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Honeydew as a food source for natural enemies: Making the best of a bad meal?

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Abstract

The majority of predators and parasitoids require non-prey food as part of their diet. The availability of suitable non-prey food can impact predator–prey and parasitoid–host dynamics and may be critical to the efficacy of biological pest control. A growing body of work addresses the role of floral nectar in conservation biological control programs. In comparison, we know relatively little about the role of honeydew as a sugar source for predators and parasitoids, in spite of the fact that honeydew is often the predominant sugar source in agroecosystems.

Here we test the hypothesis that honeydew is a less suitable food source when compared with other sugar sources, using data from parasitoid literature. We also explore whether parasitoids of honeydew-producing insects show particular adaptations allowing them to optimize the exploitation of this suboptimal food source. A review of available literature supports the general hypothesis that honeydew is inferior to other sugar sources, although there is considerable variation in the quality of honeydew depending on the honeydew producer and its host plant. The accrued dataset is not consistent with our second hypothesis that parasitoids of honeydew-producing hosts fare better on this nutritionally inferior food source as compared with parasitoid species which exploit hosts that do not produce honeydew. Finally we review evidence on the use of honeydew by predators and parasitoids under field conditions and explore implications for biological pest control programs.

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Keywords: Honeydew; Nectar; Parasitoid; Predator; Biological control

1. Introduction

Biological control agents are usually identified by their carnivorous lifestyle. However, the majority of predators and parasitoids are actually ‘omnivores’ as they also commonly feed on plant-derived foods. Exploitation of sugar sources or pollen is widespread among predaceous organisms from a broad range of orders including Hymenoptera, Diptera, Coleoptera, Heteroptera, Thysanoptera, Neuroptera, Lepidoptera, as well as from the arachnid orders Araneae and Acari (Table 1).

Non-prey feeding can have a dramatic impact on the activity, longevity and lifetime fecundity of predators and parasitoids. Thus, the availability of non-prey food can be crucial to their efficacy in biological pest control (van Rijn and Tanigoshi, 1999b; Winkler et al., 2006). Depending on the life history stages that feed on prey and/or plant-derived food, we can distinguish between true omnivory (temporal or permanent) and life-history omnivory (for examples see Wäckers and van Rijn (2005)). This is important because the type of omnivory determines the potential impact of plant-derived food on carnivore–herbivore interactions. In the case of life-history omnivores, such as hoverflies and many parasitoids, the adult stage strictly depends on sugar or pollen resources. As a consequence, the availability of suitable plant-derived foods typically

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Table 1
Exploitation of non-prey food by predators and parasitoids arranged according to order and family

| Order | Family | Plant-feeding stage | Type of non-prey food | Reference |
|--|---|---------------------|---------------------------|--|
| Neuroptera | Chrysopidae (green lacewings) | Adult and juvenile | Nectar, honeydew, pollen | Limburg and Rosenheim (2001); Stelzl (1991) |
| | Hemerobiidae (brown lacewings) | Adult and juvenile | Nectar, honeydew, pollen | Stelzl (1991) |
| Diptera | Syrphidae (hoverflies) | Adult | Nectar | Hickman et al. (1995) |
| | | | Pollen | Wratten et al. (1995) |
| | | | Honeydew | Hogervorst et al. (2007a); van Rijn et al. (2006); Zobelein (1956) |
| | Cecidomyiidae (gall midges) | Adult | Nectar | Opit et al. (1997) |
| Tachinidae (as well as many other parasitoid fly families) | Adult | Nectar | Gilbert and Jervis (1998) | |
| | | | Honeydew | Zobelein (1956) |
| Hymenoptera | Ichneumonidae, Braconidae (as well as many other parasitoid families) | Adult | Nectar | Lewis et al. (1998); Wäckers (2001) |
| | | | Pollen | Györfi (1945); Patt et al. (1997) |
| | | | Honeydew | Lee et al. (2004); Wäckers and Steppuhn (2003) |
| | Vespididae (social wasps) | Adult | Nectar, fruit | Cuautle and Rico-Gray (2003) |
| | | | Honeydew | Beggs (2001) |
| | Formicidae (ants) | Adult | Nectar | Beattie (1985) |
| | | | Honeydew | Beattie (1985) |
| Coleoptera | Meloidae (blister beetles) | Adult | Nectar, pollen | Adams and Selander (1979) |
| | Cantharidae (soldier beetles) | Adult | Nectar, pollen | Traugott (2003) |
| | | | Honeydew | Zobelein (1956) |
| | Coccinellidae (ladybirds) | Adult and juvenile | Nectar | Pemberton and Vandenberg (1993) |
| | | | Pollen | Beattie (1985) |
| | | | Honeydew | Zobelein (1956) |
| | Anthribidae | Adult | Honeydew | Zobelein (1956) |
| Heteroptera | Anthocoridae | Adult and juvenile | Pollen | Eubanks and Styrsky (2005) |
| | Lygaeidae | Adult and juvenile | Plant juice | Eubanks and Styrsky (2005) |
| | Miridae | Adult and juvenile | Plant juice | Gillespie and McGregor (2000) |
| | Nabidae | Adult and juvenile | Plant juice | Stoner (1972) |
| | Pentatomidae | Adult and juvenile | Plant juice | Ruberson et al. (1986) |
| | Reduviidae | Adult and juvenile | Plant juice | Stoner (1975) |
| Thysanoptera | Aeolothripidae, Phlaeothripidae, Thripidae | Adult and juvenile | Pollen, leaves | Kirk (1997) |
| Lepidoptera | Lycanidae (larvae are aphidophagous) | Adult | Honeydew | Nixon (1951) |
| Araneae | Araneidae (orb-web spiders) | Juvenile | Pollen | Smith and Mommsen (1984); |
| | various families | Adult and juvenile | Nectar | Taylor and Foster (1996) |
| Acari: Mesostigmata | Phytoseiidae (predatory mites) | Adult and juvenile | Nectar | van Rijn and Tanigoshi (1999a) |
| | | | Pollen | van Rijn and Tanigoshi (1999b) |

has an especially strong impact on survival and reproductive capacity of the adults (van Rijn et al., 2006; Winkler et al., 2006). In the case of temporal omnivores or permanent omnivores (including predatory mites and ladybirds), the effects of nectar, honeydew or pollen feeding are often more intricate, given that these true omnivores can (to greater or lesser extents) substitute prey with sugar/pollen feeding. Whereas the latter typically increases fitness, it may nevertheless occur at the expense of the per capita prey consumption (Eubanks and Styrsky, 2005). In spite of this, there is theoretical and experimental evidence that sugar and pollen supplements can have an important impact on carnivore–herbivore dynamics in true omnivores as well (Eubanks and Styrsky, 2005; van Rijn et al., 2002).

Many predators and parasitoids rely primarily or exclusively on carbohydrates as a source of energy to fuel physical activity and metabolic upkeep. The fact that energy from carbohydrates can be rapidly mobilized makes sugars especially suitable to supply the surge in energy required during flight (Hoferer et al., 2000). This explains why those arthropods that show high frequency wing muscle contractions such as Hymenoptera and Diptera (Smyth, 1985) primarily oxidize carbohydrates in their wing muscles.

To meet their carbohydrate requirements, predators and parasitoids may exploit a broad range of plant substrates, including floral and extrafloral nectar, fruits, plant sap exudates, as well as foods indirectly derived from plants, such as honeydew, the sugar-rich excretion product of phloem

feeding arthropods (Wäckers, 2005). The potential contribution of a given carbohydrate source to the diet of predators and parasitoids depends on its availability, apparency, accessibility, nutritional composition and the foraging risks associated with its exploitation (Wäckers, 2005).

In terms of availability, honeydew is likely the primary exogenous carbohydrate source in many ecosystems (Kloft et al., 1985). This applies in particular to agricultural ecosystems, where nectar sources are often scarce (Wäckers, 2005). Honeydew may be available from honeydew producers associated with the crop itself, with weeds growing within the crop, or with vegetation in surrounding non-crop elements. However, in comparison to nectar honeydew is often an inferior food source. Not only is honeydew less apparent when compared to the lavishly advertised floral nectar (Stapel et al., 1997; Wäckers and Swaans, 1993), it is often highly viscous, making it difficult to access, and its particular chemical composition often limits its nutritional suitability (Wäckers, 2005). Low nutritional suitability can be based on plant-derived compounds (both primary and secondary metabolites) as well as on aphid synthesized compounds (Wäckers, 2000; Wink and Römer, 1986). In contrast to floral nectar, extrafloral nectar, fruits, or fungal sugar excretions, which all have evolved to recruit sugar-feeding organisms, honeydew is primarily a waste product allowing phloem feeders to dispose of excess carbohydrates in their diet (Wilkinson et al., 1997). Consequently, there is usually little benefit to the honeydew producer in making this sugar secretion apparent or palatable. To the contrary, as any nutritional or informational benefit to predators or parasitoids can have a negative impact on the honeydew producing colony, phloem feeders are likely to be subject to a strong selection pressure to minimize honeydew apparency (Wäckers and Swaans, 1993), as well as quality and quantity excreted (Wäckers, 2000).

Here we compiled data from studies which compared honeydew to other sugar sources with regard to their impact on parasitoid longevity. On the basis of this dataset we tested the hypothesis that honeydew is a relatively unsuitable sugar source. In addition we tested whether parasitoids of honeydew-producing insects show particular adaptations allowing them to optimize the exploitation of this suboptimal food source.

2. Feeding adaptations

The suitability of a particular food source is not only a function of food source characteristics but also depends on how well consumers are attuned to its exploitation. Insects possess sensory, behavioral, morphological and physiological adaptations that enhance their ability to locate, detect and digest specific food sources. They are expected to primarily evolve adaptations to those food sources that reliably occur within their habitat. For parasitoids, which have to balance food search with the search for hosts, the exploitation of food resources likely depends on the temporal and spatial association between hosts and adult food

resources (Bernstein and Jervis, 2008; Downes and Dahlem, 1987; Sirot and Bernstein, 1996).

Parasitoids and predators can be categorized into two distinct groups according to the association between their prey and carbohydrate sources. On the one hand, there are those species whose prey is not reliably associated with a suitable carbohydrate source. These species have to alternate their search for prey with bouts of foraging for carbohydrates, which require a clear task differentiation. Parasitoids from this group often show specific adaptations to the exploitation of both host and nectar resources (see below).

The second group includes those parasitoids and predators whose prey is closely linked to carbohydrate-rich food sources. This applies to species whose prey excretes sugars, e.g. honeydew, or where prey occurs on sugar-rich substrates like fruits or nectar-bearing plant structures. For them, locating prey and carbohydrates may represent a single task. By feeding on food sources that are directly associated with prey or prey patches, their search task is simplified and they save time and energy while reducing mortality risks.

Parasitoids of honeydew-secreting hosts are a prominent example of the latter category. In the case of these parasitoids, finding hosts usually ensures a cornucopia in terms of food availability. While we may hypothesize that parasitoids of honeydew producers show few adaptations to the exploitation of additional carbohydrate sources and little or no task differentiation between food foraging and host search, they may have evolved specific adaptations to optimize the exploitation of honeydew as a food source as well.

2.1. Adaptations to nectar feeding

The mutualism between flowers and particular pollinators has resulted in the evolution of clearly distinguishable pollination syndromes that often feature intricate adaptations both from the side of plants as well as the pollinator (Fenster et al., 2004). However, also insects that contribute little or nothing to pollination may have evolved a range of adaptations to better exploit floral nectar and other resources.

Parasitoids whose hosts are not associated with adult food are equipped with a number of sensorial and behavioral mechanisms that enable them to deal with the dual task of host seeking and foraging for adult food. They possess separate categories of innate sensory responses, which are expressed relative to their physiological needs (Siekman et al., 2004; Wäckers, 1994). Food-deprived parasitoids typically express innate responses to stimuli associated with food, such as floral odors or colors. Following feeding, parasitoids lose interest in these food stimuli and start responding to host associated cues (Wäckers, 1994). In addition, parasitoids exhibit a distinct complex of task-specific innate behaviors relating to host finding and food foraging (Olson et al., 2003; Wäckers et al., 2002). Associative learning of host- and food-associated information is also

organized according to the parasitoid's physiological state. (Takasu and Lewis, 1993).

Parasitoids also show morphological adaptations to nectar feeding. Among various taxa specialized elongated mouthparts have evolved that allow parasitoids to extract nectar from long or deep tubular flower corollas (Jervis, 1998). However, the great majority of parasitoids have short mouthparts that are relatively unsuited to reach concealed floral nectaries. This restricts their feeding to exposed floral nectar from unspecialized flowers or other easily accessible sugar solutions such as honeydew or extrafloral nectar. Some parasitoids are small enough to climb into deep corollas to imbibe nectar (Baggen et al., 1999), and at least one parasitoid, *Diadegma insulare* (Cresson), is able to 'rob' floral nectar by chewing or sucking at the base of floral nectaries (Idris and Grafius, 1995).

To successfully utilize food sources, organisms must not only be able to recognize and accept food (ingestion), but their digestive system has to be able to metabolize the consumed compounds. Most nectar is primarily composed of sucrose and its hexose components glucose and fructose (Percival, 1961). Parasitoid gustatory receptors and digestive systems are well tailored to the recognition and metabolism of these principal nectar sugars, thus allowing the full exploitation of these food sources (Beach et al., 2003; Wäckers, 1999; Wäckers, 2001).

The recently described phenomenon that some parasitoids synthesize oligosaccharides when fed with nectar or a highly concentrated sucrose solution may represent a further physiological adaptation to sugar feeding (Wäckers et al., 2006). In analogy to oligosaccharide synthesis in phloem-feeders (Wilkinson et al., 1997), this metabolism may serve an osmo-regulatory function, allowing parasitoids to alleviate osmotic stress associated with the high-sucrose content of ingested nectar.

2.2. Adaptations to honeydew feeding by parasitoids

Given the fact that honeydew is often the predominant source of exogenous sugars, one can expect that sugar feeding arthropods may have evolved adaptations to optimize the exploitation of this often copious resource. The short labrum found in most parasitoids is well-suited to imbibe highly concentrated sugar solutions, including honeydew, which is typically present as small viscous droplets or as a thin film. In addition, feeding on honeydew can also be impeded by the tendency of some honeydew sugars to rapidly crystallize. At least some parasitoids can overcome this problem as they appear to be able to utilize crystalline sugar (Bartlett, 1962; Wäckers, 2000). Presumably they use excreted saliva to dissolve the sugar crystals, as has been previously shown in examples among Lepidoptera, and Diptera (Stoffolano, 1995).

Aside from exploiting honeydew as an adult food source, aphid predators and parasitoids can also use honeydew as a host-location kairomone and an oviposition stimulus (Bargen et al., 1998; Hagvar and Hofsvang,

1991). Mandour et al. (2005) showed that the whitefly parasitoid *Eretmocerus* sp. nr. *furushashii* (Aphelinidae: Hymenoptera) is arrested in patches treated with glucose, fructose, trehalulose and trehalose. The response to trehalulose, a sugar specific to whitefly honeydew, was the highest followed by trehalose, another host-synthesized sugar. In contrast, sucrose and low concentrations of melezitose did not arrest the parasitoid. The particularly strong arrestment response of *Eretmocerus* to the whitefly-synthesized sugars trehalulose and trehalose, and the fact that the parasitoids used were food satiated, indicates that this parasitoid uses these sugars as a host-searching cue (kairomone).

We hypothesize that parasitoids of honeydew-producing insects will also show particular physiological adaptations allowing them to optimize the dietary exploitation of this often nutritionally inferior food source. As a preliminary evaluation of this hypothesis, we compared the effect of honeydew and other sugar sources (such as honey, sucrose solutions and floral nectar) on longevity in parasitoids that do and do not attack honeydew-producing hosts. The results of this survey are shown in Table 2 and Fig. 1. We found data on 11 parasitoid species of hosts that *do not* produce honeydew, feeding on honeydew from a total of 13 phloem-feeder species. In the contrast group, we found data on five parasitoid species of honeydew producing hosts, feeding on honeydew from a total of ten phloem feeders (Table 2).

As a preliminary test of the hypothesis that parasitoids of honeydew producers show adaptations to optimize the exploitation of this suboptimal food source, we compared the ratio of longevities from honeydew to non-honeydew sugar sources for parasitoids that do and do not attack honeydew-producing hosts. Although the overall ratio was greater for parasitoids of honeydew-producing hosts than for parasitoids of host that do not produce honeydew (3.04 and 1.88, respectively), these differences were not significant using Wilcoxon's rank sums tests ($P > 0.1$ for tests including all data sets or ones pooled by parasitoid species when honeydew from more than one herbivore species was used). Thus, our data are not consistent with the hypothesis that parasitoids of honeydew-producing hosts are better able to utilize honeydew than are parasitoids of hosts that do not produce honeydew. A more thorough evaluation of this hypothesis will have to await more data sets like the ones reviewed in Table 1 so that a phylogenetically-corrected analysis testing for independent contrasts can be conducted. The hypothesis could also be directly addressed for pairs of parasitoid species in a multifactorial study comparing parasitoids of honeydew producing hosts and those attacking hosts not associated with honeydew on a standardized set of honeydew and control food sources.

The survey did support the general hypothesis that honeydew is inferior to other sugar sources, but with caveats. For 15 of the 17 parasitoid/honeydew combinations from parasitoids attacking hosts that *do not* produce honeydew, longevity was greater on the non-honeydew sugar source, in 10 cases more than twice as long on the non-honeydew

Table 2

Effects of honeydew and other sugar sources (sucrose solution, honey or floral nectar) on lifespan of parasitoids that either attack honeydew-producing hosts or hosts that do not produce honeydew

| Parasitoid species | Longevity on non-honeydew sugar source (source) | Longevity ^a on honeydew (honeydew-producer and host plant) | Longevity on water | Reference |
|--|---|--|--------------------|--|
| Parasitoids of honeydew-producing hosts | | | | |
| <i>Aphidius colemani</i> | 12.1 (sucrose solution) | 4.8 (<i>Aphis craccae</i> , <i>Vicia cracca</i>) | 1.9 | Campan & Wäckers (unpublished) |
| <i>Aphidius colemani</i> | 9.6 (honeydew-mimic sugar solution) | 13.4 (<i>Myzus persicae</i> , <i>Brassica nigra</i>) 4.2 (<i>Brevicoryne brassicae</i> , <i>Brassica nigra</i>) | 2.0 | Schmidt, Meyhöfer, Wäckers (unpublished) |
| <i>Aphidius ervi</i> | 15.2 (sucrose solution) | 13.2 (<i>Myzus persicae</i> ; potato) 11.1 (<i>Macrosiphum euphorbiae</i> ; potato) 12.8 (<i>Aulacorthum solani</i> , potato) | 2.5 | Hogervorst et al. (2007b) |
| <i>Aphidius ervi</i> | 14.4 (sucrose solution) | 11.6 (<i>Acyrtosiphon pisum</i> , <i>Vicia faba</i>) | 3.5 | Obrist, Völkl & Wäckers (unpublished) |
| <i>Binodoxys communis</i> | 6 (honey, sucrose solution) | 2.3 (<i>Aphis glycines</i> ; soybean) | 0.9 | Wyckhuys et al. (2008) |
| <i>Encarsia bimaculata</i> | 12.7 (sucrose solution) | 2.8 (<i>Bemisia tabaci</i> , poinsettia) | 1.8 | Mandour et al. (2007) |
| <i>Encarsia formosa</i> | 31.5 (honey, glucose solution) | 30 (<i>Trialetodes vaporariorum</i>) | 4.0 | van Lenteren et al. (1987) |
| Parasitoids of hosts that do not produce honeydew | | | | |
| <i>Apanteles fumiferanae</i> | 13.6 (honey) | 3.1 (<i>Cinara</i> sp., jack pine) | 3.0 | Elliott et al. (1987) |
| <i>Aphytis coheni</i> | 7.6 (citrus nectar, honey, sucrose water) | 0.9 (<i>Toxoptera aurantii</i> ; citrus) | 1.5 | Avidov et al. (1970) |
| <i>Aphytis coheni</i> | 7.6 (citrus nectar, honey, sucrose water) | 2.0 (<i>Icerya purchasi</i> ; citrus) | 1.5 | Avidov et al. (1970) |
| <i>Aphytis coheni</i> | 7.6 (citrus nectar, honey, sucrose water) | 4.5 (<i>Ceroplastes floridensis</i> ; citrus) | 1.5 | Avidov et al. (1970) |
| <i>Aphytis coheni</i> | 7.6 (citrus nectar, honey, sucrose water) | 5.0 (<i>Pseudococcus citriculus</i> ; citrus) | 1.5 | Avidov et al. (1970) |
| <i>Bathyplectes curculionis</i> | 7.8 (sucrose water) | 8.2 (<i>Acyrtosiphon pisum</i> ; alfalfa) | 5.7 | England and Evans (1997) |
| <i>Diadegma insulare</i> | 26.0 (buckwheat ^b nectar) | 8 (<i>Aphis glycines</i> ; soybean) | 1.8 | Lee et al. (2004) |
| <i>Diadegma semiclausum</i> | 21.3 (sucrose water) | 12.2 (<i>Brevicoryne brassicae</i> , <i>Brassica nigra</i>) | 2.2 | Wyckhuys et al., 2008 |
| <i>Glypta fumiferanae</i> | 12.7 (honey) | 4.4 (<i>Cinara</i> sp.; <i>Pinus banksiana</i>) | 4.0 | Elliott et al. (1987) |
| <i>Itopectis conquisitor</i> | 28.0 (sucrose solution) | 10.2 (<i>Aphis nasturtii</i> ; potato) | 7.0 | Leius (1961a) |
| <i>Pholetesor ornigis</i> | 24.8 (honey ^c) | 3.6 (<i>Aphis pomi</i> ; apple) | 2.6 | Hagley and Barber (1992) |
| <i>Scambus boulianae</i> | 45.3 (sucrose water, honey) | 26.0 (<i>Myzocallis Alhambra</i> ; <i>Quercus macrocarpa</i>) | 4.8 | Leius (1961b) |
| <i>Scambus boulianae</i> | 45.3 (sucrose water, honey) | 19.0 (<i>Aphis nasturtii</i> ; potato) | 4.8 | Leius (1961b) |
| <i>Trichogramma ostriniae</i> | 8.8 (honey) | 8.6 (<i>Rhopalosiphum maidis</i> ; corn) | 1.2 | Fuchsberg et al. (2007) |
| <i>Trichogramma platneri</i> | > 20 (honey) | 9.5 (<i>Dysaphis plantaginea</i> ; apple) | 1.2 | McDougall and Mills (1997) |

If multiple non-honeydew sugar sources were tested, mean lifespan over the different sugars is reported. Only data for females is reported.

^a In days. Median longevity used when possible (*Binodoxys communis*, *Aphytis coheni*) otherwise mean.

^b *Fagopyrum esculentum*.

^c Blossom of two flower species were offered as well, but it is not clear whether nectar-feeding took place, so data from the blossom treatments were not included in the mean.

sugar (Table 2 and Fig. 1). To this list can also be added the chrysomelid egg parasitoid *Edovum putleri* Grissell, for which complete longevity data are not available, but for which survival rates are higher on honey than on honeydew (Idoine and Ferro, 1988). However, for two species, honeydew was not an inferior food source from the perspective of enhancing longevity. Longevity of both *Bathyplectes curculionis* (Thomson) (a parasitoid of weevil larvae) and *Trichogramma ostriniae* (Peng & Chen) (a parasitoid of lepidopteran eggs) fed honeydew was virtually identical to that on sucrose and honey, respectively (Table 2). This underlines the variation in honeydew suitability

and should caution against a generalization that honeydew is a universally inferior sugar source.

The studies cited in Table 2 support the hypothesis that the source of honeydew has a strong influence on its nutritional quality for parasitoids. The same parasitoid was tested on honeydew from more than one hemipteran species in three of the published studies. Leius (1961b) compared the effect of honeydews of two aphid species, *Myzocallis alhambra* Davidson and *Aphis nasturtii* Kaltentbach, on *Scambus boulianae* (Htg), an ichneumonid parasitoid of lepidopteran larvae. He found that the honeydew produced by *M. alhambra* increased the lifespan

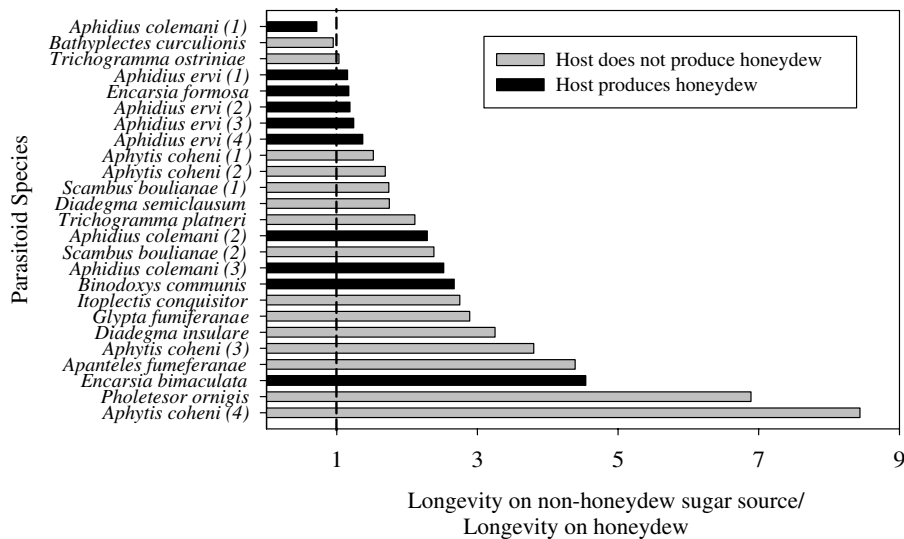


Fig. 1. The ratio of longevities on sugar sources other than honeydew over longevity on honeydew for parasitoids that attack hosts that produce honeydew or not. The vertical dotted line indicates the ratio at which longevity on honeydew equals longevity on the non-honeydew sugar source; values to the right of the line indicate that longevity is greater on the non-honeydew sugar source. Parasitoid species followed by numbers were fed honeydews from different host species as follows. *Aphidius colemani* (1): *Myzus persicae*; *A. colemani* (2) *Brevicoryne brassicae*; *A. colemani* (3): *Aphis craccae*; *A. ervi* (1): *M. persicae*; *A. ervi* (2): *Aulocarthum solani*; *A. ervi* (3) *Acyrtosiphon pisum*; *A. ervi* (4): *Macrosiphum euphorbiae*; *Scambus boulianae* (1): *Myzocallis alhambra*; *S. boulianae* (2): *Aphis nasturtii*; *Aphytis coheni* (1): *Pseudococcus citriculus*; *A. coheni* (2): *Ceroplastes floridensis*; *A. coheni* (3): *Icerya purchasi*; *A. coheni* (4): *Toxoptera aurantii*.

of *S. boulianae* by seven more days than did the honeydew of *A. nasturtii* (Table 2). Even more striking differences were uncovered by Avidov et al. (1970), who compared the longevity of the armored scale parasitoid *Aphytis coheni* DeBach on a number of sugar sources, including honeydew from four species of hemipterans, two soft-scale insects, one aphid and one mealybug. Honeydew of the mealybug, *Pseudococcus citriculus* Green, was the most effective at increasing longevity, while honeydew of the black citrus aphid, *Toxoptera aurantii* (Boyer de Fonscolombe), yielded longevity below that of water, suggesting that it contained toxins (Avidov et al., 1970). In contrast, longevities of the aphid parasitoid *Aphidius ervi* Haliday on honeydews of three aphid species did not differ much (Hogervorst et al., 2007b).

3. Sugar use in the field

Whereas there are ample laboratory data showing how feeding on nectar and honeydew affects lifetable parameters of predators and parasitoids, we know little about food source use and the impact of feeding under field conditions. It is often difficult to single out nutritional benefits in actual field studies. For instance, enhanced parasitism along a (flowering) field margin may be seen as indirect evidence that parasitoids obtain a longevity and/or fecundity bonus from food consumption. However, a range of other mechanisms may result in the aggregation of arthropods around nectar- or honeydew-providing plants as well. For one, flowering vegetation may simply attract food seeking parasitoids from the field centre to the border rows, without necessarily providing suitable food. Furthermore, preda-

tors or parasitoids may be arrested following feeding, or change to a more area restricted search pattern. Spatial learning may further enhance aggregation, as it enables parasitoids or predators to return to rewarding food sites. Finally, aggregation around food sites can also be enhanced when arthropods use their foraging sites for additional functions such as roosting or mating. To sidestep these confounding effects and to directly address the impact of sugar feeding on energy reserves, we developed a method using HPLC analysis to study the overall sugar level and sugar spectrum of individual field-collected insects (Heimpel et al., 2004; Steppuhn and Wäckers, 2004; Wäckers and Steppuhn, 2003). Using this method we have been able to demonstrate that in agricultural systems lacking suitable food sources, natural enemies can be severely food-deprived, with a high proportion of individuals failing to feed and average carbohydrate levels not exceeding unfed individuals (Olson and Wäckers, 2007). On the other hand, it has been demonstrated that parasitoids collected adjacent to suitable field margins (Lee et al., 2006; Olson and Wäckers, 2007; Wäckers and Steppuhn, 2003) or within the margins itself (Lee and Heimpel, 2003) show raised carbohydrate reserves.

Other studies found a relatively high incidence of sugar feeding in parasitoids collected from nectar-poor fields and concluded that parasitoids must have exploited alternative sugar sources, most likely honeydew (Casas et al., 2003; Lee and Heimpel, 2003; Lee et al., 2006). Although honeydew may be an important food source for biological control agents in agro-ecosystems, we still have limited quantitative data on the use of honeydew by parasitoids and predators. Based on the detection of specific aphid-

synthesized sugars in field collected parasitoids Wäckers and Steppuhn (2003) demonstrated that 80% of *Cotesia glomerata* (L.) and 55% of *Microplitis mediator* (Haliday) (Hymenoptera: Braconidae) collected in a cabbage field had indeed recently consumed honeydew. Using a modified method to account for the fact that *Aphidius* spp. synthesize oligosaccharides, Hogervorst et al., (2007a) demonstrated that at least 63% of *Aphidius* spp. with raised sugar levels had been feeding on honeydew. This shows that honeydew can be an important food source in absence of nectar sources. However, the propensity to actually engage in honeydew feeding may be determined by nectar availability. When comparing *Microplitis croceipes* (Cresson) collected from fields with and without nectar sources, only individuals from fields lacking nectar contained honeydew-specific sugars (Williams and Wäckers, unpublished). Whether aphidophagous parasitoids and predators are more inclined to exploit honeydew over nectar in comparison to predators and parasitoids of non-honeydew producers remains to be demonstrated.

3.1. Sugar use and biological control

Given the profound impact of sugar feeding on parasitoid life-span and reproduction, a clear impact on population dynamics can be expected. First of all, when no adequate sugar sources are available, the net reproductive success will often be too low to maintain a local population, even when hosts are abundant (Winkler et al., 2006).

When suitable food sources are available, the enhanced parasitoid fitness or population size will likely translate into higher parasitism rates and reduced host populations. The strongest host level reduction is to be expected when both searching rate and reproductive life-span is enhanced by nectar feeding (van Rijn and Sabelis, 2005). The extensive review by Heimpel and Jervis (2005) gives an overview over the experimental evidence for the impact of floral nectar on biological control. In a recent study, Lee and Heimpel (2008) have shown that sugar-fed *Diadegma insulare* have increased life-span and daily fecundity in the field, but paradoxically, this did not lead to higher parasitism levels of their host, the diamondback moth.

In perennial systems, basic ecological models predict that reduced host levels will ultimately feed-back to the parasitoid level, which means that, when the host–parasitoid system approaches a new equilibrium, the parasitism rate will no longer be elevated with higher sugar levels (van Rijn and Sabelis, 2005). Models that include more complex behavior such as density-dependent prey defense or predator avoidance (Vos et al., 2004) do predict an effect on equilibrium parasitism rate in perennial systems as well.

Most studies on the impact of sugars have manipulated nectar levels. In some of these studies honeydew availability may have obscured the population effects (Heimpel and Jervis, 2005; Lee and Heimpel, 2005; Wäckers and Steppuhn, 2003). Few studies have directly addressed the impact of honeydew levels on biological control. Hagen (1986) realized

the potential of honeydew to raise biological control efficacy, and advocated the use of artificial food supplements. Faria et al. (2007) showed that variation in levels of *Rhopalosiphum maidis* (Fitch) infestation between maize cultivars had a direct impact on the parasitization of *Spodoptera littoralis* (Boisduval) by *Cotesia marginiventris* (Cresson). Van Rijn, Mulder, Winkler and Wäckers (unpublished) showed in large cage studies that parasitism of *Plutella xylostella* (L.) by *Diadegma semiclausum* (Hellen) increases strongly when cabbage aphids are present in the crop.

Feeding on honeydew rather than nectar may also affect the dynamical properties of the parasitoid–host system. Population densities of parasitoids that mainly feed on honeydew of their sap-feeding hosts are likely to be strongly correlated with host densities, both in space and in time. A reduction in host density (e.g., due to top–down control by the parasitoid) will also reduce their sugar source, with apparent consequences for adult survival. Such double dependency of the parasitoids on their hosts will possibly aggravate oscillations, or (in more stable systems) increase host equilibrium densities, relative to parasitoids that have other, independent sugar sources available.

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References

- Adams, C.L., Selander, R.B., 1979. The biology of blister beetles of the *Vittata* group of the genus *Epicauta* (Coleoptera, Meloidae). *Bulletin of the American Museum of Natural History* 162, 266.
- Avidov, Z., Balshin, M., Gerson, U., 1970. Studies on *Aphytis coheni*, a parasite of the California red scale, *Aonidiella aurantii*, in Israel. *Entomophaga* 15, 191–207.
- Baggen, L.R., Gurr, G.M., Meats, A., 1999. Flowers in tri-trophic systems: mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. *Entomologia Experimentalis et Applicata* 91, 155–161.
- Bargen, H., Saudhof, K., Poehling, H.M., 1998. Prey finding by larvae and adult females of *Episyrphus balteatus*. *Entomologia Experimentalis et Applicata* 87, 245–254.
- Bartlett, B.R., 1962. The ingestion of dry sugars by adult entomophagous insects and the use of this feeding habit for measuring their moisture needs. *Journal of Economic Entomology* 55, 729–753.
- Beach, J.P., Williams, L., Hendrix, D.L., Price, L., 2003. Different food sources affect the gustatory response of *Anaphes iole*, an egg parasitoid of *Lygus* spp. *Journal of Chemical Ecology* 29, 1203–1222.
- Beattie, A.J., 1985. *The evolutionary ecology of ant–plant mutualisms*. Cambridge University Press, England.
- Beggs, J., 2001. The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. *Biological Conservation* 99, 17–28.
- Bernstein, C., Jervis, M., 2008. Food-searching in parasitoids: the dilemma of choosing between ‘immediate’ or future fitness gains. In: Wajnberg, E., Bernstein, C., van Alphen, J.J.M. (Eds.), *Behavioural Ecology of Parasitoids*. Blackwell Publishing, Oxford, pp. 129–171.
- Casas, J., Driessen, G., Mandon, N., Wielaard, S., Desouhant, E., Van Alphen, J., Lapchin, L., Rivero, A., Christides, J.P., Bernstein, C.,

2003. Energy dynamics in a parasitoid foraging in the wild. *Journal of Animal Ecology* 72, 691–697.
- Cuautle, M., Rico-Gray, V., 2003. The effect of wasps and ants on the reproductive success of the extrafloral nectaried plant *Turnera ulmifolia* (Turneraceae). *Functional Ecology* 17, 417–423.
- Downes, W., Dahlem, G., 1987. Keys to the evolution of Diptera: role of Homoptera. *Environmental Entomology* 16, 847–854.
- Elliott, N.C., Simmons, G.A., Sapio, F.J., 1987. Honeydew and wildflowers as food for the parasites *Glypta fumiferanae* (Hymenoptera: Ichneumonidae) and *Apanteles fumiferanae* (Hymenoptera: Braconidae). *Journal of the Kansas Entomological Society* 60, 25–29.
- England, S., Evans, E.W., 1997. Effects of pea aphid (Homoptera: Aphididae) honeydew on longevity and fecundity of the alfalfa weevil (Coleoptera: Curculionidae) parasitoid *Bathyplectes curculionis* (Hymenoptera: Ichneumonidae). *Environmental Entomology* 26, 1437–1441.
- Eubanks, M.D., Styrsky, J.D., 2005. The effects of plant feeding on the performance of omnivorous 'predators'. In: Wäckers, F.L., van Rijn, P.C.J., Bruin, J. (Eds.), *Plant-Provided Food for Carnivorous Insects: a protective mutualism and its applications*. Cambridge University Press, Cambridge.
- Faria, C.A., Wäckers, F.L., Turlings, T.C.J., 2007. Increased susceptibility of Bt maize to aphids enhances the performance of parasitoids of lepidopteran pests. *PLoS ONE* 2, 1–11.
- Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R., Thomson, J.D., 2004. Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics* 35, 375–403.
- Fuchsberg, J.R., Yong, T.H., Losey, J.E., Carter, M.E., Hoffmann, A.A., 2007. Evaluation of corn leaf aphid (*Rhopalosiphum maidis*; Homoptera: Aphididae) honeydew as a food source for the egg parasitoid *Trichogramma ostrinia* (Hymenoptera: Trichogrammatidae). *Biological Control* 40, 230–236.
- Gilbert, F., Jervis, M.A., 1998. Functional, evolutionary and ecological aspects of feeding-related mouthpart specializations in parasitoid flies. *Biological Journal of the Linnean Society* 63, 495–535.
- Gillespie, D.R., McGregor, R.R., 2000. The functions of plant feeding in the omnivorous predator *Dicyphus hesperus*: water places limits on predation. *Ecological Entomology* 25, 380–386.
- Györfi, J., 1945. Beobachtungen über die Ernährung der Schlupfwespenimagos. *Erdész. Kiséletek* 45, 100–112.
- Hagen, K.S., 1986. Ecosystem analysis: plant cultivars (HPR), entomophagous species and food supplements. In: Boethel, D.J., Eikenbary, R.D. (Eds.), *Interactions of Plant Resistance and Parasitoids and Predators of Insects*. John Wiley and Sons, New York, pp. 153–197.
- Hagley, E.A.C., Barber, D.R., 1992. Effect of food sources on the longevity and fecundity of *Pholetesor ornigis* (Weed) (Hymenoptera: Braconidae). *Canadian Entomologist* 124, 341–346.
- Hagvar, E.B., Hofsvang, T., 1991. Aphids parasitoids (Hymenoptera, Aphidiidae): biology, host selection and use in biological control. *Biocontrol News and Information* 12, 13–41.
- Heimpel, G.E., Jervis, M.A., 2005. An evaluation of the hypothesis that floral nectar improves biological control by parasitoids. In: Wäckers, F.L., van Rijn, P.C.J., Bruin, J. (Eds.), *Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*. Cambridge University Press, Cambridge, pp. 267–304.
- Heimpel, G.E., Lee, J.C., Wu, Z., Weisser, L., Wäckers, F.L., Jervis, M.A., 2004. Gut sugar analysis in field-caught parasitoids: adapting methods originally developed for biting flies. *International Journal of Pest Management* 50, 193–198.
- Hickman, J.M., Lovei, G.L., Wratten, S.D., 1995. Pollen feeding by adults of the hoverfly *Melanostoma fasciatum* (Diptera: Syrphidae). *New Zealand Journal of Zoology* 22, 387–392.
- Hoferer, S., Wäckers, F.L., Dorn, S., 2000. Measuring CO₂ respiration rates in the parasitoid *Cotesia glomerata*. *Mitteilungen der Deutschen Gesellschaft fuer allgemeine und angewandte Entomologie* 12, 555–558.
- Hogervorst, P.A.M., Wäckers, F.L., Romeis, J., 2007a. Detecting nutritional state and food source use in field-collected insects that synthesize honeydew oligosaccharides. *Functional Ecology* 21, 936–946.
- Hogervorst, P.A.M., Wäckers, F.L., Romeis, J., 2007b. Effects of honeydew sugar composition on the longevity of *Aphidius ervi*. *Entomologia Experimentalis et Applicata* 122, 223–232.
- Ildoie, K., Ferro, D.N., 1988. Aphid honeydew as a carbohydrate source for *Edovum putleri* (Hymenoptera: Eulophidae). *Environmental Entomology* 17, 941–944.
- Idris, A.B., Grafius, E., 1995. Wildflowers as nectar sources for *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera: Yponomeutidae). *Environmental Entomology* 24, 1726–1735.
- Jervis, M.A., 1998. Functional and evolutionary aspects of mouthpart structure in parasitoid wasps. *Biological Journal of the Linnean Society* 63, 461–493.
- Kirk, W.D.J., 1997. Feeding. In: Lewis, T. (Ed.), *Thrips as Crop Pests*. CAB International, London, pp. 217–257.
- Kloft, W.J., Maurizio, A., Kaeser, W., 1985. *Waldtracht und Waldhonig in der Imkerei*. Ehrenwirth Verlag, München.
- Lee, J.C., Heimpel, G.E., 2003. Nectar availability and parasitoid sugar feeding. In: *Proceedings of the First International Symposium on Biological Control of Arthropods*. Honolulu, Hawaii, pp. 220–225.
- Lee, J.C., Heimpel, G.E., 2005. Impact of flowering buckwheat on lepidopteran cabbage pests and their parasitoids at two spatial scales. *Biological Control* 34, 290–301.
- Lee, J.C., Heimpel, G.E., 2008. Floral resources impact longevity and oviposition rate of a parasitoid in the field. *Journal of Animal Ecology*.
- Lee, J.C., Heimpel, G.E., Leibe, G.L., 2004. Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parasitoid wasp. *Entomologia Experimentalis et Applicata* 111, 189–199.
- Lee, J.C., Andow, D.A., Heimpel, G.E., 2006. Influence of floral resources on sugar feeding and nutrient dynamics of a parasitoid in the field. *Ecological Entomology* 31, 470–480.
- Leius, K., 1961a. Influence of food on fecundity and longevity of adults of *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). *Canadian Entomologist* 93, 771–780.
- Leius, K., 1961b. Influence of various foods on fecundity and longevity of adults of *Scambus buolianae* (Htg.) (Hymenoptera: Ichneumonidae). *Canadian Entomologist* 93, 1079–1084.
- Lewis, W., Stapel, J.O., Cortesero, A.M., Takasu, K., 1998. Understanding how parasitoids balance food and host needs: importance to biological control. *Biological Control* 11, 175–183.
- Limburg, D.D., Rosenheim, J.A., 2001. Extrafloral nectar consumption and its influence on survival and development of an omnivorous predator, larval *Chrysoperla plorabunda* (Neuroptera: Chrysopidae). *Environmental Entomology* 30, 595–604.
- Mandour, N.S., Ren, S.X., Qiu, B.L., 2007. Effect of *Bemisia tabaci* honeydew and its carbohydrates on search time and parasitization of *Encarsia bimaculata*. *Journal of Applied Entomology* 131, 645–651.
- Mandour, N.S., Shunxiang, R., Baoli, Q., Wäckers, F.L., 2005. Arrestment response of *Eretmocerus* species (Hymenoptera: Aphelinidae) near *Furuhashii* to Honeydew of *Bemisia tabaci* (Homoptera: Aleyrodidae) and its component carbohydrates. In: *Proceedings of the Sixth Arabian Conference for Horticulture*, vol. 6, Ismailia, Egypt, pp. 311–319.
- McDougall, S.J., Mills, N.J., 1997. The influence of hosts, temperature and food sources on the longevity of *Trichogramma platneri*. *Entomologia Experimentalis et Applicata* 83, 195–203.
- Nixon, G.E.J., 1951. *The association of ants with aphids and coccids*. Commonwealth Institute of Entomology, London.
- Olson, D., Wäckers, F.L., 2007. Management of field margins to maximize multiple ecological services. *Journal of Applied Ecology* 44, 13–21.
- Olson, D.M., Rains, G.C., Meiners, T., Takasu, K., Tertuliano, M., Tumlinson, J.H., Wäckers, F.L., Lewis, W.J., 2003. Parasitic wasps learn and report diverse chemicals with unique conditionable behaviors. *Chemical Senses* 28, 545–549.
- Opit, G.P., Roitberg, B., Gillespie, D.R., 1997. The functional response and prey preference of *Feltiella acarissuga* (Vallot) (Diptera: Cecidomyiidae) for two of its prey: Male and female two spotted spider

- mites, *Tetranychus urticae* Koch (Acari: Tetranychidae). Canadian Entomologist 129, 221–227.
- Patt, J.M., Hamilton, G.C., Lashomb, J.H., 1997. Foraging success of parasitoid wasps on flowers: interplay of insect morphology, floral architecture and searching behavior. Entomologia Experimentalis et Applicata 83, 21–30.
- Pembererton, R.W., & Vandenberg, N. J. (1993). Extrafloral nectar feeding by ladybird beetles (Coleoptera, Coccinellidae). In: *Proceedings of the Entomological Society of Washington*, Vol. 95, pp. 139–151.
- Percival, M.S., 1961. Types of nectar in angiosperms. New Phytologist 60, 235–281.
- Ruberson, J.R., Tauber, M.J., Tauber, C.A., 1986. Plant feeding by *Podisus maculiventris* (Heteroptera: Pentatomidae): effect on survival, development, and preoviposition period. Environmental Entomology 15, 894–897.
- Siekman, G., Keller, M.A., Tenhumberg, B., 2004. The sweet tooth of adult parasitoid *Cotesia rubecula*: ignoring hosts for nectar? Journal of Insect Behavior 17, 459–476.
- Siro, E., Bernstein, C., 1996. Time sharing between host searching and food searching in parasitoids: state-dependent optimal strategies. Behavioral Ecology 7, 189–194.
- Smith, R.B., Mommsen, T.P., 1984. Pollen feeding in an orb-weaving spider. Science 226, 1330–1332.
- Smyth, T., 1985. Muscle systems. In: Blum, M.S. (Ed.), *Fundamentals of Insect Physiology*. John Wiley and Sons, New York, pp. 227–228.
- Stapel, J.O., Cortesero, A.M., De Moraes, C.M., Tumlinson, J.H., Lewis, W.J., 1997. Extrafloral nectar, honeydew and sucrose effects on searching behavior and efficiency of *Microplitis croceipes* (Hymenoptera: Braconidae) in cotton. Environmental Entomology 26, 617–623.
- Stelzl, M., 1991. Investigations on food of Neuroptera-Adults (Neuropteroidae, Insecta) in Central Europe, with a short discussion of their role as natural enemies of insect pests. Journal of Applied Entomology 111, 469–477.
- Stappuhn, A., Wäckers, F.L., 2004. HPLC sugar analysis reveals the nutritional state and the feeding history of parasitoids. Functional Ecology 18, 812–819.
- Stoffolano, J.G., 1995. Regulation of a carbohydrate meal in the adult Diptera, Lepidoptera, and Hymenoptera. In: Chapman, R.F., de Boer, G. (Eds.), *Regulatory Mechanisms in Insect Feeding*. Chapman and Hall, New York, pp. 210–224.
- Stoner, A., 1972. Plant feeding by *Nabis*, a predaceous genus. Environmental Entomology 1, 557–558.
- Stoner, A., 1975. Plant feeding by *Reduviidae*, a predaceous family (Hemiptera). Journal of the Kansas Entomological Society 48, 185–188.
- Takasu, K., Lewis, W.J., 1993. Host- and food-foraging of the parasitoid *Microplitis croceipes*: learning and physiological state effects. Biological Control 3, 70–74.
- Taylor, R.M., Foster, W.A., 1996. Spider nectarivory. American Entomologist, (Summer) 82–86.
- Traugott, M., 2003. The prey spectrum of larval and adult *Cantharis* species in arable land: an electrophoretic approach. Pedobiologia 47, 161–169.
- van Lenteren, J.C., Van Vianen, A., Gast, H.F., Kortenhoff, A., 1987. The parasite–host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). XVI. Food effects on oogenesis, oviposition, life-span and fecundity of *Encarsia formosa* and other hymenopterous parasites. Journal of Applied Entomology 103, 69–84.
- van Rijn, P.C.J., Tanigoshi, L.K., 1999a. The contribution of extrafloral nectar to survival and reproduction of the predatory mite *Iphiseius degenerans* on *Ricinus communis*. Experimental and Applied Acarology 23, 281–296.
- van Rijn, P.C.J., Tanigoshi, L.K., 1999b. Pollen as food for the predatory mites *Iphiseius degenerans* and *Neoseiulus cucumeris* (Acari: Phytoseiidae): dietary range and life history. Experimental and Applied Acarology 23, 785–802.
- van Rijn, P.C.J., Sabelis, M.W., 2005. The impact of plant-provided food on herbivore–carnivore dynamics. In: Wäckers, F.L., van Rijn, P.C.J., Bruin, J. (Eds.), *Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*. Cambridge University Press, Cambridge.
- van Rijn, P.C.J., van Houten, Y.M., Sabelis, M.W., 2002. How plants benefit from providing food to predators even when it is also edible to herbivores. Ecology 83, 2664–2679.
- van Rijn, P.C.J., Kooijman, J., Wäckers, F.L., 2006. The impact of floral resources on syrphid performance and cabbage aphid biological control. IOBC WPRS Bulletin 29, 149–152.
- Vos, M., Kooij, B.W., DeAngelis, D.L., Mooij, W.M., 2004. Inducible defences and the paradox of enrichment. Oikos 105, 471–480.
- Wäckers, F.L., 1994. The effect of food deprivation on the innate visual and olfactory preferences in the parasitoid *Cotesia rubecula*. Journal of Insect Physiology 40, 641–649.
- Wäckers, F.L., 1999. Gustatory response by the Hymenopteran parasitoid *Cotesia glomerata* to a range of nectar and honeydew sugars. Journal of Chemical Ecology 25, 2863–2877.
- Wäckers, F.L., 2000. Do oligosaccharides reduce the suitability of honeydew for predators and parasitoids? A further facet to the function of insect-synthesized honeydew sugars. Oikos 90, 197–201.
- Wäckers, F.L., 2001. A comparison of nectar- and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. Journal of Insect Physiology 47, 1077–1084.
- Wäckers, F.L., 2005. Suitability of (extra-) floral nectar, pollen, and honeydew as insect food sources. In: Wäckers, F.L., van Rijn, P.C.J., Bruin, J. (Eds.), *Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*. Cambridge University Press, Cambridge.
- Wäckers, F.L., Swaans, C.P.M., 1993. Finding floral nectar and honeydew in *Cotesia rubecula*: random or directed? Proceedings of Experimental and Applied Entomology 4, 67–72.
- Wäckers, F.L., Steppuhn, A., 2003. Characterizing nutritional state and food source use of parasitoids collected in fields with high and low nectar availability. IOBC WPRS Bulletin 26, 203–208.
- Wäckers, F.L., van Rijn, P.C.J., 2005. Food for protection: an introduction. In: Wäckers, F.L., van Rijn, P.C.J., Bruin, J. (Eds.), *Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*. Cambridge University Press, Cambridge.
- Wäckers, F.L., Bonifay, C., Lewis, W.J., 2002. Conditioning of appetitive behavior in the Hymenopteran parasitoid *Microplitis croceipes*. Entomologia Experimentalis et Applicata 103, 135–138.
- Wäckers, F.L., Lee, J.C., Heimpel, G.E., Winkler, K., Wagenaar, R., 2006. Hymenopteran parasitoids synthesize ‘honeydew-specific’ oligosaccharides. Functional Ecology 20, 790–798.
- Wilkinson, T.L., Ashford, D.A., Pritchard, J., Douglas, A.E., 1997. Honeydew sugars and osmoregulation in the pea aphid *Acyrtosiphon pisum*. Journal of Experimental Biology 200, 2137–2143.
- Wink, M., Römer, P., 1986. Acquired toxicity—the advantages of specializing on alkaloid-rich lupins to *Macrosiphon albifrons* (Aphidae). Naturwissenschaften 73, 210–212.
- Winkler, K., Wäckers, F.L., Bukovinskine-Kiss, G., van Lenteren, J.C., 2006. Nectar resources are vital for *Diadegma semiclausum* fecundity under field conditions. Basic and Applied Ecology 7, 133–140.
- Wratten, S.D., White, A.J., Bowie, M.H., Berry, N.A., Weigmann, U., 1995. Phenology and ecology of hoverflies (Diptera, Syrphidae) in New Zealand. Environmental Entomology 24, 595–600.
- Wyckhuys, K.A.G., Strange-George, J.E., Kulhanek, C.A., Wäckers, F.L., Heimpel, G.E., 2008. Sugar feeding by the aphid parasitoid *Binodoxys communis*: how does honeydew compare to other sugar sources? Journal of Insect Physiology. doi:10.1016/j.jinphys.2007.11.007.
- Zoebelein, G., 1956. Der Honigtau als Nahrung der Insekten. Zeitschrift für Angewandte Entomologie 38, 369–416.