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SHORT COMMUNICATION

Sugar in moderation: sugar diets affect short-term parasitoid behaviour

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Abstract. The biological control potential of parasitic wasps in the field is expected to increase with the provisioning of sugar sources, which increase longevity and replenish carbohydrate reserves. *Apanteles aristoteliae* is an important parasitoid of *Argyrotaenia franciscana*, the orange tortrix, an economic pest in fruit crops. In the present study, the effect of sugar diet on the physiological status of *A. aristoteliae* is investigated in the laboratory, as well as the effects of nutritional status on short-term olfactory orientation and parasitism behaviour, and the association between olfactory orientation and immediate parasitism activity. Levels of glycogen, fructose, total sugars, proportional weight gain and volume consumed are higher among females fed 25% sucrose solution than 10% sucrose solution, and lowest for those fed water. Sugar feeding also affects behaviour: wasps with higher levels of fructose or weight gain have a lower probability of making a choice in the olfactometer. Wasps with intermediate fructose levels or weight gain have a higher probability of orienting towards hosts than wasps with low or high levels. Among wasps that make a choice in the olfactometer, wasps fed 10% or 25% sucrose significantly prefer host versus food cues, whereas starved wasps are just as likely to select food cues as host cues.

Key words. *Apanteles aristoteliae*, *Argyrotaenia franciscana*, olfactometer, oviposition, parasitoid, sugar, superparasitism.

Introduction

The benefits that sugars, in the form of aphid honeydew, nectar or sugar solutions, provide to parasitoid wasps are widely documented. Parasitoid wasps that consume sugar live significantly longer than individuals that are provided only with water (Wäckers *et al.*, 2008). In addition to a longer lifespan, the lifelong fecundity of sugar fed wasps is higher (Jervis *et al.*, 1996). The physiological state of a wasp, strongly influenced by diet, is predicted to affect the foraging behaviour of female parasitoids. The model of food and host foraging decisions of parasitoids by Sirot & Bernstein (1996) predicts that when there is moderate to high food availability, parasitoids should forage for food before energy reserves become too low; but should not forage for food when food availability is very low. By contrast, the model of Tenhumberg *et al.* (2006)

predicts that parasitoids with low carbohydrate reserves should always search for food, no matter how scarce the food supply. Laboratory tests reveal that starved parasitoids ignore host cues in favour of food cues (Lewis & Takasu, 1990; Jacob & Evans, 2001).

Apanteles aristoteliae Viereck (Hymenoptera: Braconidae) is a solitary endoparasitoid of the leafroller pest known as the orange tortrix *Argyrotaenia franciscana* (Walsingham) (formerly *Argyrotaenia citrana* Fernald) (Lepidoptera: Tortricidae). Although this parasitoid is the dominant species attacking orange tortrix in caneberries, oranges, grapes and apples (Basinger, 1938; Kido *et al.*, 1981; Coop *et al.*, 1989; Walker & Welter, 2004), the degree to which *A. aristoteliae* may be limited by insufficient nectar resources in these systems is unknown. Biological information on this species is lacking in the literature. This parasitoid does not appear to host-feed based on 4 years of experience with a laboratory colony; field-collected *A. aristoteliae* lived 2.92 ± 0.37 days with water ($n = 13$) and 32.0 ± 1.8 days with 25% honey ($n = 51$) (M. Ambrosino, personal observations). Therefore, this wasp may primarily extend its longevity via sugar feeding.

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The present study first determines how starvation and sugar feeding affect weight gain, sugar, glycogen and lipid levels of female *A. aristoteliae*. Second, the effects of diet and nutritional status on the short-term behaviour of the parasitoid in terms of olfactory preferences and reproductive output are investigated. Although many factors of feeding may affect activity, the present study examines how the amount of sugar consumed would affect behaviour while keeping the post-feeding time within a narrow range. Third, the relationship between olfactory preference and actual short-term reproductive output is determined, particularly whether a preference for host odours indicates a greater likelihood to parasitize hosts.

Materials and methods

Behavioural tests were conducted with female *A. aristoteliae* that were 46–50-h old; at this age, females readily orient towards host cues and engage in reproductive behaviours, as explained below. By this time, females can mature twice their egg load compared with emergence levels (33.3 ± 1.0 , $n = 122$, 17.1 ± 1.4 , $n = 31$, respectively) and would have many eggs available for a short-term trial on parasitism activity. *Apanteles aristoteliae* were reared on orange tortrix in a laboratory culture maintained on diet at Oregon State University. Blackberry leaves (cultivar ORUS 1523-4 slated to be released commercially) used in behavioural assays were taken from plants grown in 3.8-L pots in a greenhouse.

Preparation

First, females (0–4 h old) were paired with a male in a Petri dish (100 × 25 mm) and a 10% w/w sucrose solution was provided in a 0.5-mL microcentrifuge tube plugged with cotton (Table 1). Because sucrose is odourless, females were trained to associate feeding with a novel scent (Lewis & Takasu, 1990; Patt *et al.*, 1999) by adding 10 µL of banana flavour (Kroger Co., Cincinnati, Ohio) in a 0.5-mL microcentrifuge tube covered with mesh and attaching it to the sucrose tube. Petri dishes were kept in a growth chamber under a LD 16:8 h photocycle at 25 °C and 85% relative humidity. Females were allowed to feed *ad libitum* for 24 h. Second, females were starved for the next 20.5 h and given a 0.5-mL tube containing water. Also, during the starvation period, females

(approximately 26 h old) were exposed to a leaf-host complex to condition them towards host cues. Conditioning was carried out because females reared from hosts fed artificial diet have a low probability of orienting towards host-plant cues in the olfactometer. Previously, 66% of females aged 24–48 h responded to host-plant cues after 5 min of conditioning on the previous day; whereas only 24% of naïve unconditioned wasps responded ($n = 38$) (M. Ambrosino, personal observation). Females were placed in a Petri dish (50 × 9 mm) with a host damaged blackberry leaflet and five second- to fourth-instar orange tortrix larvae, allowed to engage in host foraging and oviposition behaviour for 5 min, and then females were returned to their original dish. Approximately 70% females would parasitize at least one larva in 5 min. Third, after the starvation period, females were anesthetized with CO₂ and weighed to 1 µg on a Cahn C-35 microbalance (Thermo Electron Corp., Beverly, Massachusetts) to determine their pre-feeding weight. Fourth, females were placed in a Petri dish with one of the food treatments: (i) water with no scent (starved treatment) ($n = 46$); (ii) 10% sucrose solution coupled with banana scent ($n = 40$); or (3) 25% sucrose solution coupled with banana scent ($n = 40$). Females had 1.5 h to feed and recover from any effects of the CO₂ before the olfactometer trial began. Wasps were not weighed directly after the feeding period because preliminary trials showed that CO₂ exposure affected how the wasps behaved in the olfactometer.

Behaviour

A Y-tube olfactometer (diameter 24 mm) with carbon filtration (Analytical Research Systems, Micanopy, Florida) was used with 1.3 L min⁻¹ airflow per arm with diffused lighting from above. Females were tested for their olfactory orientation towards food versus host cues. The food cue was 35 µL of imitation banana flavour on a 50-mm filter paper. Host cues were a host damaged blackberry leaflet, one host larva and frass. Each wasp was individually introduced into the olfactometer in a small glass couplet at the base of the Y-tube. Observations began when females crossed the start line 14 cm before the junction. A ‘choice’ for one of the cues was made when the wasp spent more than 15 s beyond the finish line, 6.5 cm after the junction in one of the olfactometer arms. Wasps that did not cross the start line or make a decision after 10 min were counted as ‘no choice’. Preliminary trials suggested that naïve wasps do not innately orient towards banana odour (three banana, one air control and 25 no choice),

Table 1. Sequence of procedures applied to individual female *Apanteles aristoteliae*.

Duration (h)	Starting age (h)	Procedures
24	0–4	♀ paired with ♂, given 10% sucrose with banana odour <i>ad libitum</i>
20.5	26 ± 2	♀ and ♂ starved with water; approximately 26 h old ♀ exposed to host stimuli for 5 min, host larvae frozen for dissection
0.2	46.5 ± 2	♀ treated with CO ₂ and weighed (handling time included)
1.5	46.7 ± 2	♀ given one of the treatments: (i) water; (ii) 10% sucrose with banana odor; and (iii) 25% sucrose with banana odour
0.2	48.2 ± 2	♀ tested in olfactometer for orientation to host or food (banana) odours for 10 min (handling time included)
1.5	48.4 ± 2	♀ tested in parasitism arena, larvae frozen for dissection
	49.9 ± 2	♀ treated with CO ₂ , weighed, and frozen for ovary and nutrient analyses

and that trained and starved wasps orient towards banana (15, 0 and 11, respectively). As also mentioned previously, conditioned wasps could orient towards host-plant cues.

The same females were tested for their parasitism activity immediately after the olfactometer trial. An individual wasp was placed into the center of a clear plastic arena ($32 \times 25 \times 11$ cm). At one end of the arena was a blackberry leaf infested with 20 second- to fourth-instar orange tortrix larvae. Blackberry leaves had been infested for at least 24 h prior to the beginning of the trial. Females were allowed 1.5 h to move within the arena and host patch. The dimensions of the arena permitted females to fly, although they mostly walked. Afterwards, females were removed, weighed to determine the weight lost or gained from their last feeding and activity period, and frozen. Orange tortrix larvae used in the parasitism activity trial were also frozen.

Analyses

To determine the egg load, female wasps were dissected, their ovaries removed, and eggs counted. One forewing was removed and measured. Lipid, glycogen and sugar levels were determined in individual wasps using vanillin and anthrone in accordance with methods described by Olson *et al.* (2000). Thirty-one newly-emerged females were also dissected and tested for sugars and lipids for baseline data. All orange tortrix larvae exposed to the wasps were dissected for the presence of wasp eggs.

The effects of treatment on weight gain, volume gain (weight gain/weight of 1 μ L of 10% or 25% solution), lipid, glycogen, fructose, total sugar levels and egg load were tested using analysis of variance (ANOVA) or Kruskal–Wallis with chi-square approximation depending on the homogeneity of variances. Differences among treatments were tested with Tukey's honestly significant difference; or Wilcoxon pairwise analysis with a corrected P -value ($\alpha_{\text{new}} = 1 - (1 - 0.05)^{1/k}$, where k = pairwise comparisons; Sokal & Rohlf, 1981). Preferences for odours in the olfactometer by treatment were tested using Pearson's chi-square analysis. Because each diet treatment creates wasps with a range of nutritional states, the direct effects of nutritional status (fructose level, weight change) on olfactometer orientation were determined by logistic regression. For comparison, raw data in the form of proportions for a given fructose and weight class are presented alongside the regressions. The effects of treatment on the number of eggs laid, the number of larvae parasitized with one or more eggs, and the number of larvae superparasitized in the arena were tested using ANOVA. In addition, ANOVA tested how choices in the olfactometer (no choice, host, food) translated into oviposition behaviour in the arena. The wing lengths of females were equal across treatments (2.96 ± 0.016 mm), as were their pre-feeding weights (1.29 ± 0.023 mg) and the number of eggs laid during their conditioning period (1.07 ± 0.85); thus, size and conditioning experience were not included in the analysis (winglength: $F_{2,119} = 1.03$, $P = 0.36$; pre-treatment weight: $F_{2,123} = 0.651$, $P = 0.523$; eggs laid in conditioning: $F_{2,122} = 0.33$, $P = 0.72$). Three females from

the starved treatment escaped from the parasitism activity arena and were not assayed for nutrient levels, nor parasitism activity ($n = 43$ instead of 46). All statistics were conducted with JMP, version 7.0.1 (SAS Institute, 2007).

Results and Discussion

Effects of diet on physiological status

The study confirms that water, 10% and 25% sucrose diets affected female *A. aristoteliae* in terms of weight gain, volume of sucrose consumed and nutrient levels. There is a significant difference between all three treatments in the weight change that occurs during the 3.2-h feeding period and behaviour trial. Starved wasps lost 0.058 ± 0.004 mg, whereas wasps fed 10% sucrose solution gained 0.099 ± 0.017 mg and those fed 25% sucrose solution gained significantly more weight at 0.18 ± 0.019 mg ($\chi^2 = 77.8$, d.f. = 2, $P < 0.001$; adjusted $P = 0.017$ for pairwise comparisons). Wasps fed 10% sucrose consumed 0.123 ± 0.012 μ L, and wasps fed 25% sucrose consumed 0.166 ± 0.017 μ L ($n = 72$, $F = 4.2$, d.f. = 1, $P = 0.045$). The tendency for *A. aristoteliae* to feed more from 25% than 10% sucrose is consistent with observations that diets with higher sugar concentrations lead to greater weight gain by *Aphidius ervi* (Azzouz *et al.*, 2004) and elicit more gustatory responses among *Anaphes iole* and *Diadegma semiclausum* (Beach *et al.*, 2003; Winkler *et al.*, 2005).

The levels of fructose, total sugars and glycogen were significantly higher in sugar-fed than starved wasps, whereas the levels of total sugars and glycogen in starved wasps remained at emergence levels or below (Fig. 1). Elevated sugar and glycogen levels are consistently observed among other parasitic Hymenoptera and Diptera fed sugar diets (Olson *et al.*, 2000; Lee *et al.*, 2004; Fadamiro *et al.*, 2005). The levels of sugars and glycogen in wasps starved for only 24 h suggests that *A. aristoteliae* females must feed once a day to survive in the field. This is supported by the observation that 15 females undergoing the 20.5-h starvation protocol did not survive until the first weighing period and were not tested.

Lipid levels followed a different trend from sugars because lipid levels were greater among newly-emerged females (Fig. 1). This is consistent with other evidence suggesting that parasitic wasps cannot create lipids *de novo* (Giron & Casas, 2003; Visser & Ellers, 2008). Unexpectedly, lipid levels of starved wasps were significantly higher than the lipid levels of wasps from either sugar treatment (Fig. 1). For other parasitoids, starved females exhibit a faster decline of lipid levels than females fed sugar *ad libitum* (Ellers, 1996; Lee *et al.*, 2004; Fadamiro *et al.*, 2005). Rather than providing sugar *ad libitum*, *A. aristoteliae* females were starved for 20.5 h, given access to various diets for 1.5 h, and then frozen 1.7 h later for nutrient analysis. It is unlikely that lipids were diverted to egg production because there were no differences in the egg load of females among treatments (see below). More studies are needed to confirm that lipids levels are lower among recently fed *A. aristoteliae* and are not an artefact of this experimental design.

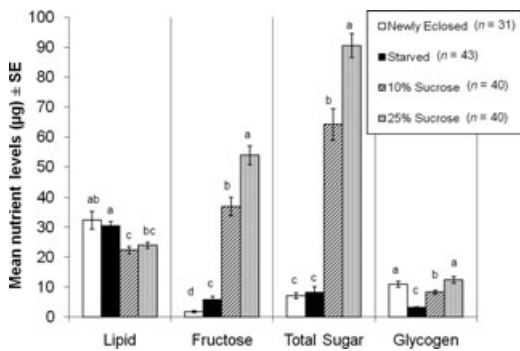


Fig. 1. Lipid and carbohydrate levels in female wasps that were newly emerged and in the three feeding treatments (lipid: $\chi^2 = 19.0$, d.f. = 3, $P < 0.001$, mean rank of newly-eclosed wasps was lower than starved wasps; fructose: $\chi^2 = 114.8$, d.f. = 3, $P < 0.001$; total sugars: $\chi^2 = 110.5$, d.f. = 3, $P < 0.001$; glycogen: $\chi^2 = 81.9$, d.f. = 3, $P < 0.001$). Letters denote significant differences between treatments using Wilcoxon pairwise analyses (adjusted $P = 0.0085$).

Lastly, diet did not affect the number of mature eggs present in females when they were in the parasitism arena (eggs dissected from ovaries + eggs laid in arena, $F_{2,120} = 0.69$, $P = 0.50$). Starved wasps had 31.0 ± 1.8 eggs, whereas 10% and 25% sucrose fed wasps had 31.5 ± 1.7 and 33.8 ± 1.9 eggs, respectively. These results contrast with more eggs being found among *Trichogramma nubilale* fed sugar *ad libitum* (Olson & Andow, 1998). However, the lack of difference may be expected because the present methods allowed little time for treatments to diverge: females were treated similarly until they were at least 44.7 h old and frozen for analysis 3.2 h later.

Effects on olfactory orientation

Diet treatment directly affected the three-way likelihood of a female choosing food, hosts or making no choice ($\chi^2 =$

22.1, d.f. = 4, $P < 0.001$; Fig. 2). Diet marginally affected the likelihood of females making a choice versus no choice ($\chi^2 = 5.1$, d.f. = 2, $P = 0.078$). Approximately 39% (starved) to 60% (fed) of females in the olfactometer trials did not choose food, nor host odours (Fig. 2). Of the wasps that made a choice, starved wasps were equally likely to select food and host odours, whereas wasps fed 10% or 25% sucrose significantly preferred host odours (Fig. 2). Similarly, starved *Cotesia rubecula* are equally likely to choose host and food cues (Siekman *et al.*, 2004), whereas the preference for host cues among well-fed wasps is observed for *C. rubecula* (Wäckers, 1994; Siekman *et al.*, 2004), *Microplitis croceipes* (Lewis & Takasu, 1990) and *Bathylplectes curculionis* (Jacob & Evans, 2001).

The nutritional status of wasps regardless of diet treatment was examined for effects on behaviour. Fructose was used as indicator of feeding and gut sugar levels (Olson *et al.*, 2000) because fructose is present at low levels ($1.74 \pm 0.37 \mu\text{g}$) in newly-emerged unfed *A. aristoteliae* (Fig. 1) and sucrose breaks into glucose and fructose moieties. Fructose levels significantly associated with the choice females made in the olfactometer. Of wasps that made a choice in the olfactometer, females with levels of fructose lower than $12 \mu\text{g}$ had a higher probability of selecting food cues, whereas females with levels above $12 \mu\text{g}$ were more likely to select host cues (Fig. 3A). Also, the probability of making no decision in the olfactometer increased as fructose levels increased past 30–40 μg . Similarly, the proportion of wasps selecting food declines, whereas the proportion making no choice rises as fructose levels increase (Fig. 3B).

The proportion of weight gained or lost after the 3.2 h period was another indicator of feeding, and also had a significant effect on the olfactometer behaviour. Females that gained the most weight had a high likelihood of not making a choice (Fig. 3C). Logistic regressions followed trends similar to the proportional data, except that females that lost the most weight had a high probability of selecting food cues according to the regression (Fig. 3C), although the proportion of these

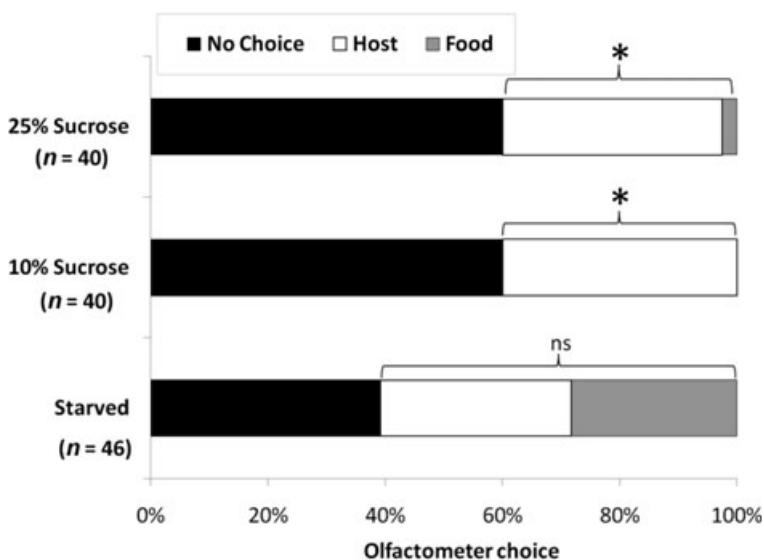


Fig. 2. Percentage of females that made no choice or oriented towards host or food cues. Among wasps that chose a cue, stars indicate a significant preference for an odour (starved: $\chi^2 = 0.14$, d.f. = 1, $P = 0.705$; 10% sucrose: $\chi^2 = 16$, d.f. = 1, $P < 0.001$; 25% sucrose: $\chi^2 = 14.7$, d.f. = 1, $P < 0.001$).

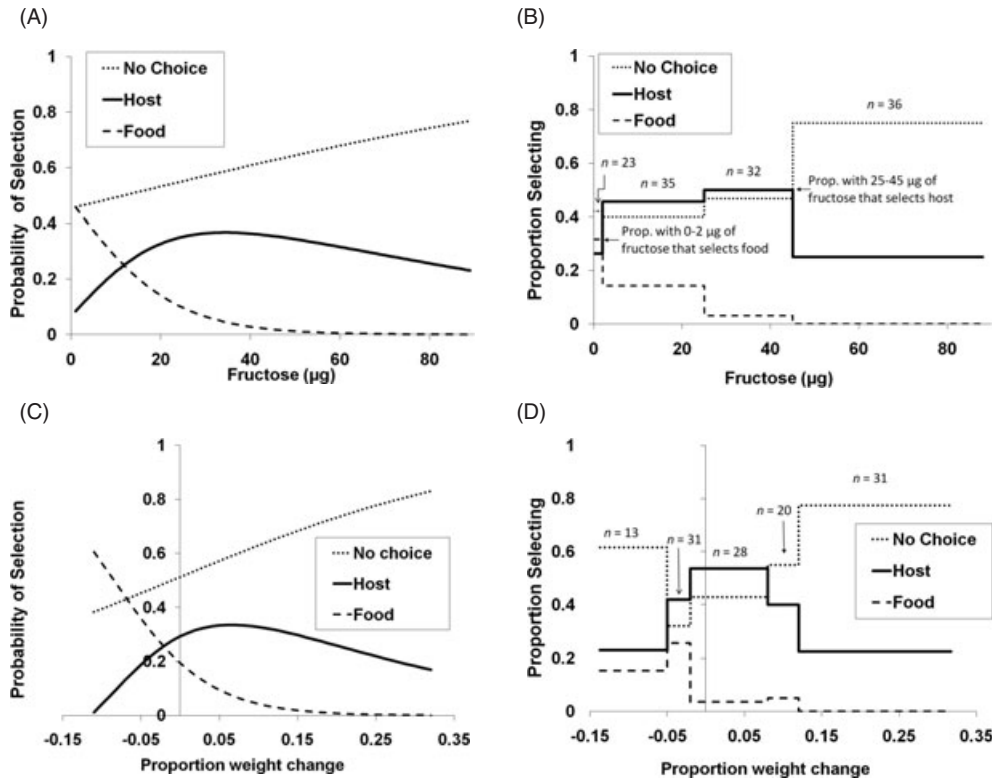


Fig. 3. (A) Probability of selecting either food cues, host cues or not making a choice in the olfactometer based on the gut fructose levels (logistic regression: $n = 122$, $\chi^2 = 20.2$, d.f. = 2, $P < 0.001$, $r^2 = 0.09$). $\text{Probability}_{\text{food}} = 1 - \{1/[1 + \exp(-0.084 - 0.086 \times \text{fructose})]\}$; $\text{Probability}_{\text{no choice}} = 1/[1 + \exp(0.18 + 0.016 \times \text{fructose})]$; $\text{Probability}_{\text{host}} = [1 - (\text{Probability}_{\text{no choice}}) - (\text{Probability}_{\text{food}})]$. (B) Proportion of females within a fructose level category that selected food, host or made no choice. (C) Probability of and (D) proportion within a weight class selecting either food cues, host cues or not making a choice in the olfactometer based on the proportion of weight that females lost or gained (logistic regression: $n = 123$, $\chi^2 = 19.0$, d.f. = 2, $P < 0.001$, $r^2 = 0.08$). $\text{Probability}_{\text{food}} = 1 - \{1/[1 + \exp(-1.42 + 16.82 \times \text{proportion weight } \Delta)]\}$; $\text{Probability}_{\text{no choice}} = 1/[1 + \exp(-0.050 + 4.8 \times \text{proportion weight } \Delta)]$.

females making no choice appeared common (Fig. 3D). Those wasps that consumed an intermediate amount of sugar with a proportional weight gain of 0.04–0.1 were more likely to select host cues than wasps with substantial weight loss or gain. A period of inactivity is reported in female *D. insulare* fed sugar *ad libitum*, where females with higher levels of fructose are less likely to move into patches containing hosts (Lee & Heimpel, 2007). *Diadegma insulare* are suggested to need a period of time to digest their sugar meal, accounting for the decreased probability of entering the patch. Similarly, *A. aristoteliae* may also need a period of time for digestion of their recent sugar meal, leading to the high probability of making no decision in the olfactometer trials when weight gain is substantial.

Effect on parasitism

Although treatment affected orientation in an olfactometer, there was no effect of treatment on the number of eggs laid, total larvae parasitized one or multiple times, and larvae superparasitized by wasps in the arena (Table 2). Although an abundance of hosts was available, *A. aristoteliae* superparasitized some hosts two to four times. The wasps were

more than 46 h old when placed into the arena and had an egg load of more than 30 eggs, and it is unlikely that the lower rates of parasitism were observed because wasps had not matured enough eggs. It is possible that *A. aristoteliae* has a maximum number of eggs that can be laid in one patch. The single patches may have been left intentionally underexploited by wasps, even though they were still capable of ovipositing, to prevent self-superparasitism (Rosenheim & Mangel, 1994). This possibility is likely given that *A. aristoteliae* on average laid 5.75 ± 0.50 eggs, still had 26.3 ± 1.1 eggs remaining in the ovaries, and did not appear to be capable of avoiding superparasitism because 5% (i.e. one out of 20) larvae were superparasitized. Moreover, field studies of *A. aristoteliae* parasitism on patches with orange tortrix larvae show that the percentage of larvae parasitized remains approximately 40%, regardless of the number of larvae in the patch (Walker & Welter, 2004). In this case, treatment differences may appear only if wasps are monitored in larger multi-patch arenas.

Lastly, when examining the behaviour of females in the arena based on their choice in the olfactometer, there was a marginal association between olfactometer choice and the number of eggs laid, and for larvae superparasitized (Table 2).

Table 2. Means \pm SE and analysis of variance on the effect of diet treatment and olfactometer choice on parasitism activity of *Apanteles aristoteliae*.

	Number of eggs laid	Number of larvae parasitized	Number of larvae superparasitized
Starved	4.65 \pm 0.83	3.81 \pm 0.65	0.70 \pm 0.22
10% sucrose	6.55 \pm 0.91	5.0 \pm 0.65	1.28 \pm 0.26
25% sucrose	6.10 \pm 0.88	4.88 \pm 0.69	1.12 \pm 0.22
d.f.	2, 120	2, 120	2, 120
<i>F</i>	1.33	0.99	1.71
<i>P</i>	0.269	0.372	0.185
No choice	4.78 \pm 0.62	3.86 \pm 0.49	0.78 \pm 0.15
Host	7.2 \pm 0.88	5.57 \pm 0.63	1.41 \pm 0.25
Food	5.25 \pm 1.86	4.33 \pm 1.42	0.83 \pm 0.51
d.f.	2, 120	2, 120	2, 120
<i>F</i>	2.67	2.24	2.57
<i>P</i>	0.073	0.11	0.08

Although comparisons were marginal, females that preferred host odours in the olfactometer later laid 44% more eggs in the arena compared with females that preferred food odours or that did not make a choice. Because *A. aristoteliae* does not host feed, the selection of host odours may indicate a preference for reproductive foraging. These observations are consistent with the assumption that the olfactory preferences of wasps in the olfactometer might reflect subsequent behavioural activity. The olfactory preferences of two-spotted spider mites *Tetranychus urticae* to host plants in the olfactometer are also consistent with their movement towards specific plants during a release–recapture study with different individuals in the greenhouse (Pallini *et al.*, 1997). To the authors' knowledge, no other studies have correlated olfactory preference of the same individual parasitoid in an olfactometer to subsequent reproductive activity. In summary, *A. aristoteliae* with moderate sugar intake are more likely to orient to hosts in the short-term. Because a laboratory experiment demonstrates 'what parasitoids can do' and not necessarily 'what they actually do' in the field (Heimpel & Casas, 2006), the present study demonstrates the need to explore how short-term effects of sugar intake can affect parasitoid foraging in the field.

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