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Review

Foraging behaviour by parasitoids in multiherbivore communities

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Parasitoid foraging decisions are often affected by community characteristics such as community diversity and complexity. As part of a complex habitat, the presence of unsuitable hosts may affect foraging behaviour of parasitoids. First, unsuitable herbivores may affect the localization of patches where hosts are present. Second, encounters with unsuitable herbivores in the food plant patch may affect parasitoid decisions during their searching behaviour in the patch. In this review, we outline the importance of the presence of unsuitable herbivores on the behavioural responses of parasitoids during both these foraging phases. Nonhosts feeding on a neighbouring plant or on the same plant individual the host is feeding from may affect odour-based searching by parasitoids in a way specific for the species combination studied. Feeding by specific host and nonhost–herbivore combinations may induce volatiles that are more, less or equally attractive compared to those from plants infested by the host only. Within the food patch, mixed presence of host and nonhost may reduce the number of hosts parasitized per time unit and reduce parasitoid foraging efficiency. Importantly, we show that a single nonhost species may have contrasting effects in terms of its effects on odour-based searching and patch residence decisions. We conclude that studying host searching behaviour at both phases of foraging is essential for our understanding of parasitoid foraging behaviour in natural and agricultural settings. We further speculate on the ecological context in which unsuitable herbivores affect either of the two phases of parasitoid foraging.

To optimize their foraging strategies, predators may use information on where their prey is located and how profitable a certain food patch may be (Vet & Dicke 1992; Schmidt et al. 2010; Kessler & Heil 2011). However, prey are members of complex communities and share their environment with nonprey that may affect predator foraging decisions. Hence, predators foraging in species-rich communities are exposed to natural selection that involves the presence of nonprey organisms and cues derived from them. Studies on parasitic wasps or parasitoids have played a major role in shaping and testing foraging theory (Godfray 1994). Parasitoids lay their eggs in or on other organisms that function as a host for the development of their offspring, eventually resulting in the death of the host in which the larvae develop (Godfray 1994). The host-searching behaviour of various parasitoids has been studied extensively in tritrophic systems consisting of a single food chain of plant, herbivore and parasitoid species (Vet & Dicke 1992; Heil 2008). In (agro)ecosystems, however, parasitoids forage in a complex habitat of a diverse plant and herbivore community (Dicke et al. 2009). Only in the last decade have experimental studies addressed parasitoid foraging behaviour in more natural, complex habitats. Results from these studies have shown that predictions on parasitoid foraging in simple tritrophic communities should be nuanced for foraging behaviour of parasitoids in more complex habitats (e.g. Rodriguez-Saona et al. 2005; Bukovinszky et al. 2012). One of the factors of a complex habitat is the presence of a community of other herbivores that may be unsuitable host species (here called nonhost herbivores). The presence of other herbivores in the habitat in which parasitoids search for hosts has been shown to have a strong effect on parasitoid foraging behaviour (Rodriguez-Saona et al. 2005; Dicke et al. 2009). These nonhost herbivores may either be present on neighbouring plants or share the same plant with host herbivores of a parasitoid. The shared food plant may be attacked simultaneously or sequentially (Vos et al. 2001; Poelman et al. 2010) and on the shared food plant the herbivores may feed on a single plant organ or may feed spatially separated on different plant organs above as well as below ground (Van Dam & Heil 2011). As a result, the presence of nonhost herbivores can affect parasitoid foraging behaviour on several levels, from finding the plant the host is feeding from to locating the host on the food plant and deciding whether or not to parasitize the host, each decision phase being an important attribute of parasitoid fitness (McArthur & Planka 1966;

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Van Alphen et al. 2003). In host location, the presence of nonhost herbivores may affect the parasitoid in two phases. First, like several other biotic and abiotic factors, nonhosts may influence the ability or efficiency of parasitoids to locate patches of host-infested plants from a distance (Gouinguené & Turlings 2002; Dicke et al. 2009). Parasitoids exploit so-called herbivore-induced plant volatiles (HIPVs) to locate their host (Vet & Dicke 1992; Heil 2008). HIPVs are blends of volatile compounds and are emitted by plants in response to attack by arthropod herbivores (Turlings et al. 1995; Arimura et al. 2005; Dicke & Baldwin 2010; Mumm & Dicke 2010). In more complex habitats, HIPV cues of host presence are surrounded by noise of volatiles induced by unsuitable hosts (Dicke et al. 2009). Second, nonhosts may affect foraging decisions in the patch: once a host-infested plant is located, encountering co-occurring nonhosts or their products on the plant could interfere with foraging decisions such as the time spent searching for hosts on the plant (Shiojiri et al. 2001; Bukovinszky et al. 2012). Both of these phases together predict parasitoid host-finding efficiency, but typically these two phases of host location are studied separately. Importantly, recent studies that did combine these two phases of parasitoid foraging have shown that effects of nonhosts on each phase may result in different predictions on foraging efficiency (Bukovinszky et al. 2012). The effect of nonhosts on parasitoid foraging decisions may be determined by the host range specialization (generalist–specialist) of parasitoids. Moreover, there is a large potential of specificity of effects that nonhosts may have on either phase of parasitoid foraging that may be determined by the feeding guild (Van Poecke et al. 2003; Delphia et al. 2007; Dicke et al. 2009), species (Hare 2011), development stage (Yamamoto et al. 2011) and density (Zhang et al. 2009) of the nonhost herbivore (Fig. 1). We review the effects of unsuitable hosts on two phases in foraging, that is (1) responses of parasitoids to HIPVs and (2) decisions of parasitoids when foraging for their hosts on a plant. For each of these phases we scale down from effects of nonhosts when located on neighbouring plants to nonhost presence on the same plant or leaf as the host herbivore is feeding on. We conclude that linking the responses of parasitoids to HIPVs and the responses to nonhost encounters on the plant is crucial for our understanding of parasitoid foraging decisions under natural conditions where plants are attacked by multiple herbivore species.

RESPONSE TO HIPVS INDUCED BY DUAL HERBIVORY

To find their herbivorous hosts, parasitoids use information from their environment. Hosts are under strong selection to be inconspicuous, minimizing cues that directly give away their presence to their enemies. However, while feeding on their food plant, herbivores may give away their presence indirectly by inducing the emission of volatiles by their food plant. Although these HIPVs that plants produce are readily detectable by parasitoids, the plant cues might not be as reliable as direct information received from the host (Vet & Dicke 1992). Parasitoids have to face this reliability–detectability problem while foraging, and on top of that they find themselves in an environment that is full of (volatile) cues that may distort information on host presence. For example, plants attacked by host herbivores may stand next to plants attacked by nonhost herbivores, both plants releasing HIPVs indicative of the presence of some kind of herbivore (Mumm & Dicke 2010). In addition, a plant that is attacked by both host and nonhost herbivores may release different cues compared to a plant under attack by the host only (Shiojiri et al. 2001; Schwartzberg et al. 2011; Zhang et al. 2013). Parasitoid species may respond differently to HIPVs of plants that harbour nonhosts. Parasitoids that have a narrow host range and are highly specialized in

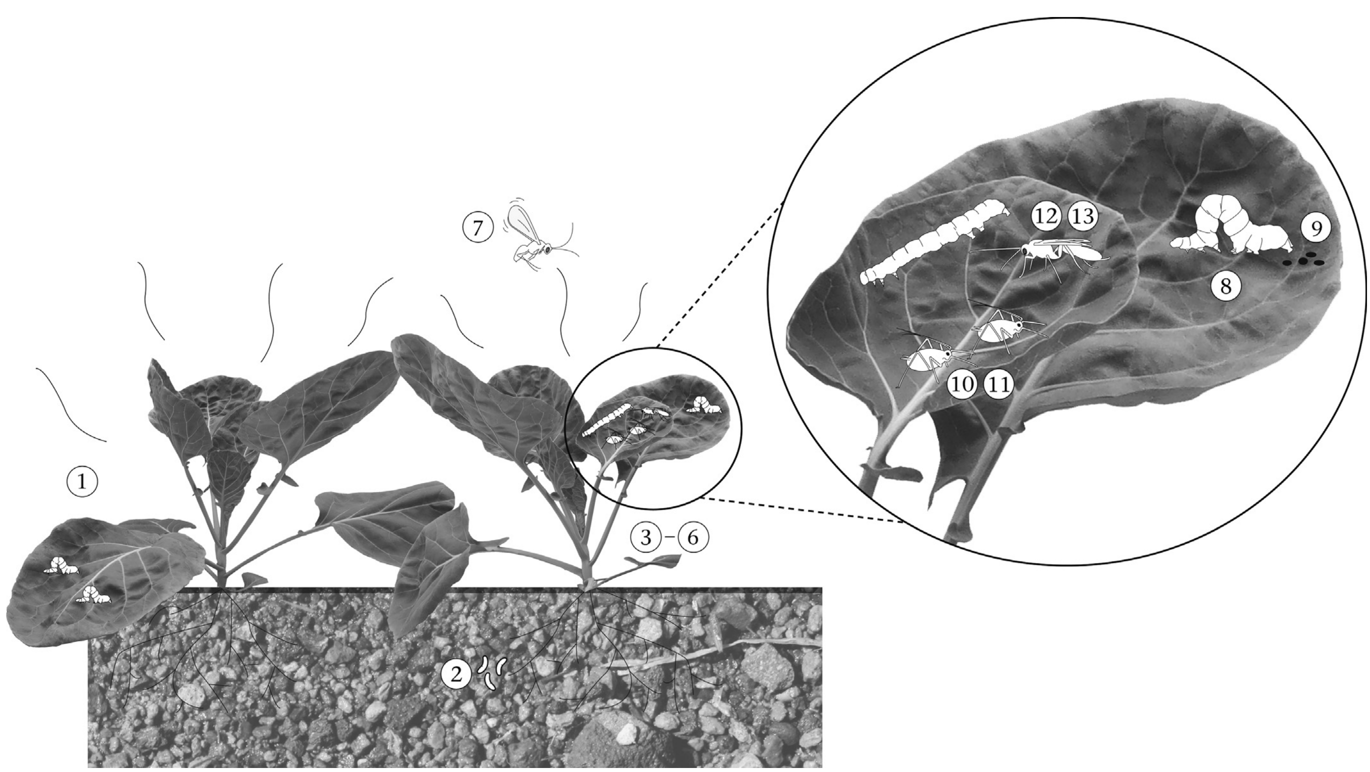

Figure 1. Factors potentially affecting the attractiveness of host-infested plants to foraging parasitoids: (1) nonhost-infested neighbouring plants; (2) feeding guild of nonhost; (3) developmental stage of nonhost; (4) density of nonhost; (5) order of host and nonhost arrival; (6) time period between infestation by host and nonhost; (7) parasitoid species. Potential factors affecting the plant residence time of parasitoids: (8) position of nonhost on plant; (9) handling of nonhost (products); (10) density of nonhost; (11) developmental stage of nonhost; (12) parasitoid species; (13) previous experience of parasitoid (associative learning). Figure created by Emma Tanis.