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Parasitoid nutritional ecology in a community context: the importance of honeydew and implications for biological control

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One focus of conservation biological control studies has been to improve the nutritional state and fitness of parasitoids by adding nectar and artificial sugars to agroecosystems. This approach has largely overlooked the presence of honeydew, which is likely the primary carbohydrate source available to parasitoids in many agroecosystems. Over the last decade, it has been demonstrated that parasitoids often utilize this sugar source and there is evidence that honeydew can indirectly impact the population dynamics of herbivores through its nutritional value for parasitoids. The consumption of honeydew by parasitoids can shape direct and indirect interactions with other arthropods. The strength of these effects will depend on: first, parasitoid biology, second, the presence of other sugar sources (mainly nectar), third, the quality and quantity of the honeydew, and fourth, the presence and competitive strength of other honeydew consumers such as ants. The combination of these four factors is expected to result in distinct scenarios that should be analyzed for each agroecosystem. This analysis can reveal opportunities to increase the biocontrol services provided by parasitoids. Moreover, honeydew can be a resource-rich habitat for insect pathogens; or contain plant secondary chemicals sequestered by hemipterans or systemic insecticides toxic for the parasitoid. Their presence and effect on parasitoid fitness will need to be addressed in future research.

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Introduction

The study of parasitoid nutritional ecology has been motivated in large part by the importance of parasitoids as biological control agents of pest insects. As adults, most parasitoids need to feed on sugar-rich foods to meet their energy requirements. The absence of sugar feeding can severely compromise the fecundity and lifespan of most parasitoid species and, consequently, their potential to control pests [1]. Since the early observations by Wolcott [2,3], who noted that the mole cricket parasitoid *Larra analis* F. (Hymenoptera: Sphecidae) was dependent upon the nectar of two flowering weed species for establishment in Puerto Rico, most biological control practitioners have focused their efforts on improving the nutritional state and fitness of parasitoids by adding flowering plants (nectar) and artificial sugars to agroecosystems [1,4]. This approach, however, has critically overlooked the potential role of honeydew, which in terms of availability is the primary carbohydrate source in many agroecosystems [5]. In fact, during the last decade, it has been demonstrated that parasitoids commonly feed on honeydew in the field using high-performance liquid chromatography (HPLC) [6,7,8,9,10,11••], or anthrone tests [12].

By feeding on honeydew, parasitoids can impact on the population dynamics of herbivores. For example, Evans and England [13] demonstrated that parasitism of the alfalfa weevil *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae) by the parasitoid *Bathyplectes curculionis* Thomson (Hymenoptera: Ichneumonidae) increases when the parasitoid has access to honeydew excreted by pea aphids *Acyrthosiphon pisum* Harris (Hemiptera: Aphididae). The usefulness of honeydew in increasing parasitoid fitness and biological control will depend, apart from its availability, on several factors: first, parasitoid biology, second, the presence of other sugar sources (mainly nectar), third, the quality and quantity of the honeydew, and fourth, the presence and competitive strength of other honeydew consumers such as ants. The two former factors have been reviewed previously for parasitoid sugar feeding in general [1]. Here, we discuss the implications of the two latter factors in the nutritional state and fitness of parasitoids. Taking into consideration the widespread availability of honeydew in agroecosystems, we also discuss the opportunities and challenges that honeydew represents for biological control.

Effect of honeydew quality and quantity on the nutritional state and fitness of parasitoids

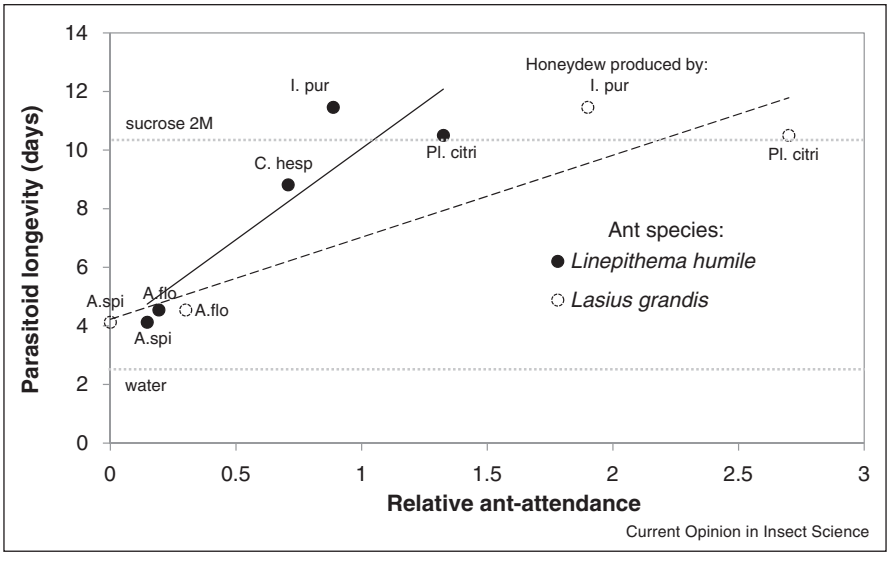
Honeydew is a sugar-rich fluid excreted by plant feeders (mostly hemipteran insects) after feeding on phloem sap. Many honeydews are inferior in quality as a sugar source for parasitoids fitness compared to nectar or plain sugar solutions ([5], but see [14]). However, there can be substantial variation among honeydew types or even in honeydew excreted by individuals of the same species [15]. The sugar content and composition of honeydew is species-specific as it contains a mixture of phloem sugars and oligosaccharides synthesized by the plant feeders [8•,16,17]. In addition, honeydew may contain low concentrations of amino acids and secondary metabolites [16], which can contribute to the variability in honeydew quality (Figure 1) [5,18,19]. Depending on the honeydew type fed upon, the impact on parasitoid longevity and fecundity can vary from negligible to substantial [19]. For example, *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) laid five times more eggs and lived twice as long when fed on honeydew excreted by *Coccus hesperidum* L. (Hemiptera: Coccidae) than by *Aphis spiraecola* Patch (Hemiptera: Aphididae) [19]. Moreover, the effect of feeding on two or more honeydew types on parasitoid fitness remains unknown. This is especially relevant in agroecosystems where multiple species of honeydew producers coexist.

The effect of honeydew on the nutritional state of parasitoids has been analyzed both under controlled conditions and in the field. Under controlled conditions, Lee *et al.* [20] and Wyckhuys *et al.* [21] demonstrated that honeydew-fed parasitoids contained more sugars and glycogen than starved parasitoids but less than individuals that had been given access to honey or sucrose. The honeydew-fed parasitoids also exhibited intermediate longevities in these studies. This latter result may be partially explained by the fact that some oligosaccharides present in honeydew cannot be metabolized by parasitoids [22]. In the field, it was also demonstrated that parasitoids feed on honeydew [6,7,8,9,1,0,11••] even in the presence of flowers [12,23,24]. Tena *et al.* [8•] showed that the sugar content of *Aphytis melinus* in citrus varied through the year and that this reflected the density and species of honeydew producers. In spring and summer, when honeydew producers were abundant, the sugar content of *A. melinus* was three-fold higher than in fall when honeydew producers were scarce [8•]. The citrus agroecosystem is particularly suitable to study complex honeydew-mediated interactions, given that up to 6–8 species of honeydew producers can coexist in a single tree [8•,25,26].

Effect of ants on the nutritional state of parasitoids

Most ant species are omnivorous, feeding on protein and plant-derived carbohydrates such as floral and extrafloral nectar, plant sap and in particular honeydew [27–29]. When they have a choice, ants prefer honeydews with high sugar concentration that are rich in oligosaccharides [16,30]. Laboratory observations producing these results were later corroborated by field observations, showing

Figure 1



Relationship between the longevity of *Aphytis melinus* and the relative ant-attendance (i.e. total number of attending ants divided by the number of hemipterans per honeydew source) of the ants *Lasius grandis* and *Linepithema humile* for different honeydew producers. Data obtained by Tena *et al.* [19,26] and Pekas *et al.* [25]. Horizontal lines indicate the parasitoid longevity when feeding on water or sucrose (2M). Linear regression: *Linepithema humile*: $F_{1,3} = 14.40$, $P = 0.03$, $R^2 = 82.7\%$, $y = 6.22x + 3.82$; *Lasius grandis*: $F_{1,2} = 13.98$, $P = 0.06$, $R^2 = 87.5\%$, $y = 2.80x + 4.22$). A.flo: *Aleurothrixus floccosus*; A.spi: *Aphis spiraecola*; I.pur: *Icerya purchasi*; P.citri: *Planococcus citri*. The relationships show that the same honeydew-producing hemipteran species that produce high longevities in parasitoids are also preferred by ants, and also that this relationship is stronger for *L. humile* than for *L. grandis*.