

# Nectar from oilseed rape and floral subsidies enhances longevity of an aphid parasitoid more than does host honeydew

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**Abstract** Many adult parasitic Hymenoptera consume floral nectar and honeydew, although the latter is in most cases a ‘bad meal’ compared to floral nectars. Parasitoids of aphids, however, may be well-adapted to consuming honeydew when it is produced by their hosts. The nutritional value of honeydew for this group of parasitoids has often been tested against that of synthetic feeding solutions, but rarely against floral nectar. In the present work, the relative nutritional values of honeydew from the aphid *Myzus persicae* (Sulzer), nectar from two cultivars of oilseed rape (OSR) and nectars from four ‘companion’ plant species were assessed by testing their effect on the longevity of *Diaeretiella rapae* (McIntosh) [Hymenoptera: Braconidae]. Parasitoids fed on nectar from OSR lived longer than those fed on nectars of companion plants, or on water only. *Diaeretiella rapae* also lived longer when fed OSR nectar than when fed honeydew from *M. persicae*.

**Keywords** *Brevicoryne brassicae* · *Myzus persicae* · *Diaeretiella rapae* · Ecosystem services · Companion plants

## Introduction

Agroecosystem diversification can improve the ecological fitness of pests’ natural enemies and consequently improve biological control (Letourneau et al. 2011; Gurr et al. 2012; Ratnadass et al. 2012). Among numerous possible habitat management measures, floral plantings subsidise agro-ecosystems with nectar, a source of food for parasitoids and other beneficial natural enemies of pests (e.g. Tylianakis et al. 2004; Zhu et al. 2014). The provision of floral subsidies in the field can enhance parasitic activity and mitigate the impact of pests on yield (Heimpel and Jervis 2005; van Rijn et al. 2008; Gontijo et al. 2013; Balmer et al. 2014).

Most parasitoid species can absorb carbohydrates and other nutrients from floral nectar, extra-floral nectar or homopteran honeydew. However, they do not benefit equally from these sugar sources. For example, nectars are not all equally nutritious to parasitoids. Some plant species, such as buckwheat (*Fagopyrum esculentum* Moench [Polygonaceae]), produce a nectar that strongly enhances longevity and fecundity of several parasitoid species, to a consistently greater extent than other nectariferous species (Fiedler et al. 2008). Furthermore, homopteran

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honeydew is for most parasitoids a ‘bad meal’, as revealed by laboratory feeding trials comparing the longevity of parasitoids when fed with this honeydew or other sugar sources such as nectar (reviewed by Wäckers et al. 2008). However, it has been hypothesised that parasitoids whose hosts produce honeydew may have evolved the capacity to metabolise honeydew sugars as efficiently as nectar. Indeed, the ability to digest honeydew efficiently would allow those parasitoids to find hosts and food at the same place, which would reduce food-foraging costs and associated risks, and has probably been selected through evolution (Wäckers 2000, 2005; Wäckers et al. 2008). Until recently, honeydew diets had been experimentally compared to synthetic sugar diets, and no study comparing nectar and honeydew diets had been performed on parasitoids whose host produce honeydew (Wäckers et al. 2008). Two recent studies provide such diet comparison in aphid parasitoids. However their results are contradictory: *Lysiphlebus testaceipes* (Cresson) [Hymenoptera: Braconidae] lived as long on buckwheat nectar as on host (*Aphis gossypii* (Glover)) honeydew (Hopkinson et al. 2013), but the longevity of *Diaeretiella rapae* (McIntosh) [Hymenoptera: Braconidae] was 3.5 times shorter when fed *Brevicoryne brassicae* L. honeydew compared with *Vicia faba* L. extra-floral nectar (Jamont et al. 2013). In that case, *D. rapae* longevity on honeydew was not significantly different from control wasps given access to water only, suggesting that *B. brassicae* honeydew has negligible nutritional value to this parasitoid.

Oilseed rape (*Brassica napus* L., OSR) hosts several guilds of pest insects (Williams 2010), including three aphid species (*Myzus persicae* (Sulzer), *Brevicoryne brassicae* L. and *Lipaphis erisimi* (Kalt.)), which are the main pests of this crop in Australasia (Lamb 1989). *Diaeretiella rapae* is the most common parasitoid of the above three aphid species worldwide (Pike et al. 1999; Desneux et al. 2006). Because these three aphid species produce honeydew, and because OSR produces nectar during flowering, aphid parasitoids can find various sugar sources in OSR crops: crop floral nectar, aphid honeydew, and, if provided, nectar from floral subsidies. To evaluate the usefulness of deploying floral subsidies in OSR crops, this study compared the value of various floral nectars, OSR nectar, and *M. persicae* honeydew, for the aphid parasitoid *D. rapae*. Also, to

investigate a potential interactive effect of honeydew and nectar, an additional diet treatment combining buckwheat nectar and aphid honeydew was performed (inspired by van Rijn et al. 2013). Changes in longevity of adult *D. rapae* when provided with the various diets mentioned above were measured in the laboratory.

## Materials and methods

### Insect and plant rearing

*Diaeretiella rapae* cultures were started in March 2012 by collecting aphid (*M. persicae*) mummies from brassica plots at the Biological Husbandry Unit, Lincoln University (<http://bhu.org.nz>). Parasitoids were maintained on *M. persicae* feeding on OSR plants (cv. Ability) in controlled-temperature rooms set at 24 °C (with a 4 °C range) and a 16:8 L:D photoperiod. Before experiments began, *M. persicae* mummies were individually placed in a 1.5 ml microcentrifuge tube with a cotton stopper. Upon emergence, parasitoids were sexed and used in bioassays on the same day.

OSR, Camelina and four companion plant species were grown in a glasshouse at the Lincoln University nursery, with natural lighting and no heating. They were sown continually over a period from September 2013 to February 2014 to ensure a continuous provision of flowers during the experiment. Two cultivars of OSR were used: Ability and Flash. The latter is a winter cultivar requiring vernalisation to initiate flowering. Vernalisation was triggered by placing 30-day old plantlets under 4 °C, 8 h of light per day for 40 days. Camelina (*Camelina sativa* L. [Brassicaceae]) was included in tests, to evaluate its potential as nectar source. It is a recently developed low-input brassica biofuel feedstock crop the oil-rich seeds of which can be used for biodiesel production (Shonnard et al. 2010). Two camelina cultivars were tested: CS3 and Suneson. The four species used here have been commonly used as floral subsidies (Fiedler et al. 2008): alyssum (*Lobularia maritima* L. [Brassicaceae], cv. Benthamii), buckwheat (*Fagopyrum esculentum*, cv. Katowase), coriander (*Coriandrum sativum* L. [Apiaceae], cv. Slowbolt), and phacelia (*Phacelia tanacetifolia* Benth. [Borraginaceae], cv. Balo).

Nectar in living inflorescences

One male and one female *D. rapae* were placed in a transparent plastic container (11 cm × 6.5 cm × 6.5 cm) through a 2 cm wide hole on one side. The hole was sealed with a foam plug. A 3 cm × 6 cm mesh-covered aperture on another side ensured proper aeration of the container. A 1.5 ml microcentrifuge tube containing a damp piece of cotton wool was pasted to the inner wall of the container and was kept moist to ensure ad libitum access to water for parasitoids. One flowering stem of the tested plant was inserted through a 2 cm wide foam-plugged hole on the base of the container, while the stem was still attached to the plant. The container was tied to a wooden stake to maintain it above the stem. Visual checks at the start of each experimental unit confirmed that the stems bore no aphids and that nectar was present in more than five fresh flowers. The only exception was camelina, which did not show nectar droplets on flowers. Plants were watered regularly throughout the experiment. It is assumed that the total volume of nectar present in the treatments (except

camelina) allowed parasitoids to feed ad libitum. There were eight nectar treatments (Fig. 1), originating from the eight plant types mentioned above as well as a control, where no flowers were inserted in the containers. There were eight experimental blocks containing one replicate of each treatment and the control. All containers within one block were started on the same day. Containers were checked daily to assess the longevity of each insect.

Nectar and honeydew droplets on Parafilm

One male and one female *D. rapae* were placed in a transparent plastic container, with ventilation and access to water as above. *M. persicae* honeydew and various floral nectars were presented as individual treatments as droplets on a 2 × 4 cm band of Parafilm and replaced daily. Nectar was taken from fresh buckwheat, phacelia, and OSR flowers by carefully dissecting the flowers and depositing droplets of nectar on the Parafilm band. Nectar droplets in buckwheat flowers are smaller than those in OSR flowers, this is due to flower morphology and this size difference was

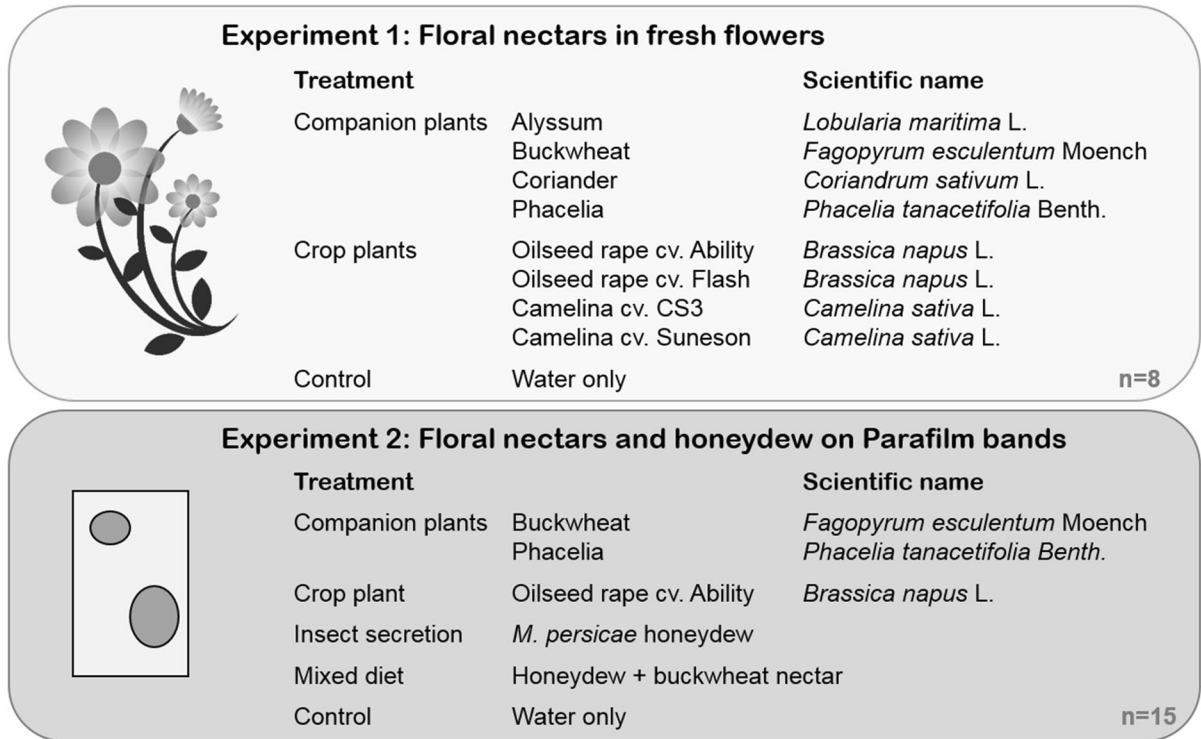


Fig. 1 Treatments used in a longevity trial on adult *Diaeretiella rapae* fed with nectars and honeydew from various sources

maintained on the Parafilm bands. The size of nectar droplets was not modified because this would have caused smearing the nectar. Honeydew was collected by placing the Parafilm bands under oilseed rape leaves bearing *M. persicae* colonies (culturing conditions as described above) for 24 h. A treatment combining buckwheat nectar and honeydew was provided by placing buckwheat nectar droplets on a Parafilm band that had been covered with honeydew as described above. Honeydew and nectars were provided in excess quantities and refreshed daily to avoid crystallisation. All diets were provided on the same substrate to avoid biases potentially induced by differing substrates (as discussed in Hopkinson et al. 2013 and Jamont et al. 2013). There were 15 blocks, each one contained one replicate of the five treatments, plus a control consisting of a band of Parafilm alone (Fig. 1). All containers within one block were started on the same day, and were checked daily to record the longevity of each insect.

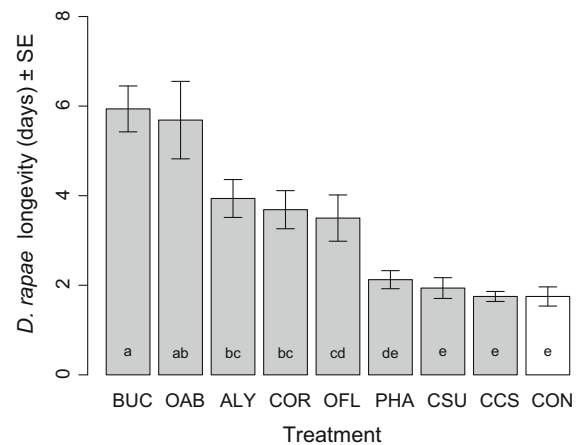
### Statistical analysis

For both experiments, the effects of sex, diet and their interaction on longevity were analysed by analysis of variance, modelling a split-plot design with diet as a plot-level factor and sex as within-plot factor. Longevity data were log-transformed to achieve ANOVA assumptions of normality and homogeneity of residuals. Post-hoc least-square difference (LSD) tests were performed to examine differences between diet treatments and sexes. All analyses were performed with GenStat.

## Results

### Nectars in inflorescences

The effect of floral diet and sex on parasitoid longevity were both significant ( $F_{8,56} = 10.72$ ,  $P < 0.001$ ;  $F_{1,63} = 6.70$ ,  $P = 0.012$ , respectively) and there was no significant interaction ( $F_{8,63} = 1.73$ ,  $P = 0.108$ ). Males lived a mean of 2.9 days, shorter than females (3.8 days). Access to buckwheat and OSR cv. Ability allowed parasitoids to reach the highest longevities (respectively, 5.9 and 5.7 days), three times longer than that of unfed parasitoids that lived only for a mean of 1.6 days (Fig. 2). Access to phacelia or

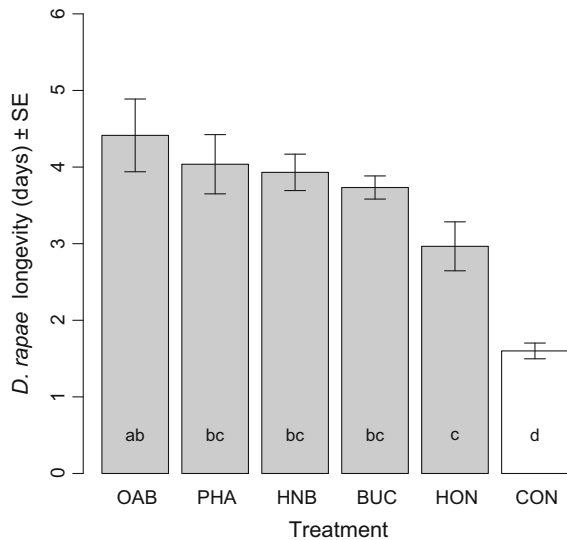


**Fig. 2** *D. rapae* longevity when fed on floral nectars from live inflorescences. Bars with the same letter are not significantly different (LSD-test,  $P < 0.05$ ). Treatments, in order of effect size: BUC: buckwheat; OAB: oilseed rape cv. Ability; ALY: alyssum; COR: coriander; OFL: oilseed rape cv. Flash; PHA: phacelia; CSU: Camelina cv. Suneson; CCS: Camelina cv. CS3; CON: control (water only).  $N = 8$  replicates

camelina did not enhance parasitoid longevity significantly compared to the control (water only). The two OSR cultivars did not increase parasitoid longevity to the same extent: the winter cultivar Flash allowed parasitoids to reach 3.5 days only, i.e. significantly less than 5.9 days on cultivar Ability. Parasitoids provided with coriander or alyssum lived significantly longer than those on water only. However, their longevities (respectively, 3.7 and 3.9 days) were significantly lower than on buckwheat.

### Nectar and honeydew droplets on Parafilm

There was a significant effect of diet on parasitoid longevity ( $F_{5,69} = 13.63$ ,  $P < 0.001$ ). However, there was no significant effect of sex ( $F_{1,79} = 0.78$ ,  $P = 0.38$ ), nor was there an interaction between sex and diet ( $F_{5,79} = 0.56$ ,  $P = 0.73$ ). All diets significantly enhanced parasitoid longevity compared to controls (Fig. 3). When fed on OSR cv. Ability nectar, parasitoids lived a mean of 4.4 days, significantly longer than those fed on *M. persicae* honeydew (2.9 days). The effect of the latter, nectars of buckwheat and phacelia, and the mixed diet (honeydew + buckwheat nectar) were not significantly different from one another. The mixed honeydew-nectar diet did not enhance parasitoid longevity more



**Fig. 3** *D. rapae* longevity when fed on various diets provided on Parafilm bands. Bars with the same letter are not significantly different (LSD-test,  $P < 0.05$ ). Treatments, in order of effect size: OAB: oilseed rape cv. Ability; PHA: phacelia; HNB: honeydew + buckwheat mixed diet; BUC: buckwheat; HON: *M. persicae* honeydew; CON: control (water only). N = 15 replicates

than the nectar alone, which indicates that there was no positive synergistic effect of co-occurring honeydew and nectar feeding.

## Discussion

### Comparison of diets

Nectars and honeydew enhanced parasitoid longevity compared with water-only controls, except for phacelia and camelina flowers. Access to phacelia flowers did not enhance parasitoid longevity (Fig. 2). However, when phacelia nectar was provided as droplets on Parafilm, it increased parasitoid longevity more than two-fold (Fig. 3). This discrepancy is probably due to flower morphology because phacelia nectaries are located at the bottom of a deep (10–15 mm) corolla which entrance is blocked by small lid-like structures on the petals. This morphology may limit exploration by the parasitoid. Other parasitoids have also been shown to be unable to consume phacelia nectar from the flowers (Vattala et al. 2006), which illustrates the importance of floral morphology for nectar exploitation by parasitoids (Patt et al. 1997). Camelina flowers

did not produce noticeable amounts of nectar. In field conditions, pollinators do visit camelina. However, the extent to which this plant provides pollen or nectar for those insects has not been studied (Groeneveld and Klein 2014). This plant is mainly self-pollinated and receives little benefit from insect pollination (Groeneveld and Klein 2014). Therefore, production of nectar is not crucial for its reproduction. These results suggest differing nutritional quality between the nectars of the two different OSR cultivars tested here, which could be explained by genetic differences between the two cultivars and plant life history. In addition, cv. Flash requires a vernalisation period whereas cv. Ability does not. Placing plants in the fridge for 40 days to ensure vernalisation is likely to have altered the plant physiology and potentially led to the production of lower quality nectar.

Buckwheat nectar confers high longevities on many parasitoid species (Fiedler et al. 2008; Russell 2015), and this was also the case for *D. rapae*, especially when nectar was provided on intact shoots. Buckwheat nectar increased the longevity of *D. rapae* to a ca. 50 % larger extent than alyssum and coriander. A similar difference in effect size has been observed on the aphid parasitoid *Aphidius ervi*. The longevity of *Microctonus hyperodae* Loan [Hymenoptera: Braconidae], a parasitoid of the Argentine stem weevil, was increased twice more by feeding on buckwheat nectar than by feeding on alyssum. These results on three parasitoids species point out buckwheat nectar as a superior food source for parasitoids.

### The value of honeydew

Honeydew enhanced *D. rapae* longevity to a certain extent but not as much as floral nectar, particularly OSR nectar. Feeding on *M. persicae* honeydew increased *D. rapae* longevity to three days on average, which represents an increase one third smaller than the increase caused by feeding on OSR nectar (on OSR cv. Ability nectar, mean longevity was ca. 4.5 days). Therefore, *D. rapae* oviposition period was extended from 3 to 4.5 days, which is a period of particularly high fecundity. Indeed, *D. rapae* is a synovigenic parasitoid, i.e. it can mature eggs during its adult stage, and the number of mature eggs in ovaries of *D. rapae* is at its highest between the second and fourth day after emergence. Feeding on OSR nectar rather than on honeydew could therefore significantly improve the



fitness of *D. rapae*. This result has to be taken with caution, however, because honeydew droplets were noticeably smaller than OSR droplets, and as a result, they may have crystallised at a faster rate than OSR, which may have impeded their uptake by parasitoids. However, when parafilm bands were placed in the experimental containers, at least 50 % of the honeydew droplets appeared liquid, therefore they were available to parasitoids for at least the first hours after the Parafilm band was refreshed.

Longevity of *D. rapae* was not significantly different when fed on honeydew or buckwheat droplets. Vollhardt et al. (2010) observed that honeydew-fed *Aphidius ervi* tended to subsequently feed on buckwheat nectar, whereas nectar-fed parasitoids did not feed on honeydew. This suggests a gustatory mechanism that signals honeydew as being a food source of lower quality than nectar.

In contrast to honeydew from *M. persicae*, that from *B. brassicae* had no effect on the longevity of *D. rapae* (Jamont et al. 2013). Similarly, the longevity of the parasitoid *Aphidius colemani* Viereck was about three times higher when fed honeydew from *M. persicae* than when fed on that from *B. brassicae* (see Table 2 in Wäckers et al. 2008). Also, the solitary bee *Osmia bicornis* L. feeds on *M. persicae* honeydew but avoids that from *B. brassicae* (Konrad et al. 2009). One potential explanation is that the latter is coated with wax (Lamb 1959; Wäckers 2005), which may limit its exploitation by parasitoids. The predatory syrphid *Episyrphus balteatus* (De Geer) seemed relatively unaffected by this wax and had increased longevity after consumption of *B. brassicae* honeydew (van Rijn et al. 2013).

#### Food sources in OSR fields

OSR fields are an agroecosystem that is not devoid of food sources for *D. rapae*: they may feed on OSR nectar and honeydew from *M. persicae*. In laboratory conditions, honeydew from *M. persicae* is not as valuable as OSR nectar, although this may have been confounded by its faster crystallisation. In the field, crystallisation might occur faster than in the laboratory, so honeydew quality might be lower than that measured in this experiment. In cases of heavy aphid infestation, honeydew can occasionally accumulate between the stem and the base of a leaf. This could prevent crystallisation and represent a food source for *D. rapae*. However, this has

not been studied to date. Therefore, even in periods of high honeydew availability, nectar provision may allow for a better enhancement of the longevity of *D. rapae*, which in turn may increase the biocontrol of pests by this parasitoid. Although not as valuable as nectar, honeydew can be considered as a resource for *D. rapae*, and could potentially complement floral nectar when aphid densities are high and nectar not available. The presence of honeydew might mitigate potential exploitative competition for nectar, by providing a sugar source when nectar is intensely consumed by other insects such as pollinators (Lee and Heimpel 2002).

In the mutualistic association between ants and aphids, ant-tended aphid species provide honeydew to ants, and these in return protect aphids against predatory or parasitic arthropods. Following this observation, it could be hypothesised that *D. rapae* and aphid parasitoids in general may mimic ant behaviour to obtain honeydew directly from the anuses of their hosts, from which honeydew is excreted. This, however, has never been reported, and was not observed during the work presented here. It is probable that providing honeydew directly to parasitoids would be very costly (in terms of fitness) to aphids, because fitter parasitoids would attack a higher number of aphids.

The nectar of OSR cv. Ability conferred a higher longevity to *D. rapae* than that from cv. Flash, but nevertheless, parasitoids are not likely to be limited by food availability during the flowering of this crop. The value of floral subsidies would therefore be more marked outside the period of crop flowering, in particular during pre-flowering, when the crop is highly sensitive to aphid infestation (Ellis et al. 1999). Furthermore, because OSR nectar is highly nutritive to *D. rapae*, and perhaps also to other natural enemies, it could be used itself as a floral subsidy for other crops. When flowering, OSR fields may also enhance the longevity of natural enemies that may subsequently disperse in surrounding crops (as hypothesised in Bowie et al. 1999). Alternatively, OSR can be used in floral strips or intercropped with other crops (as in Wang et al. 2009) to provide nutritional resources to natural enemies, and simultaneously yield a marketable seed.

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