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SCIENTIFIC NOTES

Honeydew associated with four common crop aphid species increases longevity of the parasitoid wasp, *Bracon cephi* (Hymenoptera: Braconidae)

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Abstract

The absence of sugar resources can be an important factor in limiting the success of parasitoids as biological control agents. Restoring vegetation complexity within agricultural landscapes has thus become a major focus of conservation biological control efforts, with a traditional emphasis on nectar resources. Aphid honeydew is also an important source of sugars that is infrequently considered. We carried out a laboratory experiment to examine the potential effects of honeydew from six different aphid species by crop species combinations on the longevity of *Bracon cephi* Gahan (Hymenoptera: Braconidae), the most important biological control of the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), a major pest of wheat in the northern Great Plains of North America. The benefits of honeydew for parasitoid longevity varied significantly among different aphid and crop species, illustrating the complexity of these interactions. However, honeydew produced by four aphid species commonly found in wheat, pea, and canola crops significantly increased the longevity (by two- to threefold) of the parasitoid. The study suggests that honeydew provisioning could be an important mechanism underlying the benefits of crop diversification to support biological control that merits further research.

Introduction

A majority of natural enemies of crop pests require nonhost food sources during their life time (Lundgren 2009). Sugar resources, in particular, can increase the fecundity, foraging activity, and search efficiency of adult parasitoids, strongly influencing their effectiveness as biological control agents (Evans 1994; Wäckers and Fadamiro 2005; Tena *et al.* 2015; Benelli *et al.* 2017). In simplified agricultural landscapes, low cover and diversity of vegetation are thought to result in sugar limitation that compromises the ability of natural enemies to provide consistent biological control (Mockford *et al.* 2022). Restoring vegetation complexity within these landscapes has thus become a major focus of conservation biological control efforts (Landis *et al.* 2000; Gurr *et al.* 2004). Much of the work in this field has focused on floral or extrafloral nectar as sources of sugars. However, honeydew produced by phloem-feeding hemipterans can also be an important source of sugars for parasitoids that should be more explicitly considered in the context of conservation biological control (Wäckers *et al.* 2008; Tena *et al.* 2016; Luquet *et al.* 2021).

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Table 1. Six aphid species–crop species combinations used in experiments.

Aphid species	Common name	Crop plant and variety	Common name
Acyrthosiphon pisum	Pea aphid	*Pisum sativum* Linnaeus '4010'	Pea
Acyrthosiphon pisum	Pea aphid	*Medicago sativa* Linnaeus 'Vernal'	Alfalfa
Acyrthosiphon pisum	Pea aphid	*Lens culinaris* Medikus 'Indian Head'	Lentil
Lipaphis erysimi	Turnip/mustard aphid	*Brassica napus* Linnaeus 'Hyclass 940'	Canola
Sitobion avenae	English grain aphid	*Triticum aestivum* Linnaeus 'Reeder'	Wheat
Rhopalosiphum padi	Bird cherry oat aphid	*Triticum aestivum* Linnaeus 'Reeder'	Wheat

Honeydew is often the most available carbohydrate source within agroecosystems (Wäckers and Fadamiro 2005; Wäckers *et al.* 2008) and can be present in crop fields where parasitoids are actively foraging for hosts (Evans 1994; Luquet *et al.* 2021), eliminating the travel time and energy necessary to forage for sugars in adjacent noncrop habitats (Vollhardt *et al.* 2010). Furthermore, a growing body of work demonstrates that honeydew can be as effective at enhancing parasitoid performance as sucrose solutions or high-quality floral nectar for some species (Wäckers *et al.* 2008; Benelli *et al.* 2017; Monticelli *et al.* 2020; Rand and Waters 2020). Thus, assessing the quality of commonly available honeydew resources for natural enemies provides basic information potentially useful in developing habitat and landscape management efforts to bolster biological control services (Tena *et al.* 2016).

We carried out a laboratory experiment to determine whether access to honeydew from aphids associated with dominant crops in the landscape influences the longevity of the parasitoid wasp, *Bracon cephi* Gahan (Hymenoptera: Braconidae). This species is a specialist biological control agent of the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), a major pest of wheat in the region (Buteler *et al.* 2008; Morrill *et al.* 1998; Rand *et al.* 2014). Previous work on this species has shown that access to floral nectar and honeydew can increase longevity (Reis 2018; Rand and Waters 2020) and that provisioning of sugar resources significantly increases both longevity and egg load, with similar benefits observed on sucrose, glucose, and fructose (Reis *et al.* 2019; Cavallini *et al.* 2022). In other systems, the quality of honeydew for parasitoids has been shown to vary widely across different aphid species and even for the same aphid species feeding on different host plants (Tena *et al.* 2018; Monticelli *et al.* 2020). However, the relative benefits of feeding on honeydew associated with different aphid species by host crop combinations have not been previously investigated for *B. cephi*.

Aphids were collected from the field in the diverse crop landscapes of Williams and Divide counties in North Dakota, in the northern Great Plains of the United States of America. *Cephus cinctus* is a consistent pest of wheat in the region, where wheat is commonly rotated with pulse, oilseed, and forage crops. Fields of pea, *Pisum sativum* Linnaeus (Fabaceae), lentil, *Lens culinaris* Medikus (Fabaceae), canola, *Brassica napus* Linnaeus (Brassicaceae), and alfalfa, *Medicago sativa* Linnaeus (Fabaceae) were sampled for aphids by sweep netting in July and August of 2020 and 2021. We established colonies of the most commonly encountered aphid species by crop associations to use in our experiments (Table 1). Aphid identification followed Liu and Sparks (2001) and Tharp *et al.* (2005).

Aphids (Hemiptera: Aphididae) were added to cages containing from two to eight 0.9-L pots, depending on plant and cage size, with the appropriate host crop ($\geq$ 15 cm in height), and allowed to increase in numbers until densities sufficient to produce a high yield of honeydew (more than 100 aphids/plant) were achieved. Strips of parafilm (1 $\times$ 5 cm) were then placed below the aphids to catch honeydew rain for a 24-hour period, following the approach of Tena *et al.* (2013). Only strips containing at least 10 drops of honeydew were retained for use in our experiments to ensure

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that insects could feed *ad libitum*. Similar parafilm strips to which five 2-μL drops of a 2M sucrose solution were added were also prepared to serve as positive controls (Tena *et al.* 2013). Strips were stored in a freezer (–20 °C) until deployed within a maximum of 16 months.

Bracon cephi were reared from wheat straw and stubble collected from wheat fields in Divide County, North Dakota in November 2020 and April 2021. Stubble was stored at 4 °C until removed (14 October 2021) and placed in 208-L plastic barrels (~22 °C; 14-hour:10-hour light:dark cycle), each fitted with a screen cage on top to capture emerging insects. Newly eclosed adult females were placed individually into borosilicate test tubes (1.8 × 15 cm) and assigned to one of eight experimental treatments: one of the six honeydew types (from different aphid species or the same species on different crops; Table 1), water (a negative control), or 2M sucrose (a positive control). Three to six replicates of the eight treatments were set up daily, depending on the numbers of emerging insects, between 2 and 6 November 2021 (18 replicates; 144 *B. cephi* individuals in total). A single strip of parafilm containing one of the six honeydew types, the sucrose solution, or the reverse-osmosis water (added to strips as a light mist) was placed in each tube. Tubes were then sealed with a water-saturated sponge to maintain humidity and provide water to all insects and kept in the laboratory at room temperature (mean ± standard deviation = 23.6 ± 2.3 °C) under lights set at 15:9 hours light:dark. Our negative control was also given access to water because we were interested in examining differences in the nutritional suitability among honeydew types in the absence of confounding effects of water availability. Insects were checked for survivorship, with the date recorded for individuals that died, and surviving individuals were provided new treatment strips and moistened sponges daily.

Statistical analyses were conducted in JMP®15 (SAS Institute Inc. 1989–2021). A general linear mixed model (normal distribution, identity link) was used to test for differences in *B. cephi* longevity among treatments (SAS Institute Inc. 2019a). The response variable was the number of days alive, transformed (natural-log) to normalise distributions. The model included start date as a random blocking factor, to account for variability attributable to parasitoid emergence timing, and treatment as a fixed factor, with eight levels. Tukey's honestly significant difference tests were used to compare least-squares means among treatment levels. A survival analysis was run to test treatment effects on Kaplan–Meir survival curves (SAS Institute Inc. 2019b).

The longevity of *B. cephi* females differed significantly among treatments ($df = 7$, 129.4; $F = 89.9$; $P < 0.0001$), with the positive effects of honeydew feeding on longevity varying both for the different aphid species on the same crop and for the same aphid species on different crops (Fig. 1). Although the lifespan of females on honeydew did not reach those observed on sucrose for any aphid–crop combination, longevity was significantly higher on honeydew than on water controls for four of the six honeydew types (Fig. 1). A distinct hierarchy in honeydew suitability was observed, with the highest observed longevity found on honeydew from *R. padi* and the lowest found on honeydew from *A. pisum* on alfalfa (Fig. 1).

Females fed on honeydew from *R. padi* Linnaeus on wheat lived longer than those fed on any other honeydew type (mean ± standard error = 34.2 ± 1.5 days) and lived significantly (3.5 times) longer than those fed on water (mean ± standard error = 9.6 ± 0.7). This finding parallels a greenhouse study that found similar increases in *B. cephi* longevity on *R. padi* honeydew, equalling the benefits observed on buckwheat, a high-quality floral resource (Rand and Waters 2020). The increase in longevity observed on *R. padi* honeydew in the present study was also of similar magnitude as that observed on floral resources in previous laboratory studies (Reis 2018).

Interestingly, the longevity of parasitoids that were provided with honeydew produced by *Sitobion avenae* (Fabricius), the other grain aphid examined in the present study, was significantly lower, although it still exceeded that of parasitoid controls fed on water (Fig. 1). The results suggest that *B. cephi* could benefit significantly from within-field sugar resources

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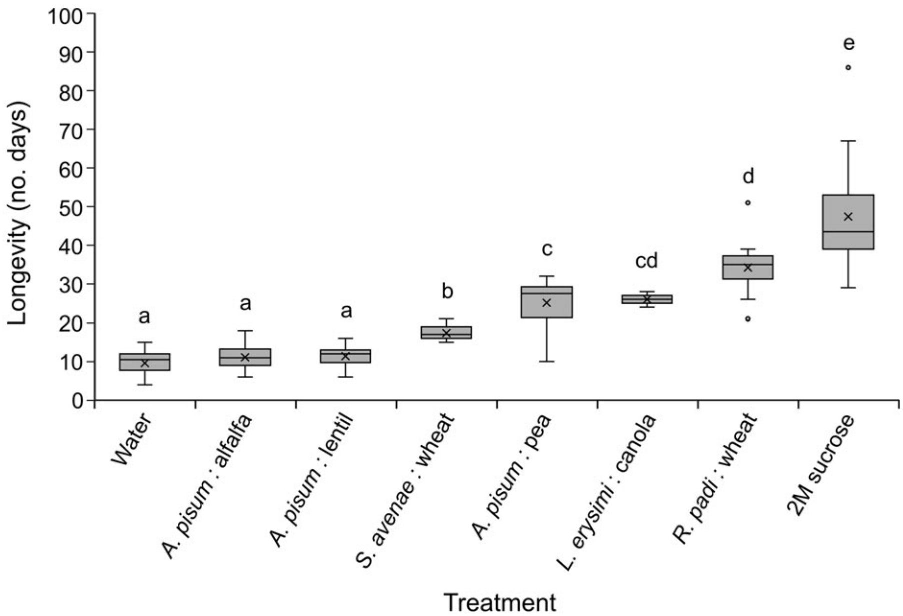

Figure 1. Longevity of *Bracon cephi* females fed on one of six different honeydew types, water (negative control), or 2M sucrose (positive control). Tukey's honestly significant difference tests comparing least squares means among treatments are presented above plots (different letters indicate significant differences, $P < 0.05$).

provided by aphids, especially *R. padi*, in wheat. The benefits of honeydew in nectar-poor crops have been documented in other cereals. For example, extensive feeding by *Aphidius* spp. aphid parasitoids on aphid honeydew appears to alleviate sugar limitation in triticale monocrops, such that parasitism levels equal those observed in nectar-rich intercrops with faba bean (Luquet *et al.* 2021). The present study further suggests that aphid honeydew from other nonhost crops could provide beneficial resources for parasitoids of wheat pests. Females fed on honeydew from both *Acyrthosiphon pisum* (Harris) on pea and *Lipaphis erysimi* (Kaltenbach) on canola lived at least 2.6 times longer on average than those fed on water (Fig. 1). In contrast, the suitability of honeydew from *A. pisum* on lentil and alfalfa appears low, with the longevity of *B. cephi* in those treatments not significantly differing from that of *B. cephi* fed on water alone (Fig. 1).

The factors underlying the differences in suitability of different honeydew types were not assessed in the present study and might reflect differences in either accessibility or quality. Previous work has found that differences in nutritional quality associated with the composition of sugars, proteins, or primary and secondary chemicals can all affect parasitoid performance (Wäckers 2005; Faria *et al.* 2008; Sabri *et al.* 2013; Monticelli *et al.* 2020). Amino acids have recently been shown to slightly increase the egg loads of *B. cephi* but had no effect on the insect's longevity (Cavallini *et al.* 2022). Factors, such as viscosity, that affect a parasitoid's ability to take in the resource can also drive variability and may be influenced by precipitation and humidity (Wäckers 2005; Faria *et al.* 2008; Sabri *et al.* 2013; Monticelli *et al.* 2020).

It seems unlikely that parasitoids would leave wheat fields to forage for sugars in adjacent crops if *R. padi* honeydew were present locally. However, aphid populations are notoriously variable, and parasitoids may benefit from other crop aphids during periods of scarcity within wheat. Furthermore, parasitoids overwinter in wheat stubble, with fields often rotated to an alternative crop the following year. Parasitoids emerging in fields that were rotated from wheat to crops that contain beneficial aphids, such as canola or pea, may benefit from

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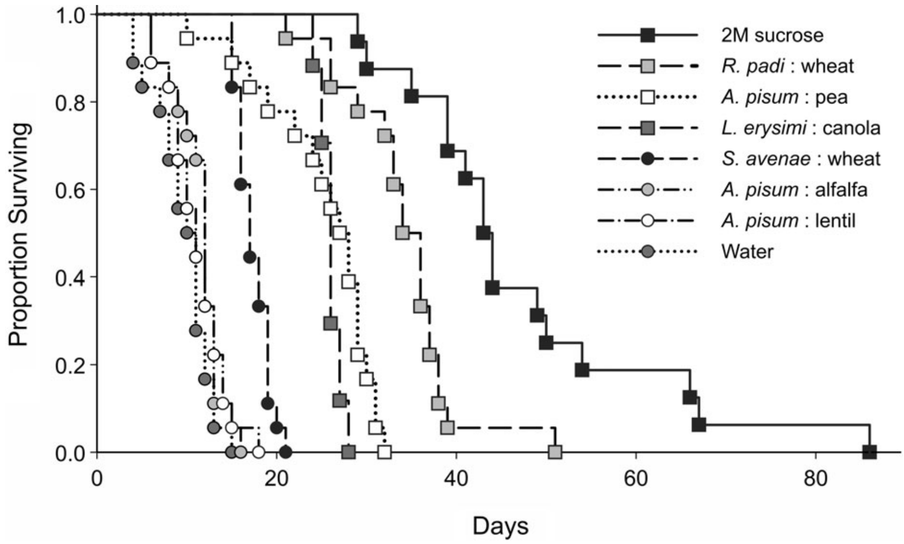

Figure 2. Kaplan–Meir survival curves for *Bracon cephi* parasitoids fed on one of six different honeydew types, water (negative control), or 2M sucrose (positive control).

honeydew resources in these rotational crops. Previous work has shown that aphids are typically present in legume and brassica crops during the period of parasitoid emergence and parasitism of host larvae in mid-June through July (Rand and Lundgren 2018; Rand *et al.* 2022). Wind tunnel experiments have documented dramatic increases in flight capacity associated with sugar feeding in the parasitoid *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) (Fahrner *et al.* 2014). Thus, honeydew feeding by *B. cephi* in canola and pea fields early in the season could increase longevity, dispersal ability, or both, thereby increasing the insects' likelihood of colonising nearby wheat fields.

Survival analysis (SAS Institute Inc. 2019b) indicated a highly significant treatment effect on Kaplan–Meir survival curves (Log-Rank ChiSquare = 230.96; $P < 0.0001$), with some notable differences in shape (Fig. 2). Females fed on *L. erysimi* honeydew did not start to die until day 24, second only to those fed on sucrose treatments, but then all these females died within a short time window. In contrast, females fed on honeydew from *A. pisum* on pea started to die much sooner (day 10) but did so over a longer period, such that mean longevity was similar in the two treatments (Fig. 1). *Bracon cephi* is a synovigenic species, continuing to mature eggs throughout adulthood. Previous work has shown that egg load more than doubles with sugar feeding for females that are between 2 and 10 days old (Reis *et al.* 2019; Cavallini *et al.* 2022). Whether sugar feeding continues to augment egg load later in the insect's lifespan (individuals older than 10 days) is unknown. This information will be critical for gauging the relative benefits of different honeydew types, and sugar feeding more generally, for parasitoid performance and biological control. For example, if more eggs are laid early in the insect's lifespan, with oviposition decreasing as females age, as has been found for other species in the *Bracon* genus (El-Basha 2015), then honeydew that maximises early survivorship may be of particularly high value.

Overall, our results suggest that *B. cephi* could benefit significantly from sugars associated with aphid honeydew, underscoring the importance of avoiding prophylactic pesticide applications on subeconomic aphid populations, given their potential benefits to natural enemies. However, the benefit of honeydew varied greatly both across crops for the same aphid species (*A. pisum* on pea, lentil, and alfalfa) and across different aphid species within a crop (*R. padi* and *S. avenae* on wheat). This finding parallels similar variability observed in parasitoid performance across

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different crop plant and aphid species combinations tested in previous work (Tena *et al.* 2018; Monticelli *et al.* 2020). The presence of crop aphid honeydew has been suggested as a potential mechanism underlying observed increases in biological control in crop fields that are embedded in landscapes with a high cover or diversity of alternative crops (Kheirodin *et al.* 2020), but this is one of only a handful of studies to demonstrate benefits of nonhost crop aphid honeydew on parasitoid performance. Future work that examines the spatial and temporal availability of aphid honeydew across different crop species and its influence on parasitism levels in the field will be important in guiding landscape-diversification strategies to bolster biological control services. In addition, recent work documenting negative effects of honeydew from insecticide-treated crops (Calvo-Agudo *et al.* 2021, 2022) adds potential complexity that needs to be investigated in the system examined in the present study, given the ubiquity of insecticide seed treatment in oilseed crops in the region (Tansey *et al.* 2008; Main *et al.* 2014).

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