoid age, different patterns were recorded in total sugar levels depending upon diet (Fig. 3). Nevertheless, no significant regression was found between age and total sugar levels for different diets. Significant differences were recorded in endpoint total sugar levels in both female and male *D. longicaudata* (females $F = 42.97$, $df = 5$, $P < 0.001$; males $F = 12.16$, $df = 5$, $P < 0.001$). Endpoint total sugar levels were highest in wasps provided with access to honey, but did not differ between newly emerged wasps and those with access to water or guava juice (Table 2). Diet significantly affected total sugar levels in both males and females, when comparing diets of honey versus guava juice and honey versus pollen (Table 3). However, when comparing pollen versus guava juice diets, neither diet, age, nor a diet × age interaction affected total sugar levels in males. For females, when comparing pollen versus guava juice, diet significantly affected total sugar levels.

Newly emerged *D. longicaudata* had fructose levels that were close to zero. With access to different food sources, body fructose levels gradually incremented (Fig. 4). For example, honey-fed wasps showed fructose levels consistently higher to 1 μg (Table 2). No significant regression was found between age and fructose levels for different diets. Diet significantly affected body fructose levels, when comparing honey vs. guava juice and honey vs. pollen (Table 3). However, when comparing pollen vs. guava juice diets, neither diet, age, nor a diet × age interaction affected fructose levels in males. For females, when comparing pollen vs. guava juice, diet significantly affected fructose levels.

Glycogen levels in newly emerged male and female *D. longicaudata* were 65.37 ± 37.14 μg and 38.40 ± 16.72 μg, respectively. With access to different food sources, glycogen levels gradually incremented (Fig. 5), although age did not significantly affect glycogen levels for different diets. Endpoint glycogen levels in newly emerged wasps did not differ from those in water, pollen- and guava juice-fed wasps (females $F = 22.40$, $df = 5$, $P < 0.001$, males $F = 5.16$, $df = 5$, $P < 0.001$). Endpoint glycogen levels in honey-fed females and males were significantly higher than those in pollen- and guava juice-fed wasps (Table 2). Diet significantly affected glycogen levels, when comparing honey versus guava juice and honey versus pollen (Table 3). However, when comparing pollen versus guava juice diets in males, diet did not affect glycogen levels. For females, diet significantly affected glycogen levels.

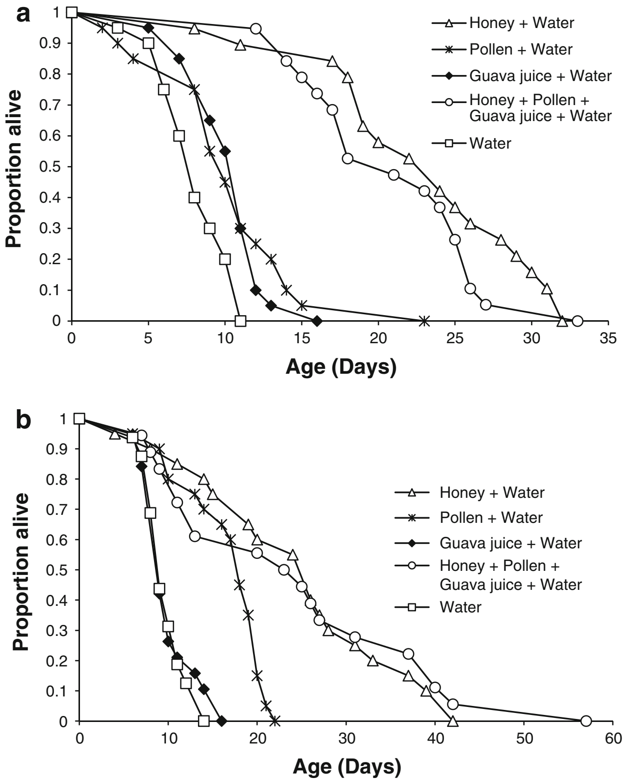

Fig. 2 Survivorship curves for female (**a**) and male (**b**) *Aganaspis pelleranoi* provided with different diets (females: honey $n = 19$, pollen $n = 20$, Guava juice $n = 20$; Honey + Pollen + Guava juice + water $n = 19$, water $n = 20$; males $n = 20, 20, 19, 18, 16$, respectively)

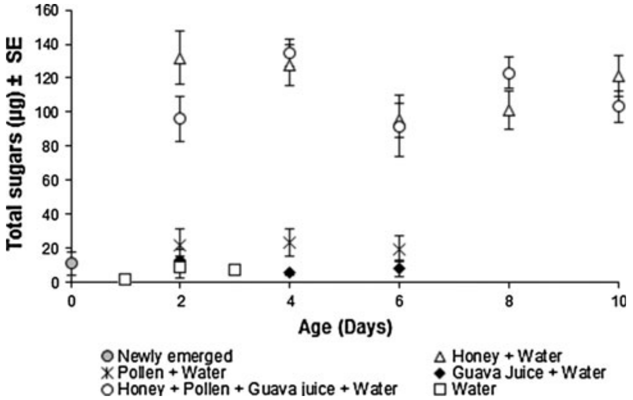

Fig. 3 Total sugar levels (±SE) in female *Diachasmimorpha longicaudata* that were newly emerged and under five diets over a period of 10 days (female emergence $n = 10$; honey $n = 9, 9, 10, 9, 10$; pollen $n = 8, 10, 8$; guava juice $n = 9, 8, 9$; honey + pollen + guava juice + water $n = 10, 9, 8, 10, 9$; water $n = 8, 9, 10$)

Table 2 Endpoint total sugar, fructose and glycogen levels in *Diachasmimorpha longicaudata* and *Aganaspis pelleranoi* adults (μg)

		D. longicaudata			*A. pelleranoi*		
		Total sugar Means ± SE	Fructose Means ± SE	Glycogen Means ± SE	Total sugar Means ± SE	Fructose Means ± SE	Glycogen Means ± SE
Females	Newly emerged	10.9 ± 6.64^{a}	0.06 ± 0.78^{a}	65.3 ± 11.7^{a}	4.18 ± 1.75^{a}	0.04 ± 2.31^{a}	42.5 ± 10.8^{a}
	Water	7.23 ± 2.81^{a}	1.85 ± 2.28^{a}	70.7 ± 8.39^{a}	5.95 ± 1.85^{a}	0.81 ± 1.14^{a}	32.5 ± 6.08^{a}
	Honey + water	121.1 ± 12.1^{b}	131.2 ± 9.4^{b}	249 ± 16.4^{b}	114 ± 14.4^{b}	100 ± 13.5^{b}	121 ± 17.2^{b}
	Pollen + water	19.53 ± 7.78^{a}	14.44 ± 9.2^{a}	102 ± 30.7^{a}	7.90 ± 1.58^{a}	8.52 ± 4.21^{a}	52.7 ± 15.0^{a}
	Guava juice + water	8.250 ± 4.85^{a}	0.340 ± 0.4^{a}	66.1 ± 11.2^{a}	3.89 ± 0.87^{a}	0.93 ± 0.79^{a}	27.5 ± 2.75^{a}
	Honey + pollen +guava juice + water	103.2 ± 9.41^{b}	108 ± 11.8^{b}	278 ± 35.2^{b}	112 ± 17.4^{b}	80.0 ± 12.2^{b}	76.0 ± 8.8^{ab}
	Mean Square	25773.54	34,174.24	89,070.23	28,940.64	19,391.75	11,756.66
	F, *df*	42.97, 5, 48	69.80, 5, 48	22.40, 5, 48	29.12, 5, 47	28.71, 5, 47	9.26, 5, 47
	P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Males	Newly emerged	12.07 ± 5.04^{a}	0.82 ± 0.76^{a}	38.4 ± 5.28^{a}	2.20 ± 1.08^{a}	0.89 ± 0.79^{a}	83.6 ± 23^{bc}
	Water	2.34 ± 0.72^{a}	1.24 ± 9.02^{a}	40.0 ± 6.17^{a}	3.73 ± 1.02^{a}	0.19 ± 1.79^{a}	33.0 ± 4.1^{a}
	Honey + water	61.05 ± 11.4^{b}	53.2 ± 12.5^{b}	89.3 ± 18.9^{b}	116 ± 16.1^{c}	108 ± 14.8^{c}	119 ± 18.2^{c}
	Pollen + water	14.93 ± 3.66^{a}	9.27 ± 4.16^{a}	47.9 ± 7.75^{a}	9.94 ± 3.01^{a}	5.08 ± 1.97^{a}	40.9 ± 6.2^{ab}
	Guava juice + water	26.99 ± 10.1^{a}	12.03 ± 8.4^{a}	97.9 ± 26.0^{b}	4.205 ± 1.4^{a}	1.79 ± 1.67^{a}	23.8 ± 3.3^{a}
	Honey + pollen + guava juice + water	70.56 ± 11.1^{b}	68.7 ± 11.9^{b}	123 ± 18.4^{c}	72.2 ± 8.52^{b}	51.3 ± 3.82^{b}	70.7 ± 6.8^{ab}
	Mean Square	7,663.42	8,376.11	12,535.71	21,299.13	18,177.12	12,174.67
	F, *df*	12.16, 5, 53	13.65, 5, 53	5.16, 5, 53	31.36, 5, 46	38.39, 5, 46	11.93, 5, 46
	P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

* Means within the same column followed by the different letters are significantly different in female and male, respectively, at $P < 0.05$ level according to Tukey HSD test

In *A. pelleranoi*, both females and males emerged with low total sugar levels (Females: 4.18 ± 3.93 μg; Males: 2.20 ± 2.16 μg). Different patterns were recorded in total sugar levels, depending upon diet (Fig. 6). Age did not affect total sugar levels for different diets. Endpoint total sugar levels were significantly higher in honey-fed wasps, while no differences were found between newly emerged wasps and those fed guava juice (females $F = 29.12$, $df = 5$, $P < 0.001$; males $F = 31.36$, $df = 5$, $P < 0.001$) (Table 2). Diet significantly affected total sugar levels, when comparing when honey vs. guava juice and honey vs. pollen (Table 4).

Fructose levels in newly emerged *A. pelleranoi* attained values close to zero. With access to the various food resources, body fructose levels gradually incremented (Fig. 7), although age did not have a significant effect on fructose levels for different diets. Endpoint fructose levels in newly emerged wasps did not differ from those fed with guava juice or with access to water (Table 2). Diet significantly affected fructose levels, when comparing honey versus guava juice and honey versus pollen (Table 4).

In newly emerged female and male *A. pelleranoi*, glycogen levels were 42.53 ± 24.20 μg and 41.01 ± 9.33 μg. Under certain diet regimes, glycogen levels rapidly increased (Fig. 8), although age did not affect these levels for different diets. Endpoint glycogen levels of honey-fed wasps were significantly higher than for those with access to guava juice, pollen, or water (females $F = 9.26$, $df = 5$, $P < 0.001$; males $F = 11.93$, $df = 5$, $P < 0.001$) (Table 2). However, endpoint levels did not differ between newly emerged wasps and those fed pollen, guava juice, or water (Fig. 8). Diet significantly affected glycogen levels, when comparing honey versus guava juice and honey versus pollen (Table 4). No effect was found of diet on glycogen levels in females, comparing guava juice versus pollen. For males though, significant effects were recorded (Table 4).

The relative importance of the different diets for each of the body nutrients is exemplified in Table 5. For both wasp species, the effect of honey and mixed diets on body nutrient levels was highly significant. Access to guava juice only had a small but significant effect on glycogen levels in males of either species. Lastly, regression models showed a significant effect of pollen on body sugar levels of *D. longicaudata* females and both sexes of *A. pelleranoi* (Table 5).

Egg load

Age significantly affected egg load in *D. longicaudata* ($F = 42.83$, $df = 7$, $P < 0.001$), with a minimum number of mature eggs found in newly emerged females (Fig. 9; Table 6). Similarly, in *A. pelleranoi,* age had a significant

Table 3 Multiple regression analyses indicating the effects of diet, age, and diet × age interaction on total sugar, fructose and glycogen levels of female and male *Diachasmimorpha longicaudata*

	df	Females			Males		
		MS	*F*	*P*	MS	*F*	*P*
Total sugar (honey vs. guava juice)							
Diet	1	22.75	161.3	<0.001	9.520	42.35	<0.001
Age	4	0.02	0.144	0.965	0.484	2.154	0.084
Diet × age	2	0.03	0.255	0.776	0.085	0.377	0.688
Total sugar (honey vs. pollen)							
Diet	1	11.92	97.85	<0.001	13.49	87.50	<0.001
Age	4	0.037	0.302	0.875	0.247	1.601	0.184
Diet × age	2	0.122	0.101	0.904	0.301	1.953	0.150
Total sugar (guava juice vs. pollen)							
Diet	1	2.139	6.137	0.018	0.259	0.753	0.390
Age	2	0.002	0.007	0.993	0.344	1.001	0.375
Diet × age	2	0.008	0.022	0.978	0.629	1.830	0.172
Fructose (honey vs. guava juice)							
Diet	1	41.27	314.6	<0.001	24.86	71.73	<0.001
Age	4	0.410	3.125	0.021	0.320	0.923	0.457
Diet × age	2	0.420	3.202	0.048	0.238	0.687	0.507
Fructose (honey vs. pollen)							
Diet	1	25.26	101.3	<0.001	23.48	106.5	<0.001
Age	4	0.064	0.256	0.905	0.432	1.958	0.112
Diet × age	2	0.254	1.019	0.367	0.371	1.682	0.194
Fructose (guava juice vs. pollen)							
Diet	1	2.701	4.890	0.033	0.035	0.061	0.807
Age	2	0.174	0.316	0.731	0.268	0.470	0.628
Diet × age	2	1.122	2.032	0.146	1.062	1.867	0.169
Glycogen (honey vs. guava juice)							
Diet	1	4.737	110.9	<0.001	0.400	4.272	0.043
Age	4	0.061	1.424	0.237	0.064	0.688	0.603
Diet × age	2	0.020	0.461	0.632	0.094	0.495	0.612
Glycogen (honey vs. pollen)							
Diet	1	2.567	47.86	<0.001	1.514	20.98	<0.001
Age	4	0.079	1.468	0.222	0.044	0.613	0.655
Diet × age	2	0.013	0.233	0.793	0.076	1.056	0.353
Glycogen (guava juice vs. pollen)							
Diet	1	0.355	5.299	0.026	0.308	3.586	0.064
Age	2	0.083	1.241	0.299	0.003	0.033	0.968
Diet × age	2	0.014	0.214	0.808	0.212	2.462	0.096

effect on maturation of eggs ($F = 8.12$, $df = 5$, $P < 0{,}001$) (Fig. 9; Table 6). Also, diet significantly affected egg load, when comparing honey versus guava juice and guava juice versus pollen.

Discussion

Throughout the world, parasitic wasps have been widely used for biological control of a diversity of fruit fly pests (e.g., Ovruski et al. 2000), and associated mass rearing and release protocols have been broadly investigated. However, basic studies on parasitoid biology and ecology, all of which directly determine parasitoid efficacy, have received far less attention. Seminal work by Bautista et al. (2001), Sivinski et al. (2006), and Yokoyama et al. (2011) all point at the key role that food sources can play in boosting fitness of certain fruit fly parasitoids. Although ecological particularities of the two fruit fly parasitoids *D. longicaudata* and *A. pelleranoi* infer recurrent contact of adult wasps with fruit pulp or juice, our work showed that both parasitoids only receive minimal benefits from access to juice of one of

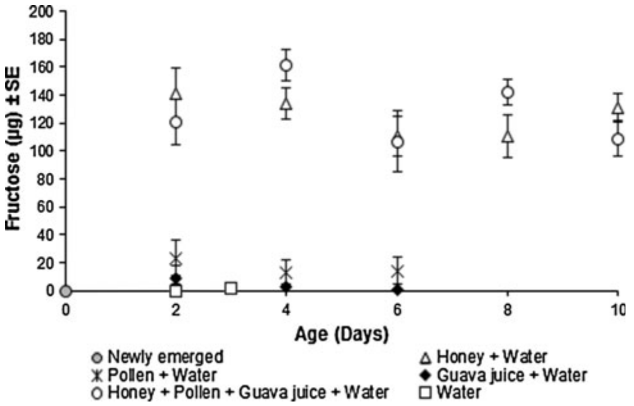

Fig. 4 Fructose levels (±SE) in female *Diachasmimorpha longicaudata* that were newly emerged and under five diets over a period of 10 days (female emergence $n = 10$; honey $n = 9, 9, 10, 9, 10$; pollen $n = 8, 10, 8$; guava juice $n = 9, 8, 9$; honey + pollen + guava juice + water $n = 10, 9, 8, 10, 9$; water $n = 8, 9, 10$)

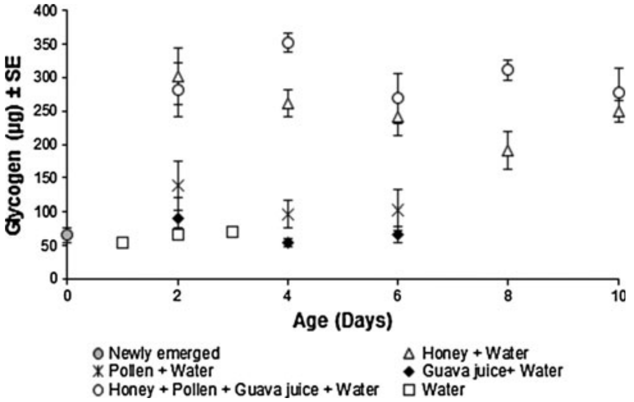

Fig. 5 Glycogen levels (±SE) in female *Diachasmimorpha longicaudata* that were newly emerged and under five diets over a period of 10 days (female emergence $n = 10$; honey $n = 9, 9, 10, 9, 10$; pollen $n = 8, 10, 8$; guava juice $n = 9, 8, 9$; honey + pollen + guava juice + water $n = 10, 9, 8, 10, 9$; water $n = 8, 9, 10$)

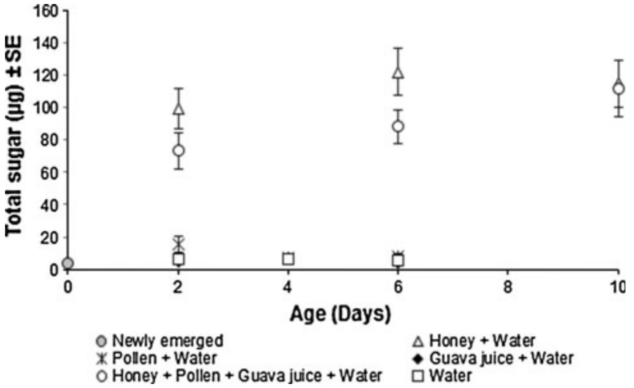

Fig. 6 Total sugar levels (±SE) in female *Aganaspis pelleranoi* that were newly emerged and under five diets over a period of 10 days (female emergence $n = 10$; honey $n = 10, 9, 10$; pollen $n = 10, 10, 10$; guava juice $n = 10, 10, 9$; honey + pollen + guava juice + water $n = 10, 9, 10$; water $n = 9, 9, 9$)

their principal host plants, that is, *P. guajava*. Guava juice did not increase body nutrient levels, nor augment longevity for either species, while bringing about very modest increases in egg load only for *A. pelleranoi*. On the other hand, both parasitoids enjoyed substantial increments in all fitness parameters through consumption of high-carbohydrate food resources such as honey.

For both parasitoids, honey more than doubled adult longevity compared with wasps with access to water or guava juice. The short lifespan of *D. longicaudata* and *A. pelleranoi* on guava juice can possibly be attributed to the type and concentration of different sugars (e.g., Lee et al. 2004; Chen and Fadamiro 2006; Wu et al. 2008; Wyckhuys et al. 2008; Luo et al. 2010; Aung et al. 2010). Compared to honey, guava juice provides relatively small amounts of sugars, such as glucose (1.30–3.04%), fructose (1.75–3.53%), and sucrose (0.81–4.21%) (De Moreno et al. 1995). Although braconid wasps are thought to assimilate all different sugar types, their content in guava juice may be too low to cause clear increases in parasitoid longevity. As indicated by Sivinski et al. (2006) and Yokoyama et al. (2011), orange juice and pulp cause fruit fly parasitoids to attain a lifespan similar to that on honey, while feeding on peach pulp led to vast increases in longevity compared with water. In a similar fashion, apple juice greatly increased longevity of the *H. pallidus* (Hein and Dorn 2008). Possibly, guava juice provides less sugar than apple juice, peach pulp, or orange juice, but analyses may be needed to further corroborate such. Aside from providing relatively low amounts of sugars (as compared to honey), guava juice possibly also contains secondary compounds that interfere with herbivores or higher trophic levels. Many fruits contain phytochemicals such as phenolics, flavonoids, or carotenoids (e.g., Sun et al. 2002), some of which act in a repellent or even toxic fashion against certain insects (e.g. Ding et al. 2000). Given that guava has one of the highest contents of phenols (Patthamakanokporn et al. 2008), the nutritional benefit of access to saccharides in its juice could potentially be offset by those compounds. Lastly, low longevity on guava juice may also hint that *D. longicaudata* and *A. pelleranoi* are unable to metabolize *P. guajava* sugars.

Access to saccharide-rich foods such as honey led to vast increases in body nutrient levels for both parasitoids. Similar results were obtained by Olson et al. (2000), Fadamiro and Heimpel (2001) and Lee et al. (2004). No evidence was found for a mobilization of fructose and glycogen to total sugars (see Fadamiro and Heimpel 2001), nor for a sustained increase in body sugar levels with age, as in *Diadegma insulare* (Lee et al. 2004). Honey-fed wasps had consistently higher sugar levels than those with access to guava juice, thus further strengthening the assumption that guava provides comparatively little sugar to both parasitoids. Glycogen levels also considerably

Table 4 Multiple regression analyses indicating the effects of diet, age, and diet × age interaction on total sugar, fructose and glycogen levels of female and male *Aganaspis pelleranoi*

	df	Females			Males		
		MS	*F*	*P*	MS	*F*	*P*
Total sugar (honey vs. guava juice)							
Diet	1	19.27	178.8	<0.001	18.66	141.8	<0.001
Age	3	0.029	0.273	0.845	0.312	2.371	0.081
Diet × age	1	0.002	0.018	0.894	0.431	3.274	0.076
Total sugar (honey vs. pollen)							
Diet	1	11.58	176.9	<0.001	9.244	59.47	<0.001
Age	3	0.036	0.548	0.652	0.064	0.409	0.747
Diet × age	1	0.265	4.048	0.049	0.465	2.989	0.090
Total sugar (guava juice vs. pollen)							
Diet	1	1.410	10.20	0.02	1.153	6.156	0.017
Age	2	0.035	0.252	0.778	0.553	3.003	0.059
Diet × age	2	0.141	1.023	0.367	0.119	0.644	0.529
Fructose (honey vs. guava juice)							
Diet	1	16.83	160.1	<0.001	0.117	146.4	<0.001
Age	3	0.138	1.316	0.283	17.15	0.151	0.928
Diet × age	1	0.258	2.458	0.125	0.018	0.052	0.821
Fructose (honey vs. pollen)							
Diet	1	12.90	105.4	<0.001	11.71	120.0	<0.001
Age	3	0.147	1.119	0.320	0.200	2.047	0.120
Diet × age	1	0.268	2.191	0.145	0.234	2.404	0.127
Fructose (guava juice vs. pollen)							
Diet	1	2.412	11.16	0.02	2.575	15.38	<0.001
Age	2	0.531	2.459	0.099	0.072	0.428	0.655
Diet × age	2	0.005	0.024	0.977	0.226	1.349	0.273
Glycogen (honey vs. guava juice)							
Diet	1	2.296	69.88	<0.001	3.961	58.45	<0.001
Age	3	0.73	2.216	0.97	0.053	0.775	0.513
Diet × age	1	0.063	1.914	0.172	0.235	3.465	0.068
Glycogen (honey vs. pollen)							
Diet	1	1.386	33.54	<0.001	1.755	34.78	<0.001
Age	3	0.005	0.130	0.942	0.003	0.069	0.976
Diet × age	1	0.001	0.021	0.887	0.123	2.440	0.124
Glycogen (guava juice vs. pollen)							
Diet	1	0.100	2.126	0.151	0.361	6.615	0.013
Age	2	0.084	1.789	0.177	0.109	2.001	0.145
Diet × age	2	0.055	1.160	0.321	0.055	1.001	0.374

increased following honey feeding, which may hint at increased nutrient storage (Boggs 1997; Lee et al. 2004) and stayed relatively constant over time (e.g., Rivero and West 2002). Females of both parasitoids emerged with a limited number of mature eggs, as is standard in synovigenic wasps (Thompson 1999). Females of *D. longicaudata* emerged with 24.0 ± 14.6 mature eggs, similar amounts as in the ichneumonid *D. insulare* (Lee et al. 2004). In contrast, *A. pelleranoi* females emerged with 102.0 ± 16.4 mature eggs. Those initial eggs primarily matured using fat reserves acquired during the immature stage (Rivero and Casas 1999). Especially for *A. pelleranoi*, the large number of initial eggs reflects a substantial energy storage capacity in immatures and, for adults, an ability to oviposit a large number of eggs in a short period of time. For the parasitoid *D. longicaudata*, diet did not affect potential fecundity or egg load, while for *A. pelleranoi*, both honey and pollen diets significantly increased egg load in comparison with water or guava juice. For several insect parasitoids, sugar feeding has been reported to benefit egg maturation. For example, females of *Ichneumon promissorius* (Hymenoptera: Ichneumonidae)

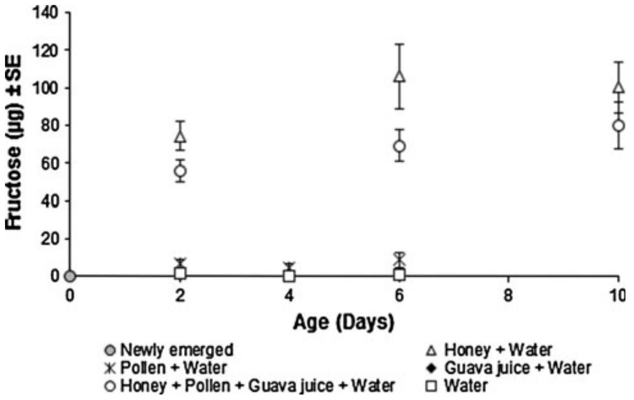

Fig. 7 Fructose levels (±SE) in female (**a**) and male (**b**) *Aganaspis pelleranoi* that were newly emerged and under five diets over a period of 10 days (female emergence $n = 10$; honey $n = 10, 9, 10$; pollen $n = 10, 10, 10$; guava juice $n = 10, 10, 9$; honey + pollen + guava juice + water $n = 10, 9, 10$; water $n = 9, 9, 9$)

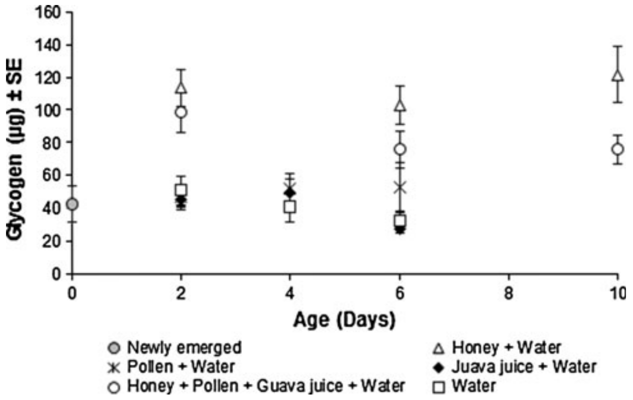

Fig. 8 Glycogen levels (±SE) in female *Aganaspis pelleranoi* that were newly emerged and under five diets over a period of 10 days (female emergence $n = 10$; honey $n = 10, 9, 10$; pollen $n = 10, 10, 10$; guava juice $n = 10, 10, 9$; honey + pollen + guava juice + water $n = 10, 9, 10$; water $n = 9, 9, 9$)

Table 5 Results of multivariate regression analyses indicating the effects of diet, age, and diet × age interaction on body nutrient levels of *Aganaspis pelleranoi* and *Diachasmimorpha longicaudata*

Independent variables	Dependent variables					
	Females			Males		
	Glycogen[a]	Fructose	Total sugar	Glycogen	Fructose	Total sugar
D. longicaudata						
Overall regression r^2	0.621***	0.760***	0.722***	0.326***	0.661***	0.575***
Intercept	1.789***	−0.097	0.451***	1.598***	−0.124	0.578***
Honey + water	0.630***	2.212***	1.578***	0.392***	1.687***	1.135***
Pollen + water	0.202**	0.783***	0.637***	0.092	0.365*	0.184
Guava juice + water	0.036	0.332	0.193	0.244**	0.325	0.312*
Honey + pollen + guava juice + water	0.708***	2.211***	1.550***	0.550***	1.791***	1.212***
Water	0	0	0	0	0	0
Age	−0.010	−0.008	0	−0.008	0.021	0.011
A. pelleranoi						
Overall regression r^2	0.446***	0.812***	0.766***	0.475***	0.762***	0.714***
Intercept	1.595***	0.293*	0.554***	1.601***	0.053	0.490***
Honey + water	0.514***	1.611***	1.431***	0.469***	1.823***	1.445***
Pollen + water	0.101	0.322**	0.311**	0.026	0.731***	0.435***
Guava juice + water	0.023	−0.214	−0.004	−0.129*	0.205	0.129
Honey + pollen + guava juice + water	0.376***	1.479***	1.326***	0.326***	1.545***	1.324***
Water	0	0	0	0	0	0
Age	−0.014	0.004	0.005	−0.008	0.008	−0.005

Values for variables are parameter estimates

[a] All body sugar data were log transformed prior to analysis

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

greatly increased egg load through consumption of honey (Wade et al. 2008). Alternative food sources such as orange juice augmented *D. longicaudata* egg load (Sivinski et al. 2006). In our study, guava juice did not benefit egg maturation of either fruit fly parasitoid. Although guava juice did not increase *A. pelleranoi* longevity nor boost parasitoid energy levels, it did, however, provide sufficient nutrients for a sustained (relatively low) fecundity over time. Contrastingly, ovarian dynamics for both species were similar under pollen and honey diets, as such hinting that pollen provides key nutrients for egg maturation in fruit fly parasitoids. Similar findings were made for different species of syrrphid flies (Irvin et al. 1999; Hickman et al. 1995) and the ichneumonid *D. insulare* (Lee et al. 2004). Our findings confirm that, even for fruit fly parasitoids with ample access to fruit juices, pollen may provide essential nutrients to parasitoids.

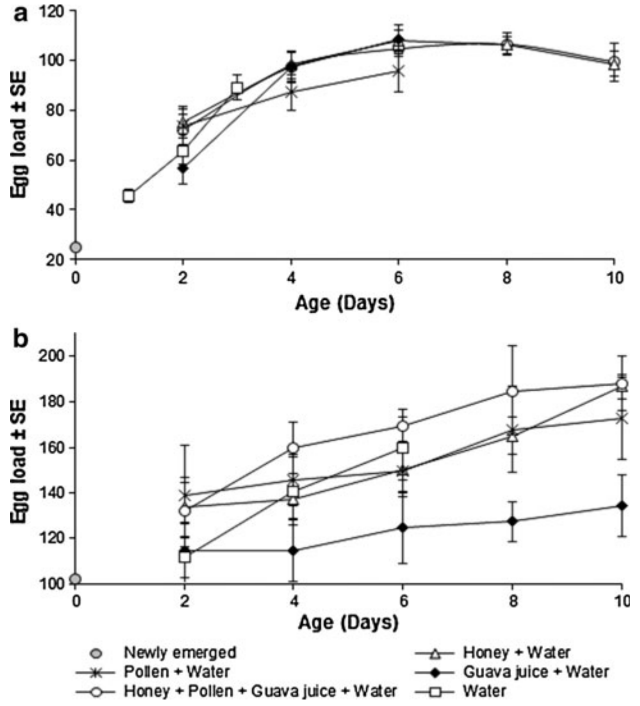

Fig. 9 Egg loads of newly emerged female *Diachasmimorpha longicaudata* (**a**) and *Aganaspis pelleranoi* (**b**) and those on five diets over a period of 10 days

Some of our findings, such as the possible positive effect of pollen on ovarian dynamics, could have been affected by experimental protocols. Concern may exist that applying pollen on wet filter paper can considerably change its nature. However, pollen is frequently consumed by parasitoid Hymenoptera when contaminating nectar, honeydew, and water sources (Jervis 1998). Also, other researchers have mixed pollen with other liquids such as honey or water and quantified its impact on key life history traits of parasitoids (Zhang et al. 2004; Geng et al. 2006). For example, mixing pollen with water improved longevity of *Trichogramma brassicae* over water alone (Zhang et al. 2004). Secondly, presence of pollen, guava juice, and honey in the same container (in combined diet treatments) not necessarily means that parasitoids actually fed on all food sources. Possibly, wasps may exhibit preference for some food source (e.g., Leius 1960), with observed fitness benefits reflecting the effect of this food. Follow-up research could help clarify whether *A. pelleranoi* or *D. crawfordi* exhibit feeding preferences for guava juice, honey, or pollen, and if (relatively) low-quality foods such as guava juice are avoided when having access to others.

Fruit juices may constitute valuable alternative food sources, as orange, peach, or apple juice all increase parasitoid fitness (e.g., Sivinski et al. 2006; Yokoyama et al. 2011), while wasps enjoy ample access to them during host foraging. However, our elucidation of the relatively poor

Table 6 Multiple regression analyses indicating the effects of diet, age, and diet × age interaction on egg loads of female *Diachasmimorpha longicaudata* and *Aganaspis pelleranoi*

	D. longicaudata				*A. pelleranoi*			
	df	MS	*F*	*P*	*df*	MS	*F*	*P*
Egg load (honey vs. guava juice)								
Diet	1	585.22	2.20	0.142	1	18,892	18.18	**<0.001**
Age	4	4,952.4	18.63	**<0.001**	4	3,331	3.207	**0.018**
Diet × age	2	531.52	1.99	0.143	4	672.4	0.647	0.631
Egg load (honey vs. pollen)								
Diet	1	1,083.7	3.064	0.084	1	1,290	0.01	0.977
Age	4	2,235.9	6.321	**<0.001**	4	5175	3.316	0.015
Diet × age	2	180.65	0.511	0.602	4	295.6	0.189	0.943
Egg load (guava juice vs. pollen)								
Diet	1	65,025	0.139	0.711	1	19,736	10.60	**0.020**
Age	2	6,961.6	14.90	**<0.001**	4	2,018	1.084	0.371
Diet × age	2	1,318.0	2.822	0.069	4	218.0	0.117	0.976
Egg load								
Diet	4	383.61	1.198	0.313	1	10,091	6.481	**<0.001**
Age	6	6,315.1	19.72	**<0.001**	4	10,108	6.852	**<0.001**
Diet × age	8	346.94	1.083	0.377	4	642.6	0.436	0.961

Bold values indicate results that are significantly different ($P < 0.05$)

effect of guava juice indicates that plant species vary considerably in their effect upon natural enemies (e.g., Ode 2006) and that not all fruit crops benefit fruit fly parasitoids to a similar extent. Parasitoid performance in fruit orchards will thus greatly depend upon the crop and the broader accessibility of alternative food sources such as (extra-)floral nectar within the orchard. The outspoken fitness benefit of high-saccharide food sources such as honey indicates that other non-prey foods could be of much greater importance for *D. longicaudata* and *A. pelleranoi*, in guava orchards. Consequently, research is urgently needed to assess whether flowering plants or plants with extra-floral nectaries provide much-needed sugars to foraging parasitoids (e.g., Lavandero et al. 2005; Berndt et al. 2006; Lee et al. 2006; Lee and Heimpel 2008). In a limited screening, Sivinski et al. (2006) showed that *D. longicaudata* only reaps marginal benefits from access to flowering plants, but more comprehensive research waits to be conducted. Also, one has to ensure that increased parasitoid fitness is readily translated into superior pest control efficacy. Along the same lines, it may be worthwhile to revisit the potential of (artificial) sugar sprays in attracting or boosting the performance of fruit fly parasitoids (see Canas and O'Neil 1998; Jacob and Evans 1998; Lundgren 2009). Even though Sivinski et al. (2006) saw little use for the rather elaborate scheme of sugar sprays, such activity may carry particular value in fruit crops that by themselves do not provide sufficient resources to natural enemies. In guava orchards, sugar sprays possibly could be important for parasitoids that receive few resources from flowering plants (Sivinski et al. 2006). Our works shows that habitat manipulation and artificial sugar sprays should merit additional research and may constitute valuable components of integrated pest management packages for fruit fly in smallholder crops (see also Bautista et al. 2001). In the meantime, our findings can help improve mass rearing and boost efficacy of augmentative release programs for both parasitoids.

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