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The influence of aphid-produced honeydew on parasitoid fitness and nutritional state: A comparative study

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Abstract

Honeydew is a sugar-rich resource excreted by many hemipteran species and is a key food source for other insect species such as ants and parasitoid wasps. Here, we evaluated the nutritional value of 14 honeydews excreted by 13 aphid species for the generalist aphid parasitoid *Lysiphlebus testaceipes* to test a series of hypotheses concerning variation in the nutritional value of honeydew. There was a positive correlation between the body sugar content of honeydew-fed parasitoids and their longevity. This information is valuable for biological control researchers because it demonstrates that the nutritional state of honeydew-fed parasitoids in the wild can indicate their fitness, independently of the honeydew source they have fed on.

Although the carbohydrate content and longevity of *L. testaceipes* differed greatly among the different honeydews, we did not find a significant effect of aphid or host plant phylogeny on these traits. This result suggests that honeydew is evolutionarily labile and may be particularly subject to ecological selection pressures. This becomes apparent when considering host aphid suitability: *Schizaphis graminum,* one of the most suitable and commonly used hosts of *L. testaceipes,* produced honeydew of the poorest quality for the parasitoid whereas *Uroleucon sonchi*, one of the few aphids tested that cannot be parasitized by *L. testaceipes*, excreted the honeydew with the highest nutritional value. These data are consistent with the hypothesis that hemipterans are subject to selection pressure to minimize honeydew quality for the parasitoids that attack them.

Keywords: Hymenoptera; Aphididae; Nutritional ecology; Biological control; Carbohydrates; *Lysiphlebus testaceipes*

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Introduction

Honeydew is a sugar-rich resource excreted by many hemipteran species, attracting insects belonging at least to 49 families, including bees and natural enemies (Zoebelein, 1956a, 1956b; Lundgren, 2009). Many adults of dipteran and hymenopteran parasitoids depend on honeydew as a food source, often the most common source of available sugar in agroecosytems (Wäckers, van Rijn, & Heimpel, 2008; Lundgren, 2009; Tena, Wäckers, Heimpel, Urbaneja, & Pekas, 2016). A great number of ant species, which tend and protect hemipterans, also feed on and would not survive without honeydew (Way, 1963; Styrsky & Eubanks, 2007; Pekas, Tena, Aguilar, & Garcia-Marí, 2011). However, the quality of honeydew as a diet for insects is highly variable (Avidov, Balshin, & Gerson, 1970; Völkl, Woodring, Fischer, Lorenz, & Hoffmann, 1999; Wäckers et al., 2008; Tena, Llácer, & Urbaneja, 2013; Tena et al., 2016).

Debate on the quality of honeydew as a diet for insects has been ongoing since before the publications of Zoebelein (1956a, 1956b). Honeydew is considered to be a mixture of plant-derived compounds that vary with several biotic and abiotic factors (Maltais & Auclair, 1962; Fischer & Shingleton, 2001; Wäckers et al., 2008). However, the composition of honeydew has a genetic component with high heritability (Völkl et al. 1999; Wäckers, 2000). Consequently, it is expected that evolution has also shaped the quality of honeydew as carbohydrate source for insects. On the one hand, high-quality honeydew may be favored to attract and retain mutualistic ant species that tend and protect hemipteran colonies, but on the other hand, it may attract and retain natural enemies and increase their fitness with potential negative consequences on hemipteran populations if ants are absent (Evans & England 1996; Wäckers et al., 2008; Tena et al., 2016). In these cases, low-quality honeydew may be favored to limit honeydew feeding by natural enemies (Wäckers, 2000; Wäckers et al., 2008). Here, we determine whether aphid honeydew varies in quality for the generalist aphid parasitoid *Lysiphlebus testaceipes* and also whether the quality exhibits a phylogenetic signal. To do this, we categorized the quality of honeydews produced by 13 aphid species as food sources for *L. testaceipes* by measuring: (i) the content of fructose and total sugars of the honeydews and (ii) their effect on the longevity and nutritional state of *L. testaceipes* females fed on these honeydews.

L. testaceipes is a solitary koinobiont and pro-ovigenic (or with a very high ovigenic index) endoparasitoid of aphids (van Steenis, 1994). It does host feed (Desneux, Barta, Delebeque, & Heimpel 2009) and parasitizes more than 100 aphid species in various genera, tribes and subfamilies (Pike et al., 2000). It is native to North America where it is an effective natural enemy of the greenbug, *Schizaphis graminum* (Royer, Pendleton, Elliott, & Giles, 2015). The parasitoid was introduced to Europe (Starý, Lyon, & Leclant, 1988) where it has achieved some success as a biological control agent (Costa & Starý, 1988; Starý et al., 1988) and also has been found to attack numerous aphid species in various ecosystems (Starý et al., 1988; Starý, Lumbierres, & Pons, 2004; Mitrović et al., 2013; Zikic et al., 2015). Therefore, this parasitoid likely feeds on honeydews from various aphid species that differ greatly in their quality as a sugar source. Moreover, some of these aphids feed on different host plants (Holman, 2009) and therefore may produce different honeydew quality for insects depending on the plant. *L. testaceipes* is thus a highly suitable model for a comparison of the quality of aphid honeydews on parasitoid fitness.

To determine whether parasitoids feed on honeydew in the field, as well as to evaluate their nutritional state, researchers have used high-performance liquid chromatography (HPLC), or anthrone tests over the last decade (Casas et al., 2003; Steppuhn & Wäckers, 2004; Heimpel et al., 2004; Lee, Andow, & Heimpel, 2006; Hogervorst, Wäckers, & Romeis, 2007a; Winkler, Wäckers, & Pinto, 2009; Tena, Pekas, Wäckers, & Urbaneja, 2013; Dieckhoff, Theobald, Wäckers, & Heimpel, 2014; Tena, Pekas, Cano, Wäckers, & Urbaneja, 2015; Calabuig et al., 2015). This information is valuable for biological control researchers, especially when parasitoid carbohydrate contents are low; as this indicates that parasitoids are sugar-limited and that providing a sugar source may increase their fitness and biological control potential (Heimpel & Jervis, 2005; Tena et al., 2016). However, an observation of high energy reserves may be misleading if low-quality carbohydrates for insects have been ingested. This is especially important when multiple hemipteran species with different honeydew qualities are present at a given field site (Pekas et al., 2011; Tena, Hoddle et al., 2013; Tena, Llácer et al., 2013; Tena, Pekas et al., 2013).

Here, we used anthrone tests to quantify the carbohydrate levels (fructose, other sugars, glycogen and total carbohydrates) of *L. testaceipes* females fed on different honeydews, and we determined (i) whether the sugar content of different honeydews is correlated with the nutritional state and longevity of parasitoids fed on these honeydews; and (ii) whether the nutritional state of parasitoids fed on different honeydews is correlated with their longevity. Positive correlations would indicate that carbohydrate level of honeydews and/or parasitoids reflect also the fitness of honeydew-fed parasitoids.

Materials and methods

Insect colonies

Our culture of *L. testaceipes* was initiated with individuals collected from parasitized soybean aphids, *Aphis glycines* in Minnesota, USA in the year preceding these studies and had thus been in culture for approximately 25 generations on soybean aphid. Just prior to these studies, the parasitoid population was transferred to *Schizaphis graminum*

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