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The nutritional value of aphid honeydew for non-aphid parasitoids

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Abstract

Intake of sugar-rich foods by adult parasitoids is crucial for their reproductive success. Hence, the availability of suitable foods should enhance the efficacy of parasitoids as biological control agents. In situations where nectar is not readily available, homopteran honeydew can be a key alternative food source. We studied the impact of honeydew feeding on the longevity of the larval endoparasitoids *Cotesia marginiventris*, *Campoletis sonorensis* and *Microplitis rufiventris*, all natural enemies of important lepidopteran pests. Females of these wasps lived longer when feeding on honeydew produced by the aphid *Rhopalosiphum maidis* on barley compared to control females provided with water only. However, they lived shorter than females fed with a sucrose solution. Further investigations with *C. marginiventris* showed that access to honeydew also increases the number of offspring produced, but less so than access to a sucrose solution. Moreover, it was found that females of this species need to feed several times throughout their life in order to reach optimal longevity and reproductive output. Analyses of the sugars in the honeydew produced by *R. maidis* on barley revealed that it contains mainly plant-derived sugars, but also several aphid-synthesized sugars. The sugar composition of the honeydew changed as a function of aphid colony size and time a colony had been feeding on a plant. In general, the higher the aphid infestation, the smaller the percentage of aphid-synthesized sugars in the honeydew. Experiments with honeydew sugar mimics allowed us to reject the hypothesis that the relatively poor performance of the parasitoid on a honeydew diet was due to the sugar composition. Instead, the results from additional feeding experiments with diluted honeydew showed that the nutritional value of pure honeydew is primarily restricted by its high viscosity. The possible consequences of these findings for biological pest control are discussed.

Zusammenfassung

Die Aufnahme von zuckerreicher Nahrung durch adulte Parasitoide ist entscheidend für ihren reproduktiven Erfolg. Daher sollte die Verfügbarkeit von geeigneter Nahrung die Effizienz von Parasitoiden als Mittel der biologischen Kontrolle steigern. Wenn Nektar nicht leicht verfügbar ist, kann der Honigtau von Homopteren eine entscheidende alternative Nahrungsquelle sein. Wir untersuchten den Einfluss des Honigtaukonsums auf die Lebensdauer der larvalen Endoparasitoide *Cotesia marginiventris*, *Campoletis sonorensis* und *Microplitis rufiventris*, die natürliche Feinde wichtiger Schadlepidopteren sind. Verglichen mit Kontroll-Weibchen, die nur Wasser erhielten, lebten die Weibchen dieser Wespen länger, wenn sie von der Blattlaus *Rhopalosiphum maidis* (auf Gerste) produzierten Honigtau aufgenommen hatten. Allerdings lebten sie kürzer als Weibchen, die mit einer Saccharose-Lösung gefüttert wurden.

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Untersuchungen an *C. marginiventris* zeigten, dass Zugang zu Honigtau auch die Nachkommenzahl erhöhte, wenn auch in geringerem Maße als Saccharose-Lösung. Für optimale Lebensdauer und Reproduktion mussten die Weibchen mehrmals während ihres Lebens trinken. Die Zucker-Zusammensetzung des Honigtaus variierte mit der Größe der Blattlauskolonie und der Dauer ihres Bestehens. Im Allgemeinen sank der von den Blattläusen synthetisierte Zuckeranteil im Honigtau mit der Stärke des Blattlausbefalls. Versuche mit gemischten Zucker-Lösungen (nachgeahmtem Honigtau) erlaubten uns die Hypothese zurückzuweisen, dass der relativ schlechte Lebenserfolg des Parasitoiden bei Honigtau-Diät auf die Zucker-Zusammensetzung zurückzuführen sei. Vielmehr zeigten zusätzliche Versuche mit verdünntem Honigtau, dass der Nährwert von reinem Honigtau primär durch seine hohe Viskosität eingeschränkt wird. Die möglichen Konsequenzen dieser Befunde für die Biologische Schädlingsbekämpfung werden diskutiert.

Keywords: Nutritional ecology; Honeydew; Carbohydrates; Parasitoids; Biological control; Aphididae; Braconidae; Ichneumonidae

Introduction

Food is essential for adult female parasitoids to optimize their reproductive success. Feeding not only increases their longevity and fecundity (Leius, 1961; England & Evans 1997; Wäckers, 2001), but also affects flight activity (Forsse, Smith & Bourchier, 1992; Wäckers, 1994) and attraction to and/or retention in an area (Stapel, Cortesero, De Moraes, Tumlinson & Lewis, 1997). The availability of suitable food should therefore be an important consideration in attempts to optimize the effectiveness of parasitoids as biological control agents.

Adult females of some parasitoids obtain essential nutrients directly from hosts through so-called host feeding, but even these species often need non-host food sources as a source of energy (Jervis, Kidd & Heimpel, 1996). Nevertheless, parasitoid females that feed on hosts or their by-products reduce the need to shift from host searching to food foraging, whereas parasitoids that only feed on food sources that are not associated with hosts will frequently have to forage for hosts and food separately (Sirot & Bernstein, 1996; Lewis, Stapel, Cortesero & Takasu, 1998). When food is located at a distance from host sites, this switching between resources may become particularly costly, since travelling to food sites limits the amount of time available for host searching, costs energy and increases the risk of mortality (Jervis et al., 1996; Stapel et al., 1997).

In nature, the primary non-host food sources available to parasitoid females are floral and extra-floral nectar, and homopteran honeydew (Wäckers & van Rijn, 2005 and references therein). Nectar availability is often limited in large monocultures, which may greatly hamper the effectiveness of parasitoids used for biological control (Winkler, Wäckers, Bukovinszkine-Kiss & van Lenteren, 2006). In such situations, honeydew can be a key alternative food for parasitoids if honeydew producing Homoptera occur in the vicinity of hosts. Feeding on nearby honeydew instead of distant nectar sources should allow parasitoids to allocate more time to searching for hosts, resulting in higher rates of parasitism.

Several laboratory studies have shown that in the presence of honeydew parasitoid females indeed live longer and achieve higher fecundity than unfed females (e.g. Hocking, 1966; England & Evans, 1997; Singh, Singh & Upadhyay, 2000). However, nectar is often a much better food source for parasitoids than honeydew (Idoine & Ferro, 1988; Wäckers, 2000; Lee, Heimpel, & Leibee, 2004; Wäckers & van Rijn, 2005). One possible explanation is that honeydew is not only composed of the main plant-derived sugars fructose, sucrose and glucose, but also contains various other compounds. These include homopteran-synthesized sugars (Mittler, 1958; Hendrix, Wei & Leggett, 1992), which may reduce the nutritional value of the honeydew (Wäckers, 2000, 2001). In fact, minimizing nutritional benefits to their natural enemies may be one of the driving forces in the evolution of honeydew sugar synthesis (Wäckers, 2000).

The composition of honeydew shows great variation both in the type of sugars present and the overall sugar concentration depending on the homopteran and plant species (Hendrix et al., 1992). Moreover, parasitoids can vary considerably with regard to the spectrum of honeydew sugars that they can utilise (Jacob & Evans, 2004; Wäckers, 2001; Winkler, Wäckers, Stingli & van Lenteren, 2005; Hausmann, Wäckers, & Dorn, 2005). This variability both from the side of the product (honeydew) and the users (parasitoids) suggests that there is an opportunity to fine-tune and manipulate the situation in crop fields to better exploit the presence of honeydew producing insects for pest control.

With the above in mind, we investigated the effect of the honeydew produced by the aphid *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae) attacking barley (*Hordeum vulgare*) on the longevity of the solitary larval endoparasitoids *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae), *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) and *Microplitis rufiventris* Kokujev (Hymenoptera: Braconidae), natural enemies of important lepidopteran pests (Hegazi,