

Effect of host diet and adult parasitoid diet on egg load dynamics and egg size of braconid parasitoids attacking *Anastrepha ludens*

LIZETTE CICERO¹, JOHN SIVINSKI² and MARTÍN ALUJA¹

¹Red de Manejo Biorracional de Plagas y Vectores, Instituto de Ecología, A.C., Xalapa, Mexico and ²Center for Medical, Agricultural and Veterinary Entomology, Gainesville, Florida, U.S.A.

Abstract. The quantity and quality of host nutrients can affect fitness-related traits in hymenopteran parasitoids, including oogenesis. The present study tested the prediction that a high host quality will influence oogenesis-related traits positively in synovigenic parasitoids, and that a high-quality adult parasitoid diet can positively affect the same parameters, potentially compensating for development on low-quality hosts. Four braconid parasitoid species with contrasting life histories are reared on a low-quality diet [*Anastrepha ludens* Loew (Diptera: Tephritidae) larvae reared on mango] or a high-quality (artificial) diet. Adult parasitoids are provided with a high-quality (honey *ad libitum*), moderate-quality (honey every other day) or low-quality (guava pulp) diet. Generalist species that encounter high variation in host quality naturally are predicted to be more flexible in dealing with nutrient shortfalls than specialist species. By contrast to the predictions, low-quality hosts yield parasitoids with higher egg loads in two species: *Opius hirtus* Fisher and *Diachasmimorpha longicaudata* Ashmead. However, as predicted, a high-quality adult diet exerts a positive effect on egg load (*Utetes anastrephae* Viereck), egg size (*Doryctobracon crawfordi* Viereck) and egg maturation rate (*D. longicaudata*, *O. hirtus* and *U. anastrephae*). The generalist *D. longicaudata* varies in egg load and maturation rate depending on host quality and adult diet, respectively. Evidence of the combined effect of both factors on parasitoid fertility is presented for the specialist *O. hirtus*. The theoretical and practical implications of these findings are discussed.

Key words. *Anastrepha ludens*, egg load, egg size, parasitoids, Braconidae.

Introduction

Oogenesis (i.e. the production of eggs) is a process that often depends on the nutritional status of the female insect. Both the number and content (i.e. size) of eggs produced may be affected by any factor that increases or decreases nutrient acquisition by the female (Wheeler, 1996; Boggs, 1997; Harvey *et al.*, 2004). Ultimately, the reproductive success of female parasitoids will be influenced by their nutritional status, which is a function of the quality and availability of food (Hagen *et al.*, 1984; Wheeler, 1996; Papaj, 2000), and this may vary according to the nature and condition of the substrate

in which the larval host develops (Eben *et al.*, 2000; Pérez-Staples *et al.*, 2008).

Proteins and lipids are essential for egg production (Ellers & van Alphen, 1997; Chapman, 1998). Nonetheless, not all adult insects are capable of assimilating or synthesizing nutrients from exogenous sources because they feed principally on sugar-rich foods such as nectar and honeydew (Heimpel *et al.*, 1997; Jervis & Kidd, 1999; Bernstein & Jervis, 2008). Most of the parasitoids that are synovigenic (i.e. they continue to mature eggs after adult emergence) and do not host-feed belong to this group, and use lipid and protein reserves that are acquired during the larval stage (endogenous nutrients) to produce eggs and adult-acquired sugars for maintenance (Jervis & Kidd, 1986; Rivero *et al.*, 2001; Rivero & West, 2002; Bezemer *et al.*, 2005; Casas *et al.*, 2005; Jervis *et al.*, 2008; Visser & Ellers, 2008).

Correspondence: Lizette Cicero, Red de Manejo Biorracional de Plagas y Vectores, Instituto de Ecología, A.C., 91000 Xalapa, México. Tel.: +52 228 8421800; e-mail: liciju@gmail.com

In addition to egg numbers matured per unit time (egg maturation rate), other reproductive investments (e.g. egg size) could be influenced by the availability of reserves acquired as larvae. In many species of insects, egg size is considered to be a reliable indicator of progeny fitness (Wallin *et al.*, 1992; Giron & Casas, 2003; Schenk & Söndgerath, 2005). However, this has not yet been established for braconid parasitoids. Besides a direct investment in egg number and size, the quantity and quality of host-derived nutrients can affect pre-imaginal developmental time, pupal weight, adult body weight, longevity without food, forewing area and hind wing area (Sarfranz *et al.*, 2008, 2009).

Sugars, as acquired by adult parasitoids that do not host-feed, are commonly used for body maintenance and to fuel other activities such as movement (Jervis *et al.*, 2008). Although adult diet is not linked directly to nutrient acquisition for oogenesis, a shortage of carbohydrates can result in proteins and lipids being used for somatic maintenance to the detriment of reproductive functions (Casas *et al.*, 2005).

The Mexican fruit fly *Anastrepha ludens* Loew (Diptera: Tephritidae) is a polyphagous fruit fly (Aluja, 1994) that attacks species of Rutaceae (*Citrus* spp. and *Casimiroa* spp.) preferentially but can also develop on mango (*Mangifera indica*; Anacardaceae), albeit not as well. Larvae derived from an artificial diet have a higher protein content than those derived from mango, as well as higher live body weights (Cicero *et al.*, 2011). For tephritid fruit flies and their synovigenic, nonhost feeding braconid parasitoids, it is predicted that a low-quality host fruit (larval host diet) will have a negative effect on parasitoid egg load, egg maturation rate [i.e. change in egg load over time (days)] and egg size because the hosts will not be able to acquire the same amount of nutrients as that obtained from a high-quality host fruit. On the other hand, a high-quality adult parasitoid diet such as honey (Sivinski *et al.*, 2006; Hein & Dorn, 2008) might have a positive effect on those same parameters if it allowed the available lipids and proteins to be used for eggs and not be diverted into somatic maintenance or movement. Thus, abundant sugars could compensate potentially for development on larval hosts that had developed on low-quality fruit and provided their parasitoids with relatively few lipids.

To test these predictions, four species of braconid parasitoids are used that share similar host species (all *Anastrepha* spp.) in nature and are potential biological control agents of *A. ludens*. However, these wasps occupy different ecological niches that require different reproductive strategies (Sivinski *et al.*, 1997). In an increasing order of specialization, *Diachasmimorpha longicaudata* Ashmead has by far the widest host range, followed by *Doryctobracon crawfordi* Viereck, *Utetes anastrephae* Viereck and *Opius hirtus* Fisher, which, in Mexico, is only reported to be recovered from *Anastrepha cordata* Aldrich and *Anastrepha alveata* Stone (López *et al.*, 1999; Sivinski *et al.*, 2000). These parasitoids also differ in longevity, host range and egg load (López *et al.*, 1999; Sivinski & Aluja, 2003; García-Medel *et al.*, 2007), and their strategies for nutrient allocation could vary accordingly.

The hypothesis tested is that parasitoids with different foraging strategies will respond differently to variation in larval

host quality and compensate differently when able to access to a rich adult diet. Specifically, it is predicted that the generalist species will be better adapted to variation in the quality and quantity of encountered resources, and will be capable of greater reproductive homeostasis than the specialists, which have evolved in the context of greater host predictability, as reflected by a lower variation in diet quality during the larval stages of parasitoid development.

Materials and methods

Insects

The parasitoids, *D. longicaudata*, *D. crawfordi*, *O. hirtus*, and *U. anastrephae*, and their host (*A. ludens*), were obtained from colonies maintained at the Red de Manejo Biorracional de Plagas y Vectores (RMBPV) of the Instituto de Ecología, A.C., in Xalapa, Veracruz, Mexico. Colonies of all parasitoid species were reared on *A. ludens* larvae (Stevens, 1991) under an LD 12 : 12 h photocycle (lights on 07.00 h) at 27 °C and 70 ± 10% relative humidity. The host larvae were reared on an artificial diet under the same conditions. Mango fruits (var. Tommy Atkins) were obtained from a local market in Xalapa, Veracruz, Mexico.

To obtain females for the experiments, the parasitoids were reared in accordance with procedures described by Aluja *et al.* (2009) using the 'sandwich-type oviposition device two (SD2)', consisting of Petri dishes (diameter 4.0 cm) covered with two pieces of organdie cloth (15 × 15 cm). Fifty larvae (third instar) of *A. ludens* in each of two devices were exposed to 100 female parasitoids in Plexiglas cages (30 × 30 × 30 cm). To make oviposition devices attractive to parasitoids, a piece of guava peel was placed over the top. This procedure was followed for all parasitoid species. Parasitoids were exposed to oviposition devices for periods of 5 h for *D. crawfordi*; 4 h for *O. hirtus* and *U. anastrephae*; and 8 min for *D. longicaudata*. Different exposure times were based on previous estimates of host-handling times. Exposed larvae were placed in 250-mL plastic containers with sterile vermiculite as a pupation substrate. Each container was labelled with the date of exposure, parasitoid species and host treatment.

The vermiculite was moistened every other day using water with 2% sodium benzoate to prevent fungal growth. Starting from day 12, containers were examined daily to record parasitoid emergence. Newly-emerged adult parasitoids were collected and offered each adult diet treatment as described below.

Host diet treatments

Anastrepha ludens larvae used for the mango treatment were obtained by exposing fruits to flies from the *A. ludens* laboratory colony. For this, 150 sexually-mature fruit flies (50 males and 100 females) were placed inside seven Plexiglas cages (30 × 30 × 30 cm) along with three mangoes that were replaced every other day. Subsequently, infested mangoes were placed in plastic trays, which were covered with a mesh

to prevent infestation with drosophilids and other Diptera, to allow larval development. After 15 days, mangoes were dissected to obtain third-instar larvae. Larvae in a similar developmental stage but fed with an artificial diet were obtained from the laboratory colony. The experiment was performed from May to November of 2006 and 2007.

Adult parasitoid diet treatments

Pairs of male and female parasitoids were placed in plastic containers covered with an organdie cloth to allow ventilation. A glass vial with a cotton wick and purified water was placed inside each container with the corresponding diet treatment. Honey is among the highest-quality adult parasitoid foods (Sivinski *et al.*, 2006) and high- and moderate-quality diets were defined on the basis of access to honey: high quality, bee honey (Miel de Abeja Carlota, Herdez, S.A. de C.V., Mexico) *ad libitum*; moderate quality, bee honey every other day (*D. longicaudata* can live no longer than 5 days on water alone). A low-quality adult parasitoid diet consisted of *ad libitum* exposure to guava pulp (*Psidium guajava*), which results in survival times similar to those obtained for water-alone diets (Stuhl *et al.*, 2011). Egg load was recorded at 3, 6, 9, 12 and 15 days (age) for each combination of host diet treatment and adult parasitoid diet treatment. These ages were chosen given that the longevity of all four species of parasitoids fed with honey *ad libitum* can exceed 15 days (Gallegos-Chan, 1999; Stuhl *et al.*, 2011). As a result of early mortality in some adult diet treatments, it was not possible to obtain sufficient replicates for the oldest ages of the three native species (*D. crawfordi*, *O. hirtus* and *U. anastrephae*). Females had no opportunity for oviposition during the course of the experiment.

Egg load and tibia measurements

Female parasitoids were dissected in a saline solution (Ringer, NaCl 0.9%) to extract the four ovarioles from the abdomen and release the eggs. Mature egg counts (egg load) and measurements were performed using a stereomicroscope with a $\times 4$ –1.6 lens (SMZ1500; Nikon, Japan) equipped with a camera (Digital Sight DS-5M; Nikon) and connected to a computer with the image-processing software NIS ELEMENTS, version 3.0 (Nikon). To quantify egg size, the mean projection areas along the major axis of the ellipsoid eggs were measured. For this, the three longest mature eggs of each individual were photographed and then the perimeter was delineated for each one, after which the egg projection area was calculated using the image-processing software. For each individual, the mean value of egg area was used for the subsequent analyses. This software was also used to measure the length of the left hind tibia of each insect with a $\times 2$ –1.6 zoom lens. This measurement was used as an indicator of adult parasitoid size.

Statistical analysis

Egg load and egg size differences were analyzed with a linear mixed model for each species (Crawley, 2007). The

response variables were egg load (number of eggs) and egg size (egg area in mm²). The main effects in both cases were larval host diet treatment (mango or artificial diet) and adult parasitoid diet (honey *ad libitum*, honey every other day and guava). Random effects were parasitoid age in days and length of tibia. In all cases, tibial length was used as an estimator of parasitoid size, and egg maturation rate was taken to be the slope of the number of eggs matured over a period of time of 3–15 days, which was analyzed in the model as the interaction between host diet treatment and age (host \times age) and parasitoid adult diet treatment and age (diet \times age) (Table 1).

The same analysis was applied to all parasitoid species except for *U. anastrephae*, for which the three-way interaction (host diet treatment \times adult parasitoid diet treatment \times age) could not be calculated by the software; consequently, the three-way interaction was not included and the fitted model for this species was host diet treatment \times adult parasitoid diet + age.

As a result of early mortality in native specialist parasitoid species, it was not possible to make comparisons among females older than 6 days for the guava treatment, and older than 12 days for the adult parasitoid diet treatment involving honey every other day.

Results

Egg load and egg maturation rate

Significant effects of both host diet treatment and adult parasitoid diet were observed on egg load for all parasitoid species except for *D. crawfordi*, although the magnitude of the differences varied among species (Table 1). In *O. hirtus*, *D. crawfordi* and *D. longicaudata*, starting at an age of 9 days and older, egg production decreased as the parasitoids aged, whereas, for *U. anastrephae*, egg production began to decrease after day 3. For *U. anastrephae*, *D. longicaudata* and *O. hirtus*, the egg maturation rate decreased more rapidly with the guava adult parasitoid diet than with the other two adult parasitoid diet treatments (honey), irrespective of the host treatment (Fig. 1)

Diachasmimorpha crawfordi did not show significant changes in egg load or egg maturation rate related to host diet treatment or the adult parasitoid diet; egg production in this species was independent from the main effects evaluated until the age of 9 days (Fig. 1).

Opius hirtus females reared on fruit fly larvae recovered from mango exhibited the highest egg loads (Fig. 2). There was also a significant interaction between host diet treatment and adult parasitoid diet treatment, with those parasitoids reared on hosts fed with mango and fed with honey (Mango–honey) having the highest egg loads (Table 1). There was no effect of adult diet alone. Similarly, significant effects of host diet treatment, adult parasitoid diet and the interaction between host diet treatment and adult parasitoid diet were observed in the egg maturation rate (Fig. 1). *Opius hirtus* reared on hosts fed with mango exhibited higher egg maturation rates compared with those reared on fly larvae reared on an artificial diet

Table 1. Results from linear mixed models for *Doryctobracon crawfordi*, *Diachasmimorpha longicaudata*, *Opius hirtus* and *Utetes anastrephae*.

Parasitoid species	Coefficients	Response variable: egg load				Response variable: egg size (area)			
		Numerator d.f.	Denominator d.f.	F	P	Numerator d.f.	Denominator d.f.	F	P
<i>Doryctobracon crawfordi</i>									
	Intercept	1	199	9.23	<0.0001	1	181	179.46	<0.0001
	HOST	1	199	0.89	0.3479	1	181	1.54	0.2167
	DIET	2	199	0.02	0.9835	2	181	3.03	0.0500
	AGE	1	2	0.03	0.8742	1	2	0.11	0.7668
	HOST:DIET	2	199	0.04	0.9561	2	181	2.40	0.0940
	HOST:AGE	1	199	0.83	0.3630	1	181	0.03	0.8691
	DIET:AGE	2	199	0.15	0.8627	2	181	2.55	0.0811
	HOST:DIET:AGE	2	199	0.23	0.7937	2	181	0.84	0.4321
<i>Diachasmimorpha longicaudata</i>									
	Intercept	1	567	356.26	<0.0001	1	538	2087.02	<0.0001
	HOST	1	567	4.46	0.0351	1	538	2.44	0.1192
	DIET	2	567	0.22	0.8011	2	538	1.28	0.2798
	AGE	1	3	7.48	0.0717	1	3	8.98	0.0578
	HOST:DIET	2	567	0.59	0.5549	2	538	1.38	0.2516
	HOST:AGE	1	567	3.52	0.0613	1	538	2.57	0.1093
	DIET:AGE	2	567	3.23	0.0405	2	538	0.32	0.7259
	HOST:DIET:AGE	2	567	0.96	0.3834	2	538	1.17	0.3097
<i>Opius hirtus</i>									
	Intercept	1	211	122.58	<0.0001	1	200	116.22	<0.0001
	HOST	1	211	5.83	0.0167	1	200	0.18	0.6718
	DIET	2	211	1.61	0.2016	2	200	1.27	0.2835
	AGE	1	2	16.19	0.0566	1	2	0.03	0.8852
	HOST:DIET	2	211	3.03	0.0500	2	200	0.17	0.8409
	HOST:AGE	1	211	8.33	0.0043	1	200	0.11	0.7432
	DIET:AGE	2	211	5.31	0.0056	2	200	0.52	0.5954
	HOST:DIET:AGE	2	211	3.40	0.0352	2	200	0.10	0.9057
<i>Utetes anastrephae</i>									
	Intercept	1	368	115.07	<0.0001	1	342	237.11	<0.0001
	HOST	1	368	0.67	0.4152	1	342	1.78	0.1830
	DIET	2	368	9.00	0.0002	2	342	0.08	0.9209
	AGE	1	3	20.51	0.0201	1	3	0.00	0.9563
	HOST:DIET	2	368	2.87	0.0579	2	342	0.17	0.8402
	HOST:AGE	1	368	1.56	0.2129	1	342	3.28	0.0710
	DIET:AGE	2	368	7.49	0.0006	2	342	2.53	0.0808
	HOST:DIET:AGE	2	368	1.51	0.2219	2	342	0.10	0.9057

Response variables were egg load and egg size (area, μm^2). Main effects were host treatment (HOST: artificial diet and mango) and adult parasitoid diet (DIET: guava, honey and honey every other day), as well as adult parasitoid age (AGE: 3, 6, 9, 12 and 15 days). Random effects were parasitoid age in days and length of tibia (μm) as an estimator of parasitoid size. Bold values are only to highlight the significant differences.

(Fig. 3). Host diet treatment had a large influence on ovarian dynamics of this parasitoid species. Although female *O. hirtus* showed higher egg maturation rates when reared on flies fed on mango, they also had shorter life spans. By contrast, female parasitoids fed with either of the two honey treatment levels had similar egg maturation rates, whereas those fed with guava had a much lower egg maturation rate (Fig. 4).

In the case of *U. anastrephae*, female egg load varied with age and adult diet. Specifically, guava resulted in the lowest egg load (Fig. 1). In addition, egg maturation rate also differed significantly among adult parasitoid diet treatments. Diets with honey resulted in the slowest decrease in egg maturation rate with age, whereas the guava treatment resulted in a significantly faster decrease in this parameter (Fig. 4).

In the case of *D. longicaudata*, egg load was influenced significantly by host diet treatment: fruit fly larvae fed on

mango produced female parasitoids with the highest egg loads (Fig. 2). By contrast to the findings of previous studies (Cicero *et al.*, 2011), there were no significant effects of host diet treatments on the initial egg load (i.e. egg load at emergence) of *D. longicaudata*. However, egg maturation rate for this species was affected significantly by adult parasitoid diet, regardless of the host diet treatment (Fig. 1). As noted previously, egg maturation rate progressively decreased with female age, although this decrease was slower for females that fed on honey compared with those that fed on guava (Fig. 4).

Mean egg size

Mean \pm SE egg size for parasitoids fed with honey for 3 days and reared on hosts stemming from an artificial

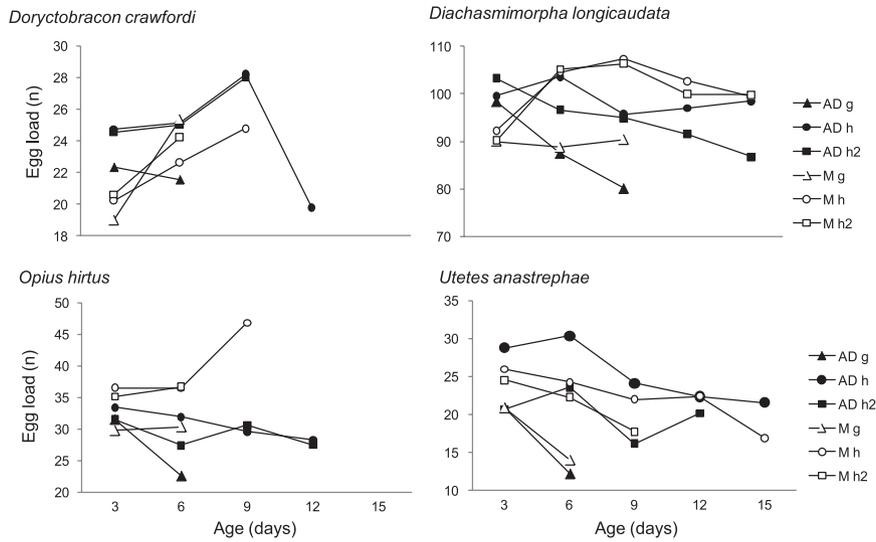


Fig. 1. Mean egg load (number of mature eggs) of female *Doryctobracon crawfordi*, *Diachasmimorpha longicaudata*, *Opius hirtus* and *Utetes anastrephae* parasitoids obtained from *Anastrepha ludens* larvae reared on either artificial diet (AD) or mango (M), and fed with three diet treatments: guava (g), honey (h) and honey every other day (h2) over a 15-day period.

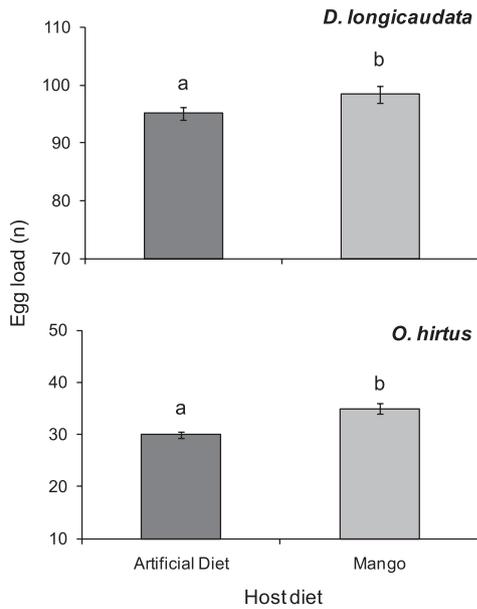


Fig. 2. Egg load (mean \pm SE) of female *Diachasmimorpha longicaudata* and *Opius hirtus* reared on two different larval host diet treatments (Artificial Diet and Mango). Different lowercase letters over the bars indicate significant differences between treatments.

diet were $0.133023 \pm 0.003502 \text{ mm}^2$ for *D. crawfordi*, $0.044694 \pm 0.000871 \text{ mm}^2$ for *D. longicaudata*, $0.08569 \pm 0.002958 \text{ mm}^2$ for *O. hirtus* and $0.077879 \pm 0.001888 \text{ mm}^2$ for *U. anastrephae* (Fig. 5). Overall, egg size did not change significantly with female age in any of the four parasitoid species examined. For *D. crawfordi*, significant differences were observed in egg size among adult parasitoid diet treatments. Specifically, females fed with honey *ad libitum* had

larger eggs compared with those that fed on guava (Fig. 5). Host diet treatment and adult parasitoid diet had no significant effects on egg size for any of the other parasitoid species (Table 1).

Discussion

By contrast to the prediction that artificial diet would yield the highest-quality fly hosts for parasitoids, fly larvae that develop in mango produce *O. hirtus* and *D. longicaudata* with higher egg loads (but apparently lower longevity) than those fed on an artificial diet. This is in agreement with the findings of Eben *et al.* (2000), and somewhat in contrast to those of Cicero *et al.* (2011), who report that *D. longicaudata* have a higher reproductive investment measured as egg load \times egg area/tibia length at 24 h when reared on hosts that develop on an artificial diet rather than on mango. This discrepancy may be a result of egg load in Cicero *et al.* (2011) being measured at parasitoid

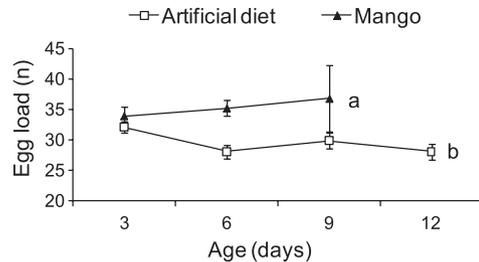


Fig. 3. Egg load (mean \pm SE) of female *Opius hirtus* parasitoids reared from laboratory *Anastrepha ludens* larvae developing in either an Artificial Diet or Mango over a 12-day period. Different lowercase letters over the bars indicate significant differences in egg maturation rate between host treatments.

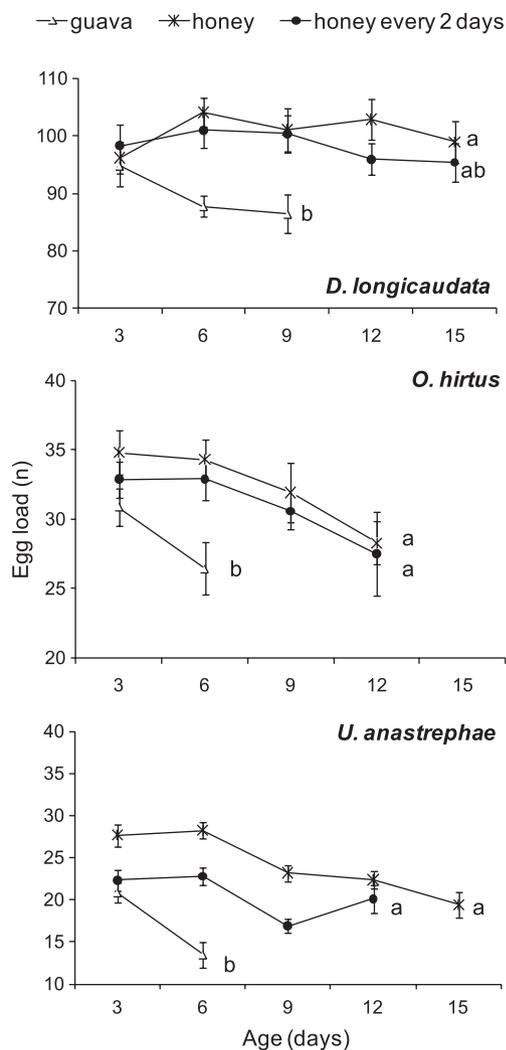


Fig. 4. Egg load (mean \pm SE) of female *Diachasmimorpha longicaudata*, *Opius hirtus* and *Uetes anastrephae* parasitoids fed with guava, honey or honey every other day over a 15-day period. Different lower-case letters over the bars indicate significant differences between diets in terms of the egg counts over time.

emergence and not at various days after feeding on a honey diet.

By contrast, the results of the present study support the prediction that a high-quality adult parasitoid diet (honey *ad libitum*) has a positive effect on egg load (*O. hirtus*) and egg maturation rate (*D. longicaudata*, *O. hirtus* and *U. anastrephae*). Guava pulp is the lowest-quality adult diet, at least in the case of *D. longicaudata*, *O. hirtus* and *U. anastrephae*. A recent study suggests that guava can have toxic effects on adult opiine parasitoids (Stuhl *et al.*, 2011), which could partly explain the findings of the present study. Moreover, the egg load (*U. anastrephae*), egg maturation rate (*D. longicaudata*, *O. hirtus* and *U. anastrephae*) and egg size (*D. crawfordi*) all increase in honey-fed parasitoids. In addition, honey every other day is equally nutritious as honey *ad libitum* in many cases (e.g. in the case of egg maturation

rate for *D. longicaudata*, *O. hirtus* and *U. anastrephae*, as well as egg size in *D. crawfordi*). Overall, these results indicate that some parasitoid species, such as *O. hirtus*, which emerge with a low egg load, can increase or maintain their fecundity over time if given access to a high-quality adult diet, depending on quality of the host diet during parasitoid larval development.

In general, the effect of host diet treatment on egg load is significant in only two of the four species studied (*D. longicaudata* and *O. hirtus*) and the adult parasitoid diet effect on egg maturation rate is significant in all species except for *D. crawfordi*.

In the case of *D. crawfordi*, parasitoids may be limited by a 'carrying capacity', in terms of matured eggs, either because of limited abdominal space (Stearns, 1977) or because they are not confronted with the need to mature more eggs when deprived of oviposition opportunities. In addition, *D. crawfordi* is the parasitoid with the largest eggs and highest egg size/tibia length ratio (*D. crawfordi*: 81.87 ± 1.21 ; *D. longicaudata*: 22.83 ± 0.54 ; *O. hirtus*: 53.97 ± 1.03 ; *U. anastrephae*: 61.13 ± 0.95), and the eggs are likely to be space demanding and metabolically more expensive to produce (at least in comparison with the other parasitoid species in the present study). It is possible that egg load could be a trait that is constrained to a certain number of eggs in species where the egg-laying expectancy does not usually exceed the number of mature eggs available at that moment. However, because *D. crawfordi* is unable to survive on some of the adult diets, comparisons are difficult and these conclusions have to be viewed with some caution.

Three out of the four of the parasitoid species do not vary egg size according to host diet treatment or adult parasitoid diet. This may be because all these species are koinobionts, and probably have hydropic eggs that are low in yolk content (Mayhew & Blackburn, 1999; Strand, 2000; Jervis *et al.*, 2008; Strand & Casas, 2008). At present, there is no evidence of a fitness advantage accruing to koinobiont parasitoid offspring that develop from larger eggs (Rosenheim, 1999; Ellers *et al.*, 2000; Strand, 2000; Lalonde, 2005). However, *D. crawfordi* may be an exception; besides having the largest eggs of the parasitoid species in the present study, it is the only species that allocates resources to increase egg size. One possibility is that investments directed to individual eggs as nutrients

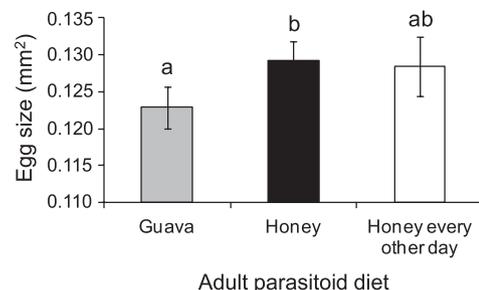


Fig. 5. Egg size (mm²) (mean egg area \pm SE) at 3 days of age of female *Doryctobracon crawfordi* parasitoids fed with three different diets: guava, honey or honey every other day. Different lowercase letters over the bars indicate significant differences between treatments.

become available, which may result in increased hatching rates that are then better able to compete in instances of super- or multiparasitism (Rosenheim, 2000).

Differences in life histories and the environments in which different species have evolved may help to explain the observed differences in reproductive strategies. *Doryctobracon crawfordi* and *D. longicaudata* are less sensitive to changes in larval and adult diet (e.g. *D. longicaudata* is the only species in the present study that survives for more than 6 days on guava) and are better able to compensate when offered a rich adult diet. Their response to diet variation can therefore be considered as being more plastic than other species. By contrast, *O. hirtus* and *U. anastrephae* are clearly affected the most by larval host quality (i.e. fly host diet treatment) and adult parasitoid diet, respectively.

Several studies report on the effects of host quality (Greenblatt & Barbosa, 1981; Eben *et al.*, 2000; Bell *et al.*, 2003; Urrutia *et al.*, 2007), as well as different adult diets (Heimpel *et al.*, 1997; Bezemer *et al.*, 2005; Eliopoulos & Stathas, 2005; Sivinski *et al.*, 2006; Hein & Dorn, 2008), with respect to parasitoid fitness parameters. Nonetheless, the interaction of these factors on parasitoid fertility has not been investigated previously. In the present study, evidence is found for such combined effects in one of the study species (*O. hirtus*), which means that this condition represents one of the multiple mechanisms that parasitoids use to deal with an unpredictable environment.

In conclusion, parasitoid resource allocation patterns are modified in response to changes in larval host quality and/or adult diet that impact on different reproductive parameters. However, the magnitude of these changes is low and variable, depending on the parasitoid species and their life-history traits (e.g. koinobionts with hydropic eggs). From the perspective of biological control, programmes involving mass rearing of koinobiont parasitoids should be aware of the relatively high nutritional tolerance that such species may possess, and perhaps use this to their advantage. Another key factor in the effectiveness of augmentative biocontrol programmes is the age at which parasitoids reach their maximum egg storage capacity. This information can be used to determine the most suitable moment for the release of parasitoids according to their egg loads (Eliopoulos *et al.*, 2003). In the case of the parasitoid species in the present study, when using high-quality adult parasitoid diets, the ideal age for field release would be 9 days for *D. crawfordi* and *D. longicaudata*, and 6 days for *O. hirtus* and *U. anastrephae*.

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