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Nectar provisioning close to host patches increases parasitoid recruitment, retention and host parasitism

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Abstract

In the adult stage, many parasitoids require hosts for their offspring growth and plant-derived food for their survival and metabolic needs. In agricultural fields, nectar provisioning can enhance biological control by increasing the longevity and fecundity of many species of parasitoids. Provided in a host patch, nectar can also increase patch quality for parasitoids and affect their foraging decisions, patch time residence, patch preference or offspring allocation. The aim of this study was to investigate the impact of extrafloral nectar (EFN) provisioning close to hosts on parasitoid aggregation in patches. The aphid parasitoid *Diaeretiella rapae* (M'Intosh) was released inside or outside patches containing *Brassica napus* L. infested by *Brevicoryne brassicae* L. aphids and *Vicia faba* L. with or without EFN. When parasitoids were released outside patches, more parasitoids were observed in patches with EFN than in patches deprived of EFN. This higher recruitment could be linked to a higher attraction of a combination of host and food stimuli or a learning process. A release–recapture experiment of labeled parasitoids released within patches showed the higher retention of parasitoids in patches providing EFN and hosts, suggesting that food close to the host patch affects patch residence time. Both attractiveness and patch retention could be involved in the higher number of parasitoids foraging in host patches surrounded by nectar and for the higher parasitism recorded. Nectar provisioning in host patches also affected female offspring allocation inside the patch.

Zusammenfassung

Viele Parasitoide benötigen im Erwachsenenstadium Wirte für ihre Reproduktion und pflanzliche Nahrung für ihr Überleben und ihren Metabolismus. Die Bereitstellung von Nektar innerhalb eines Kulturpflanzenbestandes kann die biologische Kontrolle von Schädlingen fördern, da sie die Lebensdauer und die Fekundität von vielen parasitoiden Arten erhöht. Die Verfügbarkeit von Nektar kann demnach die Attraktivität von Wirtskolonien steigern und das Suchverhalten entscheidend beeinflussen wie beispielsweise die Verweildauer in einer Kolonie, die Auswahl von Kolonien oder die Allokation von Nachkommen. Ziel der vorliegenden Studie ist es, den Einfluss von extrafloralem Nektar (EFN) auf die Parasitoidaggregation in benachbarten mit Wirten infizierten Kulturpflanzenpatches zu untersuchen. Der Blattlausparasitoid *Diaeretiella rapae* (M'Intosh) wurde auβer- und innerhalb von Kulturpflanzenpatches frei gesetzt, die aus mit Blattläusen (*Brevicoryne brassicae* L.) infiziertem Raps (*Brassica napus* L.) und Ackerbohnen (*Vicia faba* L.) mit oder ohne EFN bestanden. Bei Freisetzung auβerhalb der Patches fanden sich mehr Parasitoide in den Varianten mit EFN. Diese höhere Einwanderung von Parasitoiden konnte auf

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die Attraktivität der Kombination von Wirts- und Nahrungsstimulus oder auf einen Lernprozess zurückgeführt werden. Ein Freisetzungs- und Wiederfangexperiment zeigte eine höhere Verweildauer der Parasitoide in Patches mit EFN und Wirten, was den Einfluss pflanzlicher Nahrung auf die Parasitoidaktivität deutlich macht. Die beobachtete höhere Anzahl von Parasitoiden und die höhere Parasitierung der Wirte in Patches mit Nektar produzierenden Pflanzen können demnach sowohl durch die Attraktivität als auch durch die längere Verweildauer erklärt werden. Die Verfügbarkeit von Nektar beeinflusste ebenfalls die maternelle Ressourcenallokation in die Produktion der Nachkommen.

Keywords: *Diaeretiella rapae*; *Brevicoryne brassicae*; Resource exploitation; Extrafloral nectar; Aphids

Introduction

Parasitoids, similar to many predatory insects, are carnivorous at the larval stage and shift to other food sources as adults. While some parasitoid species can feed on host hemolymph or honeydew in the adult stage, most species rely on plant-derived sugar-rich food such as nectar for their survival and metabolic needs (Jervis, Kidd, & Heimpel 1996; Wäckers 2005; Vollhardt, Bianchi, Wäckers, Thies, & Tscharntke 2010). Nectar availability influences the lifetime reproductive success of many parasitoid species (Heimpel, Rosenheim, & Mangel 1997; Lewis, Stapel, Cortesero, & Takasu 1998; Olson, Fadamiro, Lundgren, & Heimpel 2000) by increasing longevity and fecundity, especially in the case of synovigenic species, in which egg maturation continues over adult lifetime (Lewis et al. 1998; Tylianakis, Didham, & Wratten 2004; Wäckers 2005; Jamont, Crépellière, & Jaloux 2013a).

High quality sugar sources are typically scarce in modern agroecosystems, dominated by monocultures (Landis, Wratten, & Gurr 2000; Wäckers 2003) and only few nectar sources are accessible to parasitoids (Patt, Hamilton, & Lashomb 1997). Moreover, hosts and food are often highly spatially segregated (Jervis, Kidd, Fitton, Huddleston, & Dawah 1993; Heimpel & Jervis 2005), with hosts concentrated in the field and floral or extrafloral nectar restricted to field margins or non-cultivated areas. Adult parasitoid females have to tradeoff searching for hosts to ensure immediate reproduction but decreasing their energy reserves and searching for food to increase their reserves but missing opportunities to lay eggs (Heimpel, Rosenheim, & Mangel 1996; Krivan & Sirot 1997). Both the internal state (satiation, age or egg load) and environmental cues influence this trade off and interact in the parasitoid foraging strategy (Lucchetta, Desouhant, Wajnberg, & Bernstein 2007). Among the environmental cues, the spatial distribution of plants providing food and hosts in the environment can strongly influence female decisions, such as which patch to visit and how much time to forage for hosts vs. food. This often translates into successive search for hosts and for food (Krivan & Sirot 1997; De Moraes, Lewis, Paré, Alborn, & Tumlinson 1998) and commuting between the different agroecosystem compartments (Lewis et al. 1998; Heimpel & Jervis 2005). This phenomenon leads to high traveling costs and mortality risk during nectar foraging, which could decrease the time spent searching for hosts (Sirot & Bernstein 1996; Sisterson & Averill 2002; Tenhumberg, Siekmann, & Keller 2006). Energy costs increase with the distance between hosts and food, and reducing this distance may improve parasitoid efficiency (Lavandero, Wratten, Shishehbor, & Worner 2005; Vollhardt et al. 2010; Nilsson, Eriksson, Ramert, & Anderson 2012).

Optimal foraging models have been implemented to describe this trade-off and to predict when the parasitoid female should search for hosts or for food, considering host or food density, distance between resource patches and parasitoid nutritional state (Sirot & Bernstein 1996; Desouhant, Driessen, Amat, & Bernstein 2005; Tenhumberg et al. 2006). However, the predictions of these models have been poorly investigated in the wild due to the lack of appropriate methodologies that can be used to track parasitoid movements (Hagler & Jackson 2001; Lavandero, Wratten, Hagler, & Tylianakis 2003).

The availability of sugar sources in space and time may play a major role in the population dynamics of parasitoids (Takasu & Lewis 1993) and pest population control (Gurr, Wratten, Tylianakis, Kean, & Keller 2005; Winkler, Wäckers, Bukovinszkine-Kiss, & van Lenteren 2006). Conservation biological control strategies have been explored to decrease the time parasitoids search for food and hence to increase parasitism rate, such as planting companion plants providing nectar (Landis et al. 2000) or sugar spraying (Wade, Zalucki, Wratten, & Robinson 2008). The impact of nectar provisioning on parasitoid longevity and fecundity has been well studied in laboratory experiments (Winkler et al. 2006) but much less studied in the field (but see Tylianakis et al. 2004; Lee & Heimpel 2008; Desouhant, Lucchetta, Giron, & Bernstein 2010; Segoli & Rosenheim 2013). Moreover, the impact of the spatial distribution of nectar on parasitoid movements in the field remains widely unknown (Desouhant et al. 2010). These aspects have been identified as one of the main issues to investigate in conservation biological control. When hosts and food are close to each other, the value of the host patch may increase for parasitoids, leading to higher parasitoid recruitment (Nilsson et al. 2012) and/or increased parasitoid retention in these patches (De Moraes et al. 1998). The relative importance of these two mechanisms and their impact on host parasitism has never been studied.

This study explores intercropping plant producing extra floral nectar (EFN) in Brassica crop as a way to provide