

REVIEW

En route to resources: Foraging strategies of plant-associated insects to identify resources in complex dynamic environments

Q. Rusman¹  | A. Cusumano²  | I. Vosteen³ 

¹Department of Systematic and Evolutionary Botany, University of Zürich, Zürich, Switzerland

²Department of Agricultural, Food and Forest Sciences, University of Palermo, Palermo, Italy

³Division of Agricultural Entomology, University of Göttingen, Göttingen, Germany

Correspondence

Q. Rusman

Email: quint.rusman@systbot.uzh.ch

I. Vosteen

Email: ilka.vosteen@uni-goettingen.de**Handling Editor:** Mayra Vidal**Abstract**

1. In plant-associated communities, foraging insects aim to find different resources of interest. Herbivores look for the most nutritious plant tissues, pollinators for sweet nectar and protein-rich pollen, and carnivores for their preferred prey. Although these foragers look for different resources, they face similar problems: resource cues are often highly variable and need to be detected in complex environments among non-resources. Search templates—a subset of stimuli that is likely correlated with the occurrence of a particular resource—help foragers across trophic levels to find their resources. However, search-template-based foraging can also cause perception errors.
2. Here, we synthesize knowledge on foraging by insects from functional groups belonging to different trophic levels to reveal common problems experienced by foragers and strategies to solve such problems. We focus mostly on volatile-based foraging because this searching strategy is best studied across functional groups.
3. We argue that search templates are both multimodal (including multiple trait types, e.g. odour and visual) and hierarchical (including multiple foraging steps). Search templates are plastic and updated by experience to match the dynamic foraging environment over time.
4. By comparing insects from different functional groups spanning multiple trophic levels, we have identified important missing gaps on cue use and foraging strategies which should be addressed in the future in order to reduce knowledge asymmetries among functional groups about search-template-based foraging. We propose a way to achieve this goal arguing that studies on less well investigated functional groups can advance rapidly by borrowing, testing and adjusting already available hypotheses and theories formulated for other insect groups. Knowledge of search-template-based foraging across functional groups will give new insights into the evolution of foraging behaviour in complex ecological communities, help predict ecological consequences of large-scale human-made disturbances and help optimize insect-delivered ecosystem services (pollination and biological control) in cropping systems.

KEYWORDS

herbivores, HIPVs, host plant, learning, plant volatiles, pollinators, search template, trophic levels

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2024 The Author(s). *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Plant-associated insects search for food and oviposition sites in complex environments in which these resources are interspersed among non-resources (Rusch et al., 2016; Webster & Cardé, 2017). Pollinators, herbivores, their natural enemies and higher-order carnivores do not forage randomly, but are attracted to olfactory, visual and acoustic stimuli that have a high probability to be associated with the occurrence of the desired resource. Hence, these insects have an expectation on the appearance of the resource they search for. The subset of stimuli a foraging insect is focusing on and that is likely correlated with the occurrence of a particular resource (i.e. food or oviposition site), has been referred to as a search template and includes the innate and learned preferences for certain stimuli that may be fine-tuned or broadened with additional foraging experience (Aartsma et al., 2019).

Search-template-based foraging can be found across trophic levels of plant-associated insects and strong evidence comes from studies that focus on odour-guided foraging. Plant-associated insects from functional groups across trophic levels use plant volatiles as an important source of information: Herbivores are attracted by volatiles emitted by their host plants (Bruce et al., 2005; Bruce & Pickett, 2011; Visser et al., 1992) and pollinators use flower scent to detect flowers (Raguso, 2008; Rusch et al., 2016; Schiestl, 2015). Predators, parasitoids and hyperparasitoids use herbivore-induced plant volatiles (HIPVs) to detect plants infested with their host or prey insects (Poelman et al., 2022; Turlings & Erb, 2018; Vet & Dicke, 1992). Although the use of plant volatiles as an important source of information is well established across trophic levels, it is less clear how foragers deal with the high variability of volatile cues. In this review, we discuss the problem of high cue variability in olfactory-based foraging. We propose that foragers may use search templates which are broad enough to cover the variability of cues to optimize foraging under complex environments but have to face discrimination problems if cues from resources and non-resources are highly similar. Such perception errors in turn can be reduced via multimodal integration, hierarchical cue use and learning. Although we discuss problems and strategies in the context of volatile-based foraging, they apply to the use of other cues (e.g. visual) also. We mostly include examples of volatile-based foraging, but when suitable examples are lacking or when discussing multimodal integration and hierarchical cue use, studies on foraging based on other cues, such as visual, are also included. We integrate knowledge of foraging insects from multiple functional groups—from herbivores and pollinators to predators, parasitoids and hyperparasitoids—to reveal the ubiquity of variability and perception error problems and the use of common strategies to solve these problems. Syntheses across functional groups allows for the identification of knowledge gaps for specific groups and formulation of clear predictions to fill those gaps based on knowledge of other specific groups. This will not only guide future research on search-template-based foraging for specific insect groups, but also encourage researchers to directly compare different functional groups to further refine our

understanding of the evolution of foraging behaviour in complex multi-species communities.

In this review, we focus on the behavioural ecology of foraging: we compare the foraging behaviour of multiple functional groups from an ecological perspective. Such ecological synthesis is essential for a complete understanding of the evolution of foraging behaviour under complex ecological conditions. We are very well aware of the sensory and neurobiological processes underpinning search templates and we refer to recent reviews on odour perception and neural processing (Clifford & Riffell, 2013; Haverkamp et al., 2018; Ho & Riffell, 2016; Kanwal & Parker, 2022; Martin et al., 2011; Renou, 2014; Zhao & McBride, 2020), odourscape (Conchou et al., 2019), multi-sensory integration (Kinoshita et al., 2017; Leonard & Masek, 2014) and the evolution of olfaction (Hansson & Stensmyr, 2011) that extensively covered these topics, which will hence not be discussed here. In addition, by comparing the foraging behaviour of multiple functional groups we take a broader comparative approach compared with other recent reviews that focus on herbivores (Carrasco et al., 2015; Silva & Clarke, 2020), pollinators (Rusch et al., 2016) and specialist herbivore-parasitoid systems (Aartsma et al., 2019).

2 | OLFATORY SEARCH-TEMPLATE COMPLEXITY: OCCURRENCE, CAUSES AND STRATEGIES

2.1 | Complexity as the rule in odour-guided foraging

Most odour-guided foraging insects use a complex blend of volatiles, and only few foragers use single volatile compounds under natural conditions. For example, female flies from the genus *Botanophila* use a single volatile compound to find their endophytic fungi host (Schiestl et al., 2006). The minute pirate bug *Elatophilus hebraicus* uses one compound of a two-compound pheromone blend to find its scale insect prey (Mendel et al., 1995). In other cases, one volatile compound is the dominant cue used in foraging, but other compounds are needed to successfully complete foraging, for example, by inducing host acceptance or guide host location. Research on fruit flies (Dekker et al., 2006; Dweck et al., 2013; Joseph et al., 2009; Linz et al., 2013) and oil-collecting bees (Schäffler et al., 2015) nicely illustrate this. In general, however, the search template of foragers consists of a blend of multiple compounds. Herbivores often use between 3 and 10 compounds during foraging (Bruce & Pickett, 2011), and pollinators between two and nine (Huber et al., 2005; Kobayashi et al., 2012; Riffell et al., 2009; Schäffler et al., 2015). For carnivores, the sparse information available so far suggests that these insects can use blends of between 3 and 15 compounds (Morawo & Fadamiro, 2016; Zuk & Kolluru, 1998). Importantly, the function of compounds is highly context-dependent: Foragers respond differently if compounds from a blend are presented individually and often respond more strongly to blends compared with individual

compounds (Bruce & Pickett, 2011; Mumm & Dicke, 2010; Zito et al., 2019). For example, when 10 volatile compounds of faba bean (*Vicia faba*) that are individually repellent to black bean aphids (*Aphis fabae*) are combined in a blend, the mixture becomes attractive (Webster, Bruce, et al., 2010). In contrast, many species of euglossine bees can be attracted by individual volatile compounds of orchids pollinated by euglossine bees, but the complete blends of plants often only attract one or a few species (Dodson et al., 1969; Williams & Dodson, 1972). Focussing research activity on single compounds can grossly under- or overestimate the actual number of compounds used when presented in a blend (Morawo et al., 2016; Morawo & Fadamiro, 2016). Taken together, most plant-associated foragers include volatile blends consisting of more than two compounds in their search template to find their resource of interest.

2.2 | Diet breadth and resource rarity modify search template strategies

Resources provide different cues, and therefore, the cue diversity that a forager has to deal with is partially dependent on diet breadth and resource rarity. We assume that insects generally use one search template for each resource type, such as oviposition site or food, which incorporate those stimuli that allow recognition of potential resources and to distinguish them from non-resources. Generalists may use a limited number of very general stimuli such as green leaf volatiles or common floral volatiles that are shared not only by many potential resources but also by some non-resources (narrow search template) (Knudsen et al., 2006; McCormick, 2016). Alternatively, generalists may respond to a large number of specific stimuli from different resources (broad search template) or may be attracted to a larger range of compound ratios as compared to specialists. Please note that both the narrow and the broad search template of generalists would result in the recognition of a large number of resources. The search template of specialists may contain mostly stimuli that are specifically linked to their resource potentially in combination with more general stimuli. Hence, their search template can be narrow or broad depending on the number of stimuli used. Herbivores specialized on Brassicaceae and their natural enemies for example are usually attracted by specific breakdown products of glucosinolates (Bruce, 2014). Oligolectic (specialized) bees likely use a combination of general and specific floral scent compounds to find their host flowers, while polylectic (generalized) bees focus on a broader range of general compounds (Brandt et al., 2017; Polidori et al., 2020). The degree of specialization of an insect may thus not necessarily provide much information about the absolute number of stimuli incorporated into the search template, neither about the width of the search template (narrow/broad).

Resource rarity is another key factor likely to shape search-template-based foraging. This applies especially to high-order natural enemies such as obligate hyperparasitoids. In fact, their primary parasitoid hosts are scarcer (and thus likely harder to locate) than

herbivore hosts of primary parasitoids. Parasitoid host larvae do not feed on plants and often are even hidden within the herbivore body (Poelman et al., 2022). Hyperparasitoids have to deal with large stimuli diversity due to the fact that: (1) the same herbivore species may be attacked by several parasitoid host species and (2) the same parasitoid host may develop on/in different herbivore species (Cusumano et al., 2019; Poelman et al., 2022). Because of all these challenges, hyperparasitoids are expected to adopt flexible search templates that make the best use of all available information to locate and recognize the host resource, but little is known about their search template complexity. Taken together, although diet breadth and resource rarity influence the cue diversity foraging insects are exposed to, these factors do not necessarily predict the complexity of the search template.

2.3 | Complex search templates counter blend overlap

Many plant species overlap in the volatile compounds that constitute the emitted blend and the same compounds can be emitted by plants that provide suitable and non-suitable resources (Knudsen et al., 2006; Pichersky & Gershenzon, 2002; Schiestl, 2010). Such blend overlap negatively influences foraging: Flower visiting hawkmoths have reduced foraging efficiency when flowers of their *Datura wrightii* hosts are surrounded by creosote bush (*Larrea tridentata*), which emit similar volatile compounds as *D. wrightii* (Jardine et al., 2010; Riffell et al., 2014). Still, quantitative blend composition is often unique for plant species (Levin et al., 2001; Schoonhoven et al., 2005; Wright et al., 2005). Third-trophic level carnivores use quantitative differences in HIPV blends to distinguish between different herbivore species attacking the plant (Danner et al., 2018; Dicke & Hilker, 2003; Hare, 2011). Therefore, foragers can incorporate quantitative blend characteristics in their search templates to solve blend overlap between resources and non-resources. Indeed, herbivores only respond to volatile compounds emitted by their host plants if these are presented in 'correct' combinations and ratios (Bruce et al., 2005; Bruce & Pickett, 2011; Webster, Bruce, et al., 2010; Webster, Gezan, et al., 2010). Their search template thus contains the composition of certain attractive volatile blends, while blends that do not match with the properties of the search template are not perceived as attractive. This strategy allows herbivores to ignore volatile blends emitted by non-host plants even if the non-host blends contain the same or similar compounds as the host plant blend. For pollinators and carnivores, it is less well explored how such quantitative blend characteristics are incorporated into the search template, but studies on quantitative variation in blend composition suggest they matter (Leonhardt et al., 2014; Wright et al., 2005, 2008). For example, herbivore attack in *Brassica* plants has been shown to change volatile emission quantitatively but not qualitatively, and these quantitative changes influence both pollinator and parasitoid foraging (Rusman, Poelman, et al., 2019; Schiestl et al., 2014).

Fourth-trophic level hyperparasitoids discriminate between quantitatively different HIPV blends induced by parasitized and non-parasitized caterpillars (Poelman et al., 2022). These examples indicate that already small changes in the composition of a volatile blend can result in changes in the behaviour of pollinators and carnivores. Therefore, it seems highly likely that the volatile search template of all functional groups contains a strong quantitative component.

2.4 | Search template strategies to detect highly variable cues

Although quantitative cues can help foragers distinguish resources with qualitative blend overlap, such cues can be highly variable. Plant volatile blends, for example, vary considerably between individuals of the same species (Delle-Vedove et al., 2017; Hare, 2011). Individual variation can be caused by genotypic differences (Degen et al., 2004; Gols et al., 2011), plant ontogeny (Desurmont et al., 2015; Hare, 2010; Schuman et al., 2016) or phenotypic differences caused by abiotic or biotic factors (Mumm & Dicke, 2010; Possell & Loreto, 2013; Rusman, Lucas-Barbosa, et al., 2019). Volatile emission from plants follows certain diurnal rhythms (Fenske & Imaizumi, 2016; Schuman et al., 2016). Changes in weather conditions affect information availability in seconds to minutes under field conditions (Aartsma et al., 2017), while blend composition changes with increasing distance to the odour source (Cai et al., 2022). Thus, variation in information availability to any foraging insect under natural conditions is inevitable.

To incorporate cue variability and to match search templates with resource-associated cues emitted under various biotic and abiotic conditions, we expect foragers to use a combination of two strategies: (1) broad multi-component search templates and (2) stimulus generalization (Figure 1). We suggest that volatile search templates consist of several components (Figure 1). The core components are compounds which are ubiquitous for most host plants, and some of them need to be present to make a blend attractive (Bruce & Pickett, 2011; Reinhard et al., 2010). Redundancy in some core components of the search template allows for the identification of attractive blends even if some compounds are missing or present at an unusual ratio (Bruce & Pickett, 2011; Reinhard et al., 2010). Optional components may further increase the attractiveness of a blend and their absence or presence determines the rank of blends in the preference hierarchy, as evident from polyphagous insects and parasitoids with polyphagous hosts (Carrasco et al., 2015; Geervliet et al., 1996; Janz, 2008; Thompson & Pellmyr, 1991). Optional components may also be used by specialists to evaluate the quality of the resource, as suggested by data available for polylectic and oligolectic bees (Brandt et al., 2017; Milet-Pinheiro et al., 2013).

In order to match their search templates with the variable cues associated with resources, insects use stimulus generalization. Stimulus

generalization is achieved by evaluating the similarity of the perceived stimuli and the search template, and requires a gradual decrease in responses with decreasing similarities between the perceived stimuli and the search template (Giurfa & Menzel, 2013). Redundancy in the core components of a volatile search template, additional optional components that modulate the attractiveness of a blend and stimulus generalization allow insects from functional groups across trophic levels to identify resource-associated blends despite the high variability of volatile cues (Figure 1). However, as discussed in detail below, problems may arise while employing these strategies.

3 | PERCEPTION ERRORS CAUSE CONFUSION AND MISSED OPPORTUNITIES

3.1 | Confusion in herbivores: Utilization of non-resources can have detrimental effects

Search-template-based foraging and stimulus generalization can cause perception errors (Cunningham, 2012), meaning that resources are perceived as non-resources or that non-resources are perceived as resources. When non-resources are perceived as resources, search templates are too unspecific, which can 'confuse' and misguide foraging insects. A search template is too unspecific when the subset of stimuli included lead to the recognition of a non-resource as resource. Note that this applies for the recognition of each individual (non)-resource and is independent of diet breadth and the absolute number of stimuli. Research on confusion in herbivores focussed on the attempt of herbivores to utilize non-resources, with obvious detrimental fitness consequences. This research started with observations that a surprising amount of herbivore species oviposit on non-host plants/genotypes on which all offspring die (Fox & Lalonde, 1993; Janz, 2008; Larsson & Ekblom, 1995; Steward & Boggs, 2020). In agreement with search-template-based foraging, this behaviour was among others explained with the 'confusion hypothesis' (Fox & Lalonde, 1993). According to this hypothesis, adjusting the search template to exclude all non-resources will inevitably also exclude some resources when non-resource and resource cues are relatively similar, that is this leads to a too specific search template (Cunningham, 2012). When the fitness benefit of a too unspecific search template is larger than the fitness benefit of a too specific search template, the more unspecific search template will be retained, despite including lethal non-resources. This has been shown for gall-forming cecidomyiids and is suggested to be common among other herbivores such as certain lepidopterans and flies, scale insects and aphids (Larsson & Ekblom, 1995). If non-resources are common and preferred, this can result in an 'evolutionary trap' when foragers experience reduced survival or reproduction (Schlaepfer et al., 2002; Steward, 2019; Steward & Boggs, 2020). A classic example of an evolutionary trap is the invasive garlic mustard (*Alliaria petiolata*), which is accepted for oviposition by pierid butterflies but is a lethal host for their caterpillars (Steward, 2019;

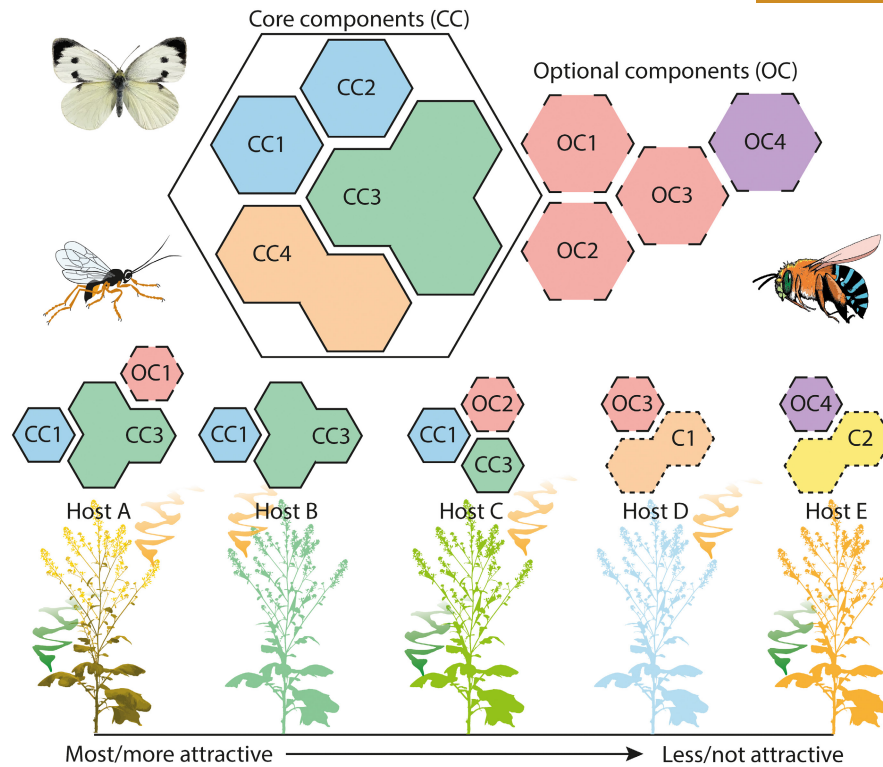


FIGURE 1 Visualization of the search template containing core components (CC, solid contour lines) and optional components (OC, rough dashed contour lines). Compounds not included in the search template are indicated by C and fine dashed contour lines. Numbers correspond to different compounds. Colour corresponds to hypothetical chemical classes. Merged compound tiles correspond to relative abundances. Incorrect ratios make hosts less or not attractive. The most attractive host A emits CC1 and CC3 in the correct ratio and the optional compound OC1 makes it more attractive than host B. Host C is less attractive than A and B because it emits CC3 in incorrect ratios. The blue host D is more attractive than the orange host E due to generalization: C1 is a similar chemical class as CC4, while C2 is not included in the search template, neither shares a chemical class with any of the compounds included in the search template. Illustration credits: Yavanna Aartsma, Dani Lucas-Barbosa, Paula Peeters—Pollinator Link, Quint Rusman.

Steward & Boggs, 2020). Thus, too unspecific search templates induce confusion which reduces foraging efficiency and can result in the attempted utilization of non-resources with detrimental effects on fitness.

3.2 | Confusion in pollinators and parasitoids: Reduced foraging efficiency in environments containing non-resources

In addition to non-resource utilization by confused herbivores, foragers should also be considered 'confused' when they experience a reduction in foraging efficiency from the presence of non-hosts without actual attempts to utilize the non-host as resource (Croijmans et al., 2022; de Rijk et al., 2016; Goulson, 2000; Vosteen et al., 2019). Confusion resulting from perceiving non-resources as resources can influence any foraging step and is not limited to host acceptance. Therefore, we consider foraging insects confused when the forager experiences reduced searching efficiency and/or tries to utilize a non-resource because of search-template-based foraging. Indeed, research on pollinators and parasitoids has shown that the perception of non-resources as resources can lead to a reduction in foraging efficiency.

In an environment dominated by multiple non-host species with yellow flowers, bumblebees foraging on hosts with yellow flowers have reduced foraging efficiency compared with bumblebees foraging on hosts with purple flowers (Goulson, 2000). Naïve *Cotesia glomerata* parasitoids are equally attracted to plants infested by their caterpillar hosts as to plants infested with non-host caterpillars. In the presence of non-host-infested plants, parasitoids need more time to find a host-infested plant and occasionally oviposit in non-hosts (Vosteen et al., 2019, 2020). Perception errors that cause confusion and reduced foraging efficiency are expected to be most likely if cues from resources and non-resources are highly similar. Parasitoids associated with caterpillar hosts more often chose a non-host-infested plant if the non-hosts are caterpillars compared to aphids (de Rijk et al., 2016). This is likely because different feeding guilds induce distinct HIPV blends, while herbivores from the same feeding guild induce blends that are more similar to each other (Danner et al., 2018). To distinguish such highly similar blends induced by host and non-host caterpillars, parasitoids would need to increase the specificity of their search template, with the risk of becoming too specific to deal with cue variability. The fitness costs/benefits of having a too specific or too unspecific search template will determine the evolution of the accuracy of search templates.

Results show that confusion occurs across functional groups, despite a research focus on different foraging steps in herbivores as compared to pollinators and parasitoids. Future work should reduce this asymmetry by clarifying the incidence of confusion in early foraging steps of herbivores and the extent to which it reduces foraging efficiency, while non-host utilization in pollinators and parasitoids has received little attention so far (but see de Bruijn et al., 2022; Vosteen et al., 2019, 2020).

3.3 | Benefits of confusion

Although confusion was found to be detrimental by reducing foraging efficiency and failed attempts to utilize non-hosts, confusion can also provide benefits when it leads to the successful utilization of non-hosts (Barron, 2001). Exposure of the crucifer specialist *Plutella xylostella* to non-host plant volatiles during oviposition or larval development on a host plant can lead to subsequent oviposition on the non-host plant (Zhang et al., 2007), which can be incorporated into the diet if suitable for larval development. Bumblebees that were more prone to make errors during foraging by visiting non-rewarding flowers, also discover new high-rewarding flowers more quickly (Evans & Raine, 2014). Such 'minoring' behaviour, visiting specific flowers at low frequency, reduces foraging behaviour in stable environments but can be beneficial when foraging conditions change over time (Evans & Raine, 2014; Keasar et al., 2013). Taken together, confusion-driven utilization of non-hosts can be instrumental to host range expansions and successful foraging across functional groups in ever-changing environments.

3.4 | Too specific search templates can lead to missed opportunities

Perceiving a suitable resource as a non-resource would result from employing a too specific search template. A search template is too specific when the subset of stimuli included are not sufficient to recognize all suitable resources. Note that this applies for the recognition of each individual resource and is independent of diet breadth and the absolute number of stimuli. Too specific search templates are nicely illustrated by restrictions on host plant ranges driven by adult choice behaviour rather than larvae feeding compatibility, and can be found across functional groups, that is in herbivores (Janz, 2008; Thompson, 1988), bees (Williams, 2003) and carnivores (Noriyuki & Osawa, 2012). Too specific search templates consequently yield missed opportunities, which can have severe fitness consequences if resources are scarce. For example, specialized aphids reject a non-host plant after brief probing, and rather die than trying to establish phloem feeding (Caillaud & Via, 2000; Powell et al., 2006; Schwarzkopf et al., 2013). Larvae of specialist *Osmia californica* bees develop normally or even better on pollen from novel non-natural host plants compared to pollen from the normal host (Williams, 2003). However, adult bees often do not

accept to collect such novel pollen, thereby producing no offspring in environments with only novel pollen (Williams, 2003). Missed opportunities are likely to occur if the search template of an insect is too specific so that it does not cover large parts of the cue variability caused by changing biotic and abiotic conditions. This is exemplified by the disruptive effect of herbivory on flowering plants on pollinator foraging (Kessler & Halitschke, 2009; Moreira et al., 2019; Rusman, Lucas-Barbosa, et al., 2019), and co-occurrence of host and non-host herbivores on parasitoid foraging (Croijmans et al., 2022; de Rijk et al., 2013; Hu et al., 2020; McCormick, 2016). Thus, perceiving suitable resources as non-resources resulting from a too specific search template is a missed opportunity that can lead to severe fitness consequences across functional groups and even extinction under strong environmental change (Singer & Parmesan, 2018).

Across functional groups, we identified perception errors resulting from too specific or unspecific search templates, with potential severe fitness consequences for the forager. If a too specific or too unspecific search template result in a severe fitness reduction (e.g. in the case of an evolutionary trap), this would lead to strong selection pressures to develop a 'better' search template. However, insects that are not strict specialists that only use one species as a resource need to make compromises in their search template to incorporate a maximum number of potential resources, while excluding non-recourses, which restricts the ways in which a search template can evolve (Cunningham, 2012). Additionally, the search template needs to be broad enough to incorporate cue variability. There is thus no 'perfect' search template that allows the entire avoidance of perception errors. Such imperfect search templates and accompanying perception errors are prone to exploitation by both natural and farming systems.

4 | EXPLOITATION OF PERCEPTION ERRORS OF FORAGING INSECTS BY NATURE AND HUMANS

A number of systems evolved to exploit perception errors caused by search-template-based foraging of insects. The most well-known are deceptive orchids. About one-third of all 25,000 orchid species is deceptive (Nilsson, 1992). These plants attract pollinators with the promise of food or sex but offer none. Food-deceptive orchids can exploit search templates of pollinators in two different ways: via Batesian mimicry (model mimics) or via generalized food deception (non-model mimics) (Jersáková et al., 2006; Nilsson, 1992). Model mimic orchids have flower traits that closely match the search templates of pollinators fine-tuned to their host plants (Anderson et al., 2005; Johnson, 2000). The success of foragers to exclude these non-rewarding flowers by experience mostly depends on the similarity of the model and mimic as well as relative abundances of mimics and model plants (Anderson et al., 2005; Jersáková et al., 2012; Schiestl, 2005). Non-model mimics provide more general signals, often produce conspicuous floral displays and match flower phenology with the

emergence of new or hibernating insects (Jersáková et al., 2006; Nilsson, 1992). Because these orchids exploit the generalization ability of foraging insects, insects quickly learn to avoid them (Gumbert & Kunze, 2001; Schiestl, 2005). Interestingly, it seems that non-model mimic orchids reduce avoidance learning via two mechanisms: unimodal signals and high signal variability. Indeed, non-model mimic orchids are often unimodal and only provide visual signals because: (1) providing both visual and odour signals enhances the discrimination ability of the forager, (2) scent signals are learned faster and provide better discrimination of the mimic (Kunze & Gumbert, 2001). Non-model mimic orchids often display highly intraspecific variation in floral signals (Gigord et al., 2001; Juillet & Scopece, 2010; Moya & Ackerman, 1993; Schiestl, 2005). Such variation might delay or inhibit avoidance learning and modify pollinator behaviour rather than leading to complete avoidance (Juillet & Scopece, 2010; Schiestl, 2005). Complete avoidance of food-deceptive orchids by naïve insects could be achieved by adapting a highly specific innate search template for choosing which plants to visit but at the risk of becoming too specific. Alternatively, foragers could add an additional foraging step to check for plant reward status before deciding to visit the flowers of a chosen plant (see section below on hierarchical cue use).

Perception errors of foraging insects are also exploited by humans to optimize farming systems. Push and pull systems are a prime example (Cook et al., 2007; Pickett et al., 2014). Such systems can use dead-end trap crops to deal with herbivores: plants highly attractive to adults but not or poorly suitable for larval development are grown in the vicinity of the crop that should be protected (Shelton & Badenes-Perez, 2006; Shelton & Nault, 2004). A successful example is Napier grass (*Pennisetum purpureum*). This trap crop is used in push-pull programmes to protect maize and sorghum crops in sub-Saharan Africa (Cook et al., 2007). Stem-borer pests oviposit heavily in this species despite the strong mortality experienced by the developing larvae. Other companion plants can be used to attract parasitoid wasps of the stem-borer pests (Sobhy et al., 2022; Thomas et al., 2023). Due to the constitutive emission of plant volatiles generally included in HIPV blends, parasitoid wasps are attracted to such companion plants even in the absence of hosts, but there is always the risk that parasitoids would learn to avoid such unreliable cues (Poelman et al., 2023). Examples of other suggested but not widely used dead-end trap crops are yellow rocket (*Barbarea vulgaris*) and early yellow rocket (*B. verna*) against the Diamondback moth (*Plutella xylostella*) (Badenes-Perez et al., 2014; Shelton & Nault, 2004), and radish (*Raphanus sativus*) against pollen beetles (*Meligethes* spp.) (Veromann et al., 2014). For crops with various pest insects, the ideal dead-end trap crop would be effective for multiple species. This can be realized by exploiting overlap in search templates, as has been shown for diamondback moths and cabbage root flies (*Delia radicum*) in the yellow rocket-cabbage system (Siekmann & Hommes, 2007). The generalization ability of foraging insects is exploited in several farming systems. For example, providing crop mimic odours within beehives can improve crop pollination by biasing honeybee foraging on the crop (Farina et al., 2023), even when potential better resources are available. The exogenous application of few natural

or synthetic compounds can enhance the attraction of natural enemies of pest insects (Thomas et al., 2023), even when pest abundance is low or absent. Future challenges to optimize farming systems by manipulating foraging behaviour include dealing with multiple herbivores and attracting/repelling pollinators and higher trophic levels (predators, parasitoids and hyperparasitoids).

4.1 | Human disturbance can cause perception errors

In addition to the intentional exploitation of perception errors of foraging insects, large-scale human disturbances like climate change and air pollution can influence insect foraging behaviour by forcing perception errors. Note that effects of large-scale human disturbances like climate change and air pollution can be more extreme than perception errors: Detection of both resources and non-resources can be disrupted altogether (Fuentes et al., 2013; Langford et al., 2023; Vanderplanck et al., 2021). The most likely perception error forced by human disturbance is the perception of a resource as non-resource. Drought, elevated temperatures and concentrations of CO₂, volatile reactive oxygen species (ROS) like ozone (O₃) and NO_x, and other volatile pollutants can induce changes in the volatile blends emitted by resources either by changing the active/passive emission by the resource or by altering the composition of the blend in the air (Blande et al., 2014; Farré-Armengol et al., 2016; Jürgens & Bischoff, 2017; Kuppler & Kotowska, 2021). When such variation falls outside the search template or essential compounds disappear from the blend, resources will be perceived as non-resource. Indeed, such perception errors have been shown for herbivores (Duque et al., 2019), natural enemies (Boullis et al., 2015; McCormick, 2016) and pollinators (Chan et al., 2024; Otieno et al., 2023). Interestingly, even human-disturbance-induced cue variation can quickly be incorporated into the search template by multimodal cue use and learning. For example, ozone-altered floral scent of *Nicotiana glauca* is unattractive for foraging *Manduca sexta* moths (Cook et al., 2020). When moths find flowers with ozone-altered floral scent based on visual cues, however, they learn to associate the ozone-altered floral scent with a nectar reward, and the ozone-altered blend becomes attractive. Learning in bumblebees offsets reduced foraging efficiency of ozone-altered volatile blends (Saunier et al., 2023). Concerning however is the fact that some large-scale human disturbances such as elevated ozone levels can impair learning (Leonard, Pettit, et al., 2019; Leonard, Vergoz, et al., 2019) or lead to higher generalization, which could result in more perception errors when non-resources are perceived as resources (Demares et al., 2022). Hence, understanding forager perception errors forced by human disturbances will help predict their ecological consequences.

Although perception errors of foraging insects are prone to exploitation by various organisms and may increase under rapid environmental change, foragers themselves evolved ways to avoid such exploitation and increase in perception errors as a consequence of rapid environmental change. In the following sections,

we discuss strategies foraging insects may use to mitigate problems associated with too specific or unspecific search templates and highlight important knowledge gaps associated with specific functional groups.

5 | MULTIMODAL AND HIERARCHICAL CUE-USE HELP TO CONFIRM FORAGING INFORMATION

5.1 | Multimodal integration is mainly studied in pollinators

Volatiles provide information about the presence of a potential resource already from a distance and are usually considered as long-range cues. Since perception errors cannot be prevented at this stage of foraging, insects need to confirm the information contained in the volatile blend. If different modalities of long-range cues are available, insects may use multimodal integration to confirm information from long-range cues. Multimodal cue use has been most extensively studied in pollinators (Junker & Parachnowitsch, 2015; Kinoshita et al., 2017; Leonard et al., 2012; Leonard & Masek, 2014). Multimodal integration helps pollinators to: (1) recognize resources in the case of cue similarities between hosts and non-hosts; (2) recognize host plants more successfully or quickly, compared to using unimodal cues; (3) assess different aspects of host plant selection at the same time, for example host plant/flower identity and quality (e.g. reward provision); and (4) cope with cue variability (Leonard et al., 2012). Multimodal integration thereby is important to confirm information from long-range cues and optimize foraging, as extensively shown for pollinators (Burger et al., 2010; Gegear & Lavery, 2005; Klahre et al., 2011; Riffell & Alarcón, 2013). Multimodal integration is not unique for pollinators, and it can also be found in herbivores and higher trophic levels. Herbivores such as butterflies (Janz, 2008), bark beetles (Campbell & Borden, 2006a, 2006b, 2009), cabbage root flies (Nottingham, 1988), apple maggot flies (Aluja & Prokopy, 1993; Prokopy & Owens, 1983) and several parasitoid species (Jang et al., 2000; Morehead & Feener, 2000) integrate visual and volatile cues to discriminate between hosts and non-hosts. For apple maggot flies, it has also been shown that multimodal cue use leads to faster recognition of host fruits and help the forager cope with cue variability: odour cues are important when visual cues are poor but less so when visual cues are strong (Aluja & Prokopy, 1993). Thus, the functional hypotheses of the benefits of multimodal integration outlined above for pollinators likely apply across functional groups. Still, we need more studies to clarify the overall use of multimodal integration for predators, parasitoids and higher-order carnivores such as hyperparasitoids. Moreover, future studies should specifically test which of the functional hypotheses of the benefits of multimodal integration apply to herbivores and higher trophic levels.

5.2 | Evidence for hierarchical cue use comes mostly from studies on herbivores and carnivores

Most foragers are expected to employ hierarchical cue use in addition to, or in the absence of, multimodal long-range cues. Foragers that employ hierarchical cue use follow several hierarchical foraging steps and use different cue modalities (volatile, visual, gustatory or tactile) or their multimodal combination to confirm their decision at each foraging step. More than three decades ago, hierarchical cue use was extensively studied for specialist herbivores such as cabbage root flies and apple maggot flies (Aluja & Prokopy, 1993; Nottingham, 1988) and several Lepidopteran species (Janz, 2008). More recently, this strategy has been suggested to be important for polyphagous herbivores as well with the 'sequential cues hypothesis', which argues that polyphagous herbivores use different cues sequentially in host location (Silva & Clarke, 2020). Due to the cryptic behaviour of herbivores and the resultant assumption that multimodal long-range cues are not available, research on predatory insects and (hyper)parasitoids has mostly focussed on hierarchical foraging (Aartsma et al., 2019; Vinson, 1998). For example, the parasitoid *C. glomerata* leaves an attractive smelling plant infested by non-host caterpillars already after a brief inspection when host-related cues such as host-frass are missing (Bukovinszky et al., 2012). Non-host encounters on the contrary do not induce patch-leaving behaviour, probably because hosts and non-hosts often co-occur on the same plant (Bukovinszky et al., 2012; Vosteen et al., 2020). Hyperparasitoids use differences in the HIPV blends induced by parasitized and non-parasitized caterpillars (Cusumano et al., 2019; Poelman et al., 2012). Once landed on a plant, they confirm their foraging decision by detecting contact chemicals associated with silk, frass and walking traces left by the parasitized herbivores (AC personal observation). Although less well investigated, pollinators also employ hierarchical cue use during foraging. After choosing a plant, bumblebee and honeybees assess flowers for characteristics like damage (Goulson et al., 2007) and reward status using odour and/or visual cues of nectar and pollen (Dobson & Bergström, 2000; Lunau, 2000). Interestingly, bees can skip this step by learning reliable cues: particular odour or colour cues associated with high reward levels (Knauer & Schiestl, 2015; Wright & Schiestl, 2009). In this way, two foraging steps ('selecting a plant' and 'assessing reward levels') are integrated as one, which could increase foraging efficiency (Amaya-Márquez et al., 2008; Gegear & Lavery, 2005; Grüter & Ratnieks, 2011; Spiesman et al., 2017). It is very likely that just as for herbivores and carnivores, hierarchical cue use is widespread among pollinators for several reasons: (1) most flowers share common flower volatile compounds that could be used as general volatile cues (Knudsen et al., 2006; Silva & Clarke, 2020), (2) most pollinators use both visual and odour cues, but these cues are perceived at different distances from the plant/flower (Hempel de Ibarra et al., 2014; Riffell et al., 2014), (3) pollinators choose among plants and subsequently among individual flowers which differ in cue provision/intensity due to, among others, size differences.

For example, honeybees can use leaf volatiles to find suitable host plants and switch to floral volatiles to find suitable flowers (Beker et al., 1989). Hence, it is very likely that hierarchical cue use is widespread across functional groups. However, this has not received much attention so far for pollinators and higher-order carnivores such as hyperparasitoids.

6 | LEARNING RESULTS IN BROADENING OR FINE-TUNING OF SEARCH TEMPLATES

During foraging, insects acquire information about the environment, and we argue that they use this information to adapt their search template to the current environmental conditions (Figure 2). Positive experience with a resource can result in a general sensitization towards resource-related cues (Reinhard et al., 2010; Vosteen et al., 2019; Wright et al., 2008) or in associative learning of those cues experienced prior or during this resource experience (Haverkamp & Smid, 2020; Jones & Agrawal, 2017). Associative learning can lead to fine-tuning of the search template by temporary specialization on the experienced cues. For hierarchical search templates, learning can shift

the innate preference hierarchy of different resource-related cues (Geervliet et al., 1998) or omit whole steps and their related cues (Dobson, 1987; Dobson & Bergström, 2000; Nicholls & Hempel de Ibarra, 2017). For example, learning of reliable cues by bumblebees leads to temporary specialization on one or few cues that correlate with flower reward levels and merges two foraging steps: host plant recognition and floral reward assessment (Knauer & Schiestl, 2015; Wright & Schiestl, 2009). Learning can also change the importance of different cues in the multimodal search image (Dobson, 1987; Dötterl et al., 2011). Positive experience can reinforce the reliability of certain cues which subsequently move up in the cue ranking. Such alteration of reliable cue ranking has consequences for which modality information is favoured over others. In contrast to fine-tuning, associative learning can also result in broadening of the search template if novel cues are incorporated into the search template after a positive experience (Chittka & Raine, 2006; Wright & Schiestl, 2009). For example, experienced individuals of some species of oligolectic solitary bees use more volatile compounds to find flowers of the same plant species compared with naive individuals (Burger et al., 2012; Milet-Pinheiro et al., 2013). A potential explanation why experience broadens the search template could be that these learned compounds provide

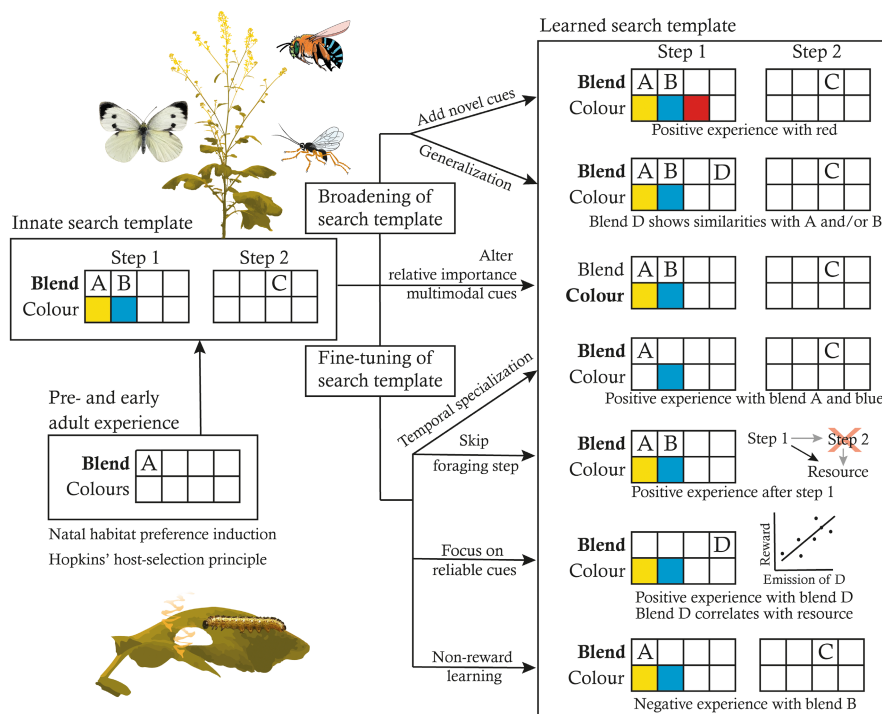


FIGURE 2 Different mechanisms by which learning can alter the search template of foraging insects. For simplicity, we only depict two trait modalities and two foraging steps. The modality in bold is preferred over the non-bold modality. The hypothetical innate search template consists of two foraging steps, after which the resource is successfully located. In Step 1, blend A and/or B are used in combination with yellow and/or blue colour. In Step 2, blend C is used. Experience can broaden or fine-tune the innate search template. Broadening happens by adding novel cues while retaining the innate cues or generalize the innate cues so novel cues that resemble the innate cues are also incorporated into the template. Fine-tuning happens by specializing on particular cues (innate or new), omitting one of the foraging steps, or a combination of both (reliable cues). Dropping a cue due to a negative experience also result in fine-tuning. In addition, experience can alter the relative importance of cues or cue modalities during foraging. The innate search template is shaped partly by pre- and early adult experience. Illustration credits: Yavanna Aartsma, Jitte Groothuis, Dani Lucas-Barbosa, Daan Mertens, Paula Peeters—Pollinator Link, Quint Rusman.

additional information for example about the reward level of the respective flower. Thus, associative learning can result in fine-tuning or broadening of the search template.

Associative learning through experience has been studied intensively across insects from different trophic levels, showing that insects have evolved a tailor-made memory to optimally deal with the specific ecologies of their foraging environments (Jones & Agrawal, 2017; Smid & Vet, 2016). Learning to select a balanced diet over an unbalanced one, for example increased the growth rate of grasshoppers in a predictable environment compared with grasshoppers in a non-predictable environment, demonstrating the adaptive value of learning reliable cues (Dukas & Bernays, 2000). The ability to learn is found in a large number of insect species (Dukas, 2008; Smid & Vet, 2016), even though learning is expected to be only adaptive in environments with a high between-generations predictability and a low within-generation predictability (Stephens, 1991, 1993). It has been suggested that ability to learn is an emergent property of all nervous systems and that learning would be absent only in cases when it is clearly maladaptive (Hollis & Guillette, 2015). Selection against learning may occur when foraging insects experience strong limitations on egg laying rate or total reproductive output, or high mortality rates (Dukas & Duan, 2000). It is important to keep in mind that the benefit of learning can depend on the foraging situation. For example, if the learned behaviour does not match the current environmental conditions, learning can result in decreased foraging efficiency (de Bruijn et al., 2018; de Bruijn, Vosteen, et al., 2021; Internicola et al., 2009). In a study by de Bruijn et al. (2018), the parasitoid wasp *C. glomerata* was allowed to forage in either a 'congruent' environment (i.e. a patch with hosts on the conditioned plant species and non-hosts on the unconditioned plant species) and a 'conflicting' environment (i.e. a patch with non-hosts on the conditioned plant species and hosts on the non-conditioned plant species). It was found that wasps foraged less efficiently when released in a conflicting environment compared with unconditioned individuals and wasps that were released in a congruent environment (de Bruijn et al., 2018). Similar adverse effects of learning were found in bumblebees (Internicola et al., 2009). Therefore, in dynamic environments we expect learning to be a continuous process during the lifetime of an organism and search templates proficiently flexible. Honeybees and bumblebees encounter different resource plants over the growing season. To increase foraging efficiency, these bees temporarily specialize on one of these plants. To keep their search templates matched with the dynamic foraging environment, they often visit alternative plants (Chittka et al., 1997; Grüter et al., 2011; Grüter & Ratnieks, 2011). Alternative plants are chosen by generalization of the learned search template (Bhagavan & Smith, 1997; Gumbert, 2000; Internicola et al., 2009; Lichtenberg et al., 2020), or by using the innate search template (Gumbert, 2000; Lichtenberg et al., 2020). Indeed, learning can further alter responses to unconditioned stimuli (Lichtenberg et al., 2020; Sobhy et al., 2019; Takemoto, 2016; Takemoto & Yoshimura, 2020). This may be the result of sensitization towards general resource-associated cues or of stimulus

generalization (Bhagavan & Smith, 1997; Ghirlanda & Enquist, 2003; Gumbert, 2000; Internicola et al., 2009). Generalization of learned olfactory stimuli can occur at compound level, that is compounds that are structurally similar to the conditioned compound are also perceived as attractive (Meiners et al., 2002), or at blend level, that is compounds from a conditioned blend are also attractive when perceived alone or as part of a different blend (Meiners et al., 2002; Milet-Pinheiro et al., 2013; Reinhard et al., 2010; Sobhy et al., 2019), or in 'incorrect' ratios (Wright et al., 2008).

The association of stimuli with the absence of rewards (non-reward learning) (Kandori & Yamaki, 2012; Papini, 2003) may further help foraging insects in fine-tuning their search template. Memory extinction and habituation are important mechanisms to update search templates in a changing environment (Haverkamp & Smid, 2020). Several studies document fading of positive-conditioned responses after repeated non-rewarding experiences with the previously conditioned stimulus, indicating the formation of extinction memory that suppresses the expression of conditioned behaviour (Chittka, 1998; de Bruijn, Vet, et al., 2021; Eisenhardt, 2014; Iizuka & Takasu, 1998; Papaj et al., 1994; Takasu & Lewis, 2003). Interestingly, memory suppression can be short, after which the conditioned response recovers (de Bruijn, Vet, et al., 2021; Papaj et al., 1994). This likely has to do with the optimization of learning during hierarchical cue use: short-term suppression of the conditioned response could be adaptive if certain foraging steps are temporarily less reliable than others and the current lack of resource does not predict future opportunities (de Bruijn, Vet, et al., 2021; Papaj et al., 1994). Changes in innate preferences after non-reward learning have been found in pollinators and a predatory bug (Ardanuy et al., 2016; Jones & Agrawal, 2017; Kandori & Yamaki, 2012), but not in parasitoids (Costa et al., 2010; Desurmont et al., 2018; Wardle & Borden, 1989). Repeated encounters with resource-related cues in the absence of the resource can result in habituation as it was shown for stink bug parasitoids that spend less time on examining stink bug footprints after repeated encounters of these footprints in the absence of hosts (Abram et al., 2017). Similarly, previous experience with attractive non-resources can decrease the time insects spend on examining the same type of non-resources in subsequent encounters, as it was shown for aphids (Mathews, 2018), pollinators (Townsend-Mehler & Dyer, 2012) and parasitoids, and can result in increased foraging efficiency in simple environments (Vosteen et al., 2019). This reduction in time spent on examining non-resources might be the result of habituation or increased discrimination abilities. Interestingly, oviposition in non-host caterpillars had the opposite effect and increased the motivation of the parasitoid *C. glomerata* to forage on a non-host-infested leaf but did not result in associative learning of the presented odour (de Bruijn et al., 2022; Vosteen et al., 2019).

Taken together, learning (positive, aversion, non-reward and generalization) in insects from functional groups across trophic levels keep the search template constantly adapted to dynamic foraging environments.

6.1 | Natal habitat preference induction might contribute to the adult search template

There is evidence that stimuli from the larval environment may be incorporated into the search template of adult insects. Considering all functional groups, a broad definition of this phenomenon is called natal habitat preference induction (NHPI) (Davis & Stamps, 2004). For herbivorous insects, the same principle has been termed Hopkins' host-selection principle (HHSP) (Barron, 2001; Jones & Agrawal, 2017). If polyphagous herbivores developed on high-quality food (host plant or artificial diet), they may show as adults a strong preference for volatile cues presented together with this food source. If they developed on poor quality food, they may either avoid the respective volatile cues as adults or show no change in preference (Anderson & Anton, 2014; Lhomme et al., 2018; Webster et al., 2013). A number of studies finding no evidence for the HHSP triggered an extensive debate on the generality of the hypothesis for herbivores (Barron, 2001; Janz et al., 2009). Despite this, we may expect NHPI to occur in insects from other functional groups that are in direct contact with the plant such as ectoparasitoids, predators and two groups of pollinators: those with larvae that develop on the plant such as butterflies, moths and hoverflies, and those that use plant material in the construction of their brood cells such as leafcutter bees (Brunet & Syed, 2017; Kantsa et al., 2019) and stingless bees (Leonhardt, 2017; Leonhardt et al., 2011). Indeed, Lepidoptera often flower forage on their larval host plants (Altermatt & Pearse, 2011), and hawkmoths have been shown to use leaf volatiles during flower foraging (Kárpáti et al., 2013). On the contrary, larvae of many (bee) pollinators and endoparasitoids are not in direct contact with the plant and plant-emitted volatiles. Still preferences of adults for the plant species on which it developed are found (Dobson, 1987; Dobson et al., 2012; Fors et al., 2018; Sheehan & Shelton, 1989). For bee pollinators, this is likely due to volatiles emitted by the food stored in the natal cell (Linsley, 1978) or the colony (Ramírez et al., 2016). Nectar and pollen often emit volatiles which are plant species specific (Dobson & Bergström, 2000). Exposure of larvae, preimaginal stages or adults upon emergence of these volatiles could lead to olfactory learning (Dobson et al., 2012). For parasitoids, this preference is only expressed if adults had contact with their cocoons or mummies while they emerged. It is assumed that traces of herbivore-induced plant volatiles which are adsorbed by the cocoons or mummies are learned during adult emergence in a process referred to as 'emergence conditioning' or 'early adult learning' (Emden et al., 2008; Giunti et al., 2016; Storeck et al., 2000; Turlings et al., 1993). Interestingly, learning of volatile cues can also occur in the last larval instar of the aphid parasitoid *Aphidius ervi* and persists through metamorphosis (Gutiérrez-Ibáñez et al., 2007). Thus, NHPI potentially occurs across functional groups.

We expect NHPI to be more important for generalist insects than specialists. For generalist insects, NHPI can be a reliable cue indicating the species/types of locally abundant resources.

A second factor that may influence if NHPI provides a fitness benefit to the insect is the similarity between the environments in which the larvae developed and in which the adults are foraging. Species that hibernate may search for oviposition sites in an entirely different environment than the one in which the larvae developed and NHPI would provide no benefit (Janz et al., 2009). NHPI may be most suited to cope with differences in the seasonal availability of resources if subsequent generations are more likely to encounter the same resources compared with generations developing early and late in the season (Anderson & Anton, 2014). If the short phenology of their resources forces insects to switch resource with every generation, as it is the case for *Pieris brassicae*, a preference for the natal habitat would be maladaptive. Females of this butterfly species indeed avoid ovipositing on their natal plant species when given a choice, while no effect of rearing history was found in its parasitoid *C. glomerata* (Fei et al., 2016). Similarly, the innate search template of *Andrena bicolor*, a bivoltine species which generations forage on different host plants, did not differ between generations (Milet-Pinheiro et al., 2016). The innate search template of this species is broad enough to include all host plants, while generations clearly differ in host plant use. Specialist foragers are expected to make less use of NHPI because important host-related cues should be present in the innate search template. However, it might help them to optimize their search template with respect to intraspecific variation in host-related volatile emission, which is common across plant and insect hosts (Delle-Vedove et al., 2017; Groot et al., 2009; Hare, 2011). Taken together, given the right conditions, that is predictability of the oviposition environment from the (quality of the) larval environment, preimaginal conditioning contributes to search templates across trophic levels even before the adults start to forage.

To the best of our knowledge, we are not aware of any studies that investigated the effects of learning of volatile cues in higher-order carnivores such as hyperparasitoids. Nonetheless, it is likely that negative and positive rewarding experiences affect the subsequent foraging decisions of these top carnivores in response to volatile cues. Primary and secondary hyperparasitoids such as *Baryscapus galactopus* and *Lysibia nana* have longer lifespan compared with their parasitoid host *C. glomerata* (Harvey & Witjes, 2005; Lee & Heimpel, 2008) (A. Cusumano, personal observation), so there is a larger time window for potential learning opportunities to occur. On the contrary, the importance of learning will depend on host encounter rate which may be low in the field given the foraging constraints typical of fourth-trophic-level organisms (Cusumano et al., 2020).

7 | CONCLUSIONS

Search-template-based foraging is a widely shared feature among functional groups across trophic levels of plant-associated insects. To identify resources among non-resources and to cope with cue variability, search templates consist of multiple cues and foragers use stimulus generalization. To avoid and reduce perception errors,

insects employ multimodal and/or hierarchical search templates. These complex search templates are plastic, and constantly expanded or simplified by learning to match the ever-changing foraging environment.

The ideal foraging strategy in complex dynamic environments for plant-associated insects would favour employing combined hierarchical and multimodal plastic search templates for all functional groups across trophic levels. Unfortunately, information on cue use and foraging strategies is highly asymmetric among functional groups. For herbivores and predators, most information on foraging shows the use of volatiles and hierarchical-foraging strategies, while it is well established that pollinators use both visual and odour cues integrated into multimodal strategies. It is very likely however that predators, parasitoids and higher-order carnivores such as hyperparasitoids also employ multimodal strategies (Aartsma et al., 2019). Unfortunately, little is known about the use of visual cues for these insects. Similar, most pollinators likely employ hierarchical foraging (Dobson & Bergström, 2000; Lunau, 2000), but knowledge is limited. For hyperparasitoids, we have very limited information on foraging behaviour overall as the ecology of such top carnivores is often overlooked despite being common components of plant-based food webs (Poelman et al., 2022). We suggest closing these knowledge gaps by studying multimodal foraging in herbivores and predators, hierarchical foraging in pollinators, and both strategies in hyperparasitoids. By consulting the literature of different functional groups of plant-associated insects, such study can advance rapidly through borrowing, testing and adjusting already formulated hypotheses and theories. For example, the functional hypotheses developed to explain multimodal cue use in pollinators (Leonard et al., 2012; Leonard & Masek, 2014) very likely apply for herbivores as well (Aartsma et al., 2019). Comparing search templates across functional groups will give new insights into the evolution of foraging behaviour across complex ecological communities. Moreover, it will help to predict the ecological consequences of human-made habitat alterations such as habitat destruction, fragmentation and climate change. Can foraging, and thereby the links between species in complex ecological communities, be maintained under strong, large-scale alterations of the environment? Information on foraging strategies employed by plant-associated insects can also be applied to optimize cropping systems. With knowledge of foraging strategies employed by functional groups across trophic levels of plant-associated insects, insect-delivered ecosystem services such as pollination and biological pest control can be optimized in cropping systems (Thomas et al., 2023).

AUTHOR CONTRIBUTIONS

All authors contributed substantially to the idea, writing and revision of the final version of the manuscript.

ACKNOWLEDGEMENTS

We thank Erik Poelman for fruitful discussions and Liza Holeski for valuable feedback on an earlier version of the manuscript. Open access funding provided by Universitat Zurich.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data were used or produced for this study.

GLOSSARY

Stimuli: Any change in the external or internal environment of an organism that provokes a physiological or behavioural response in the organism.

Cue: Stimulus that provides information to a forager but has not evolved for the benefit of the sender (Schiestl 2017). We also use this term when an explicit benefit for the sender has not been shown, is irrelevant, or when discussing foragers that include both mutualists (pollinators, natural enemies) and antagonists (herbivores); stimuli used by antagonists usually do not provide a benefit to the sender.

Signal: Stimulus that provides information to a forager that has evolved for the benefit of the sender or both the sender and receiver (Schiestl 2017).

Host: The organism from which a forager obtains its nutrition or shelter. We use forager instead of parasite used in more classic definitions (Levin et al. 2009) to include plants used by pollinators.

Search template: A subset of stimuli used by foragers that is likely correlated with the incidence of a particular resource (Aartsma et al. 2019). The width of the search template is determined by the number of components included: narrow search templates contain relatively few components, while broad search templates contain relatively many components. Search templates can be too unspecific (non-resources are perceived as resources) or too specific (resources perceived as non-resources).

Perception error: Forager perceives resources as non-resources, or non-resources as resources.

Confusion: Forager perceives non-resources as resources as a result of a too unspecific search template. This can result in 1) the attempted utilization of a non-resource, 2) a reduction in foraging efficiency on a resource due to the presence of a non-resource without actual attempts to utilize the non-resource.

Cue modalities: Different types of cues classically grouped into olfactory, visual, tactile, auditory, and gustatory cues. More recently, temperature, humidity, and electric field have been added (Clarke et al. 2017).

Multimodal cue use/integration: Processes by which information arriving from individual sensory modalities interact and influence processing of other sensory modalities, including how these sensory inputs are combined together to yield a unified perceptual experience of multisensory events (Talsma et al. 2010).

Hierarchical cue use: Foragers follow several ordered foraging steps and use cues from the same or different cue modalities or their multimodal combination to confirm their decisions at each foraging step. Note that the foraging steps are not fixed but vary depending on forager genetic makeup and experience as well as environmental conditions (Vinson 1998).

Qualitative volatile blend characteristics: Characteristics of a volatile blend related to the identity and presence/absence of specific compounds.

Quantitative volatile blend characteristics: Characteristics of a volatile blend related to the amounts and relative abundances of compounds.

Oligolectic: Bees regarded as pollen specialists that collect pollen from plants of a single family, genus or species.

Polylectic: Bees regarded as pollen generalists that collect pollen from plants of multiple families.

Learning: Adaptive change in individual behaviour as the result of experience (Thorpe 1956).

Habituation: Decreasing response to a stimulus after repeated exposure.

Reliable cue: Cue associated with an item of interest such as resource quantity and/or quality, that provide reliable information to the receiver.

Natal habitat preference induction: Experience of the natal habitat shapes the habitat/resource preferences of individuals (Davis & Stamps 2004).

ORCID

Q. Rusman  <https://orcid.org/0000-0003-0285-7967>

A. Cusumano  <https://orcid.org/0000-0001-9663-9164>

I. Vosteen  <https://orcid.org/0000-0001-8825-2170>

REFERENCES

- Aartsma, Y., Bianchi, F. J. J. A., van der Werf, W., Poelman, E. H., & Dicke, M. (2017). Herbivore-induced plant volatiles and tritrophic interactions across spatial scales. *New Phytologist*, 216, 1054–1063.
- Aartsma, Y., Cusumano, A., Fernández de Bobadilla, M., Rusman, Q., Vosteen, I., & Poelman, E. H. (2019). Understanding insect foraging in complex habitats by comparing trophic levels: Insights from specialist host-parasitoid-hyperparasitoid systems. *Current Opinion in Insect Science*, 32, 54–60.
- Abram, P. K., Cusumano, A., Abram, K., Colazza, S., & Peri, E. (2017). Testing the habituation assumption underlying models of parasitoid foraging behavior. *PeerJ*, 5, e3097.
- Altermatt, F., & Pearce, I. S. (2011). Similarity and specialization of the larval versus adult diet of European butterflies and moths. *The American Naturalist*, 178, 372–382.
- Aluja, M., & Prokopy, R. J. (1993). Host odor and visual stimulus interaction during intratree host finding behavior of *Rhagoletis pomonella* flies. *Journal of Chemical Ecology*, 19, 2671–2696.
- Amaya-Márquez, M., Hill, P. S. M., Barthell, J. F., Pham, L. L., Doty, D. R., & Wells, H. (2008). Learning and memory during foraging of the blue orchard bee, *Osmia lignaria* Say (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society*, 81, 315–327.
- Anderson, B., Johnson, S. D., & Carbutt, C. (2005). Exploitation of a specialized mutualism by a deceptive orchid. *American Journal of Botany*, 92, 1342–1349.
- Anderson, P., & Anton, S. (2014). Experience-based modulation of behavioural responses to plant volatiles and other sensory cues in insect herbivores. *Plant, Cell & Environment*, 37, 1826–1835.
- Arduany, A., Albajes, R., & Turlings, T. C. J. (2016). Innate and learned prey-searching behavior in a generalist predator. *Journal of Chemical Ecology*, 42, 497–507.
- Badenes-Perez, F. R., Reichelt, M., Gershenson, J., & Heckel, D. G. (2014). Using plant chemistry and insect preference to study the potential of *Barbarea* (Brassicaceae) as a dead-end trap crop for diamondback moth (Lepidoptera: Plutellidae). *Phytochemistry*, 98, 137–144.
- Barron, A. B. (2001). The life and death of Hopkins' host-selection principle. *Journal of Insect Behavior*, 14, 725–737.
- Beker, R., Dafni, A., Eisikowitch, D., & Ravid, U. (1989). Volatiles of two chemotypes of *Majorana syriaca* L. (Labiatae) as olfactory cues for the honeybee. *Oecologia*, 79, 446–451.
- Bhagavan, S., & Smith, B. H. (1997). Olfactory conditioning in the honey bee, *Apis mellifera*: Effects of odor intensity. *Physiology & Behavior*, 61, 107–117.
- Blande, J. D., Holopainen, J. K., & Niinemets, Ü. (2014). Plant volatiles in polluted atmospheres: Stress responses and signal degradation. *Plant, Cell & Environment*, 37, 1892–1904.
- Boullis, A., Francis, F., & Verheggen, F. J. (2015). Climate change and tritrophic interactions: Will modifications to greenhouse gas emissions increase the vulnerability of herbivorous insects to natural enemies? *Environmental Entomology*, 44, 277–286.
- Brandt, K., Dötterl, S., Francke, W., Ayasse, M., & Milet-Pinheiro, P. (2017). Flower visitors of *Campanula*: Are oligoleges more sensitive to host-specific floral scents than polyleges? *Journal of Chemical Ecology*, 43, 4–12.
- Bruce, T. J. A. (2014). Glucosinolates in oilseed rape: Secondary metabolites that influence interactions with herbivores and their natural enemies. *Annals of Applied Biology*, 164, 348–353.
- Bruce, T. J. A., & Pickett, J. A. (2011). Perception of plant volatile blends by herbivorous insects—Finding the right mix. *Phytochemistry*, 72, 1605–1611.
- Bruce, T. J. A., Wadhams, L. J., & Woodcock, C. M. (2005). Insect host location: A volatile situation. *Trends in Plant Science*, 10, 269–274.
- Brunet, J., & Syed, Z. (2017). Enhancing pollination by attracting & retaining leaf cutting bees (*Megachile rotundata*) in alfalfa seed production fields. In *WASGA winter seed conference* (pp. 67–73). Western Alfalfa Seed Growers Association.
- Bukovinsky, T., Poelman, E. H., Kamp, A., Hemerik, L., Prekatsakis, G., & Dicke, M. (2012). Plants under multiple herbivory: Consequences for parasitoid search behaviour and foraging efficiency. *Animal Behaviour*, 83, 501–509.
- Burger, H., Dötterl, S., & Ayasse, M. (2010). Host-plant finding and recognition by visual and olfactory floral cues in an oligolectic bee. *Functional Ecology*, 24, 1234–1240.
- Burger, H., Dötterl, S., Häberlein, C. M., Schulz, S., & Ayasse, M. (2012). An arthropod deterrent attracts specialised bees to their host plants. *Oecologia*, 168, 727–736.
- Cai, X., Guo, Y., Bian, L., Luo, Z., Li, Z., Xiu, C., Fu, N., & Chen, Z. (2022). Variation in the ratio of compounds in a plant volatile blend during transmission by wind. *Scientific Reports*, 12, 6176.
- Caillaud, M. C., & Via, S. (2000). Specialized feeding behavior influences both ecological specialization and assortative mating in sympatric host races of pea aphids. *The American Naturalist*, 156, 606–621.
- Campbell, S. A., & Borden, J. H. (2006a). Close-range, in-flight integration of olfactory and visual information by a host-seeking bark beetle. *Entomologia Experimentalis et Applicata*, 120, 91–98.
- Campbell, S. A., & Borden, J. H. (2006b). Integration of visual and olfactory cues of hosts and non-hosts by three bark beetles (Coleoptera: Scolytidae). *Ecological Entomology*, 31, 437–449.
- Campbell, S. A., & Borden, J. H. (2009). Additive and synergistic integration of multimodal cues of both hosts and non-hosts during host selection by woodboring insects. *Oikos*, 118, 553–563.
- Carrasco, D., Larsson, M. C., & Anderson, P. (2015). Insect host plant selection in complex environments. *Current Opinion in Insect Science*, 8, 1–7.
- Chan, J. K., Parasurama, S., Atlas, R., Xu, R., Jongebloed, U. A., Alexander, B., Langenhan, J. M., Thornton, J. A., & Riffell, J. A. (2024). Olfaction in the Anthropocene: NO₃ negatively affects floral scent and nocturnal pollination. *Science*, 383, 607–611.

- Chittka, L. (1998). Sensorimotor learning in bumblebees: Long-term retention and reversal training. *Journal of Experimental Biology*, *201*, 515–524.
- Chittka, L., Gumbert, A., & Kunze, J. (1997). Foraging dynamics of bumble bees: Correlates of movements within and between plant species. *Behavioral Ecology*, *8*, 239–249.
- Chittka, L., & Raine, N. E. (2006). Recognition of flowers by pollinators. *Current Opinion in Plant Biology*, *9*, 428–435.
- Clarke, D., Morley, E., & Robert, D. (2017). The bee, the flower, and the electric field: Electric ecology and aerial electroreception. *Journal of Comparative Physiology A*, *203*, 737–748.
- Clifford, M. R., & Riffell, J. A. (2013). Mixture and odorant processing in the olfactory systems of insects: A comparative perspective. *Journal of Comparative Physiology A*, *199*, 911–928.
- Conchou, L., Lucas, P., Meslin, C., Proffit, M., Staudt, M., & Renou, M. (2019). Insect odorscapes: From plant volatiles to natural olfactory scenes. *Frontiers in Physiology*, *10*, 1–20.
- Cook, B., Haverkamp, A., Hansson, B. S., Roulston, T. A., Lerdau, M., & Knaden, M. (2020). Pollination in the anthropocene: A moth can learn ozone-altered floral blends. *Journal of Chemical Ecology*, *46*, 987–996.
- Cook, S. M., Khan, Z. R., & Pickett, J. A. (2007). The use of push-pull strategies in integrated pest management. *Annual Review of Entomology*, *52*, 375–400.
- Costa, A., Ricard, I., Davison, A. C., & Turlings, T. C. (2010). Effects of rewarding and unrewarding experiences on the response to host-induced plant odors of the generalist parasitoid *Cotesia marginiventris* (Hymenoptera: Braconidae). *Journal of Insect Behavior*, *23*, 303–318.
- Croijmans, L., Valstar, R. T., Schuur, L., Jacobs, I., van Apeldoorn, D. F., & Poelman, E. H. (2022). Intraspecific plant variation and non-host herbivores affect parasitoid host location behaviour. *Animal Behaviour*, *194*, 169–184.
- Cunningham, J. P. (2012). Can mechanism help explain insect host choice? *Journal of Evolutionary Biology*, *25*, 244–251.
- Cusumano, A., Harvey, J. A., Bourne, M. E., Poelman, E. H., & de Boer, J. G. (2020). Exploiting chemical ecology to manage hyperparasitoids in biological control of arthropod pests. *Pest Management Science*, *76*, 432–443.
- Cusumano, A., Harvey, J. A., Dicke, M., & Poelman, E. H. (2019). Hyperparasitoids exploit herbivore-induced plant volatiles during host location to assess host quality and non-host identity. *Oecologia*, *189*, 699–709.
- Danner, H., Desurmont, G. A., Cristescu, S. M., & van Dam, N. M. (2018). Herbivore-induced plant volatiles accurately predict history of coexistence, diet breadth, and feeding mode of herbivores. *New Phytologist*, *220*, 726–738.
- Davis, J. M., & Stamps, J. A. (2004). The effect of natal experience on habitat preferences. *Trends in Ecology & Evolution*, *19*, 411–416.
- de Bruijn, J. A. C., Vet, L. E. M., & Smid, H. M. (2018). Costs of persisting unreliable memory: Reduced foraging efficiency for free-flying parasitic wasps in a wind tunnel. *Frontiers in Ecology and Evolution*, *6*. <https://doi.org/10.3389/fevo.2018.00160>
- de Bruijn, J. A. C., Vet, L. E. M., Smid, H. M., & de Boer, J. G. (2021). Memory extinction and spontaneous recovery shaping parasitoid foraging behavior. *Behavioral Ecology*, *32*, 952–960.
- de Bruijn, J. A. C., Vet, L. E. M., Smid, H. M., & de Boer, J. G. (2022). Effects of oviposition in a non-host species on foraging behaviour of the parasitoid *Cotesia glomerata*. *Ecological Entomology*, *47*, 668–678.
- de Bruijn, J. A. C., Vosteen, I., Vet, L. E. M., Smid, H. M., & de Boer, J. G. (2021). Multi-camera field monitoring reveals costs of learning for parasitoid foraging behaviour. *Journal of Animal Ecology*, *90*, 1635–1646.
- de Rijk, M., Dicke, M., & Poelman, E. H. (2013). Foraging behaviour by parasitoids in multiherbivore communities. *Animal Behaviour*, *85*, 1517–1528.
- de Rijk, M., Yang, D., Engel, B., Dicke, M., & Poelman, E. H. (2016). Feeding guild of non-host community members affects host-foraging efficiency of a parasitic wasp. *Ecology*, *97*, 1388–1399.
- Degen, T., Dillmann, C., Marion-Poll, F., & Turlings, T. C. J. (2004). High genetic variability of herbivore-induced volatile emission within a broad range of maize inbred lines. *Plant Physiology*, *135*, 1928–1938.
- Dekker, T., Ibbá, I., Siju, K. P., Stensmyr, M. C., & Hansson, B. S. (2006). Olfactory shifts parallel superspecialism for toxic fruit in *Drosophila melanogaster* sibling, *D. sechellia*. *Current Biology*, *16*, 101–109.
- Delle-Vedove, R., Schatz, B., & Dufay, M. (2017). Understanding intra-specific variation of floral scent in light of evolutionary ecology. *Annals of Botany*, *120*, 1–20.
- Desurmont, G. A., Guiguet, A., & Turlings, T. C. J. (2018). Invasive insect herbivores as disrupters of chemically-mediated tritrophic interactions: Effects of herbivore density and parasitoid learning. *Biological Invasions*, *20*, 195–206.
- Desurmont, G. A., Laplanche, D., Schiestl, F. P., & Turlings, T. C. J. (2015). Floral volatiles interfere with plant attraction of parasitoids: Ontogeny-dependent infochemical dynamics in *Brassica rapa*. *BMC Ecology*, *15*, 17.
- Démare, F., Gibert, L., Creusot, P., Lapeyre, B., & Proffit, M. (2022). Acute ozone exposure impairs detection of floral odor, learning, and memory of honey bees, through olfactory generalization. *Science of the Total Environment*, *827*, 154342.
- Dicke, M., & Hilker, M. (2003). Induced plant defences: From molecular biology to evolutionary ecology. *Basic and Applied Ecology*, *4*, 3–14.
- Dobson, H. E. M. (1987). Role of flower and pollen aromas in host-plant recognition by solitary bees. *Oecologia*, *72*, 618–623.
- Dobson, H. E. M., Ayasse, M., O'Neal, K. A., & Jacka, J. A. (2012). Is flower selection influenced by chemical imprinting to larval food provisions in the generalist bee *Osmia bicornis* (Megachilidae)? *Apidologie*, *43*, 698–714.
- Dobson, H. E. M., & Bergström, G. (2000). The ecology and evolution of pollen odors. *Plant Systematics and Evolution*, *222*, 63–87.
- Dodson, C. H., Dressler, R. L., Hills, H. G., Adams, R. M., & Williams, N. H. (1969). Biologically active compounds in orchid fragrances. *Science*, *164*, 1243–1249.
- Dötterl, S., Milchreit, K., & Schäffler, I. (2011). Behavioural plasticity and sex differences in host finding of a specialized bee species. *Journal of Comparative Physiology A*, *197*, 1119–1126.
- Dukas, R. (2008). Evolutionary biology of insect learning. *Annual Review of Entomology*, *53*, 145–160.
- Dukas, R., & Bernays, E. A. (2000). Learning improves growth rate in grasshoppers. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 2637–2640.
- Dukas, R., & Duan, J. J. (2000). Potential fitness consequences of associative learning in a parasitoid wasp. *Behavioral Ecology*, *11*, 536–543.
- Duque, L., Poelman, E. H., & Steffan-Dewenter, I. (2019). Plant-mediated effects of ozone on herbivores depend on exposure duration and temperature. *Scientific Reports*, *9*, 19891.
- Dweck, H. K. M., Ebrahim, S. A. M., Kromann, S., Bown, D., Hillbur, Y., Sachse, S., Hansson, B. S., & Stensmyr, M. C. (2013). Olfactory preference for egg laying on citrus substrates in *Drosophila*. *Current Biology*, *23*, 2472–2480.
- Eisenhardt, D. (2014). Molecular mechanisms underlying formation of long-term reward memories and extinction memories in the honeybee (*Apis mellifera*). *Learning & Memory*, *21*, 534–542.
- Emden, V. H. F., Storeck, P. A., Doulopak, S., Eleftherianos, I., Poppy, M. G., & Powell, W. (2008). Plant chemistry and aphid parasitoids (Hymenoptera: Braconidae): Imprinting and memory. *European Journal of Entomology*, *105*, 477–483.
- Evans, L. J., & Raine, N. E. (2014). Foraging errors play a role in resource exploration by bumble bees (*Bombus terrestris*). *Journal of Comparative Physiology A*, *200*, 475–484.

- Farina, W. M., Arenas, A., Estravis-Barcala, M. C., & Palottini, F. (2023). Targeted crop pollination by training honey bees: Advances and perspectives. *Frontiers in Bee Science*, 1. <https://doi.org/10.3389/frbee.2023.1253157>
- Farré-Armengol, G., Peñuelas, J., Li, T., Yli-Pirilä, P., Filella, I., Llusia, J., & Blande, J. D. (2016). Ozone degrades floral scent and reduces pollinator attraction to flowers. *New Phytologist*, 209, 152–160.
- Fei, M., Harvey, J. A., Weldegergis, B. T., Huang, T., Reijngoudt, K., Vet, L. M., & Gols, R. (2016). Integrating insect life history and food plant phenology: Flexible maternal choice is adaptive. *International Journal of Molecular Sciences*, 17, 1263.
- Fenske, M., & Imaizumi, T. (2016). Circadian rhythms in floral scent emission. *Frontiers in Plant Science*, 7. <https://doi.org/10.3389/fpls.2016.00462>
- Fors, L., Mozuraitis, R., Blažytė-Čereškienė, L., Verschut, T. A., & Hambäck, P. A. (2018). Selection by parasitoid females among closely related hosts based on volatiles: Identifying relevant chemical cues. *Ecology and Evolution*, 8, 3219–3228.
- Fox, C. W., & Lalonde, R. G. (1993). Host confusion and the evolution of insect diet breadths. *Oikos*, 67, 577–581.
- Fuentes, J. D., Roulston, T. A. H., & Zenker, J. (2013). Ozone impedes the ability of a herbivore to find its host. *Environmental Research Letters*, 8, 014048.
- Geervliet, J. B. F., Vet, L. E. M., & Dicke, M. (1996). Innate responses of the parasitoids *Cotesia glomerata* and *C. rubecula* (Hymenoptera: Braconidae) to volatiles from different plant-herbivore complexes. *Journal of Insect Behavior*, 9, 525–538.
- Geervliet, J. B. F., Vreugdenhil, A. I., Dicke, M., & Vet, L. E. M. (1998). Learning to discriminate between infochemicals from different plant-host complexes by the parasitoids *Cotesia glomerata* and *C. rubecula*. *Entomologia Experimentalis et Applicata*, 86, 241–252.
- Gegear, R. J., & Laverty, T. M. (2005). Flower constancy in bumblebees: A test of the trait variability hypothesis. *Animal Behaviour*, 69, 939–949.
- Ghirlanda, S., & Enquist, M. (2003). A century of generalization. *Animal Behaviour*, 66, 15–36.
- Gigord, L. D. B., Macnair, M. R., & Smithson, A. (2001). Negative frequency-dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid *Dactylorhiza sambucina* (L.) Soð. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 6253–6255.
- Giunti, G., Benelli, G., Messing, R. H., & Canale, A. (2016). Early adult learning affects host preferences in the tephritid parasitoid *Psytalia concolor* (Hymenoptera: Braconidae). *Journal of Pest Science*, 89, 529–537.
- Giurfa, M., & Menzel, R. (2013). Chapter 3—Cognitive components of insect behavior. In R. Menzel & P. R. Benjamin (Eds.), *Handbook of behavioral neuroscience* (pp. 14–25). Elsevier.
- Gols, R., Bullock, J. M., Dicke, M., Bukovinszky, T., & Harvey, J. A. (2011). Smelling the wood from the trees: Non-linear parasitoid responses to volatile attractants produced by wild and cultivated cabbage. *Journal of Chemical Ecology*, 37, 795–807.
- Goulson, D. (2000). Are insects flower constant because they use search images to find flowers? *Oikos*, 88, 547–552.
- Goulson, D., Cruise, J. L., Sparrow, K. R., Harris, A. J., Park, K. J., Tinsley, M. C., & Gilburn, A. S. (2007). Choosing rewarding flowers; perceptual limitations and innate preferences influence decision making in bumblebees and honeybees. *Behavioral Ecology and Sociobiology*, 61, 1523–1529.
- Groot, A. T., Inglis, O., Bowdridge, S., Santangelo, R. G., Blanco, C., López, J. J. D., Vargas, A. T., Gould, F., & Schal, C. (2009). Geographic and temporal variation in moth chemical communication. *Evolution*, 63, 1987–2003.
- Grüter, C., Moore, H., Firmin, N., Helanterä, H., & Ratnieks, F. L. W. (2011). Flower constancy in honey bee workers (*Apis mellifera*) depends on ecologically realistic rewards. *Journal of Experimental Biology*, 214, 1397–1402.
- Grüter, C., & Ratnieks, F. L. W. (2011). Flower constancy in insect pollinators: Adaptive foraging behaviour or cognitive limitation? *Communicative & Integrative Biology*, 4, 633–636.
- Gumbert, A. (2000). Color choices by bumble bees (*Bombus terrestris*): Innate preferences and generalization after learning. *Behavioral Ecology and Sociobiology*, 48, 36–43.
- Gumbert, A., & Kunze, J. (2001). Colour similarity to rewarding model plants affects pollination in a food deceptive orchid, *Orchis boryi*. *Biological Journal of the Linnean Society*, 72, 419–433.
- Gutiérrez-Ibáñez, C., Villagra, C. A., & Niemeier, H. M. (2007). Pre-pupation behaviour of the aphid parasitoid *Aphidius ervi* (Haliday) and its consequences for pre-imaginal learning. *Naturwissenschaften*, 94, 595–600.
- Hansson, B. S., & Stensmyr, M. C. (2011). Evolution of insect olfaction. *Neuron*, 72, 698–711.
- Hare, J. D. (2010). Ontogeny and season constrain the production of herbivore-inducible plant volatiles in the field. *Journal of Chemical Ecology*, 36, 1363–1374.
- Hare, J. D. (2011). Ecological role of volatiles produced by plants in response to damage by herbivorous insects. *Annual Review of Entomology*, 56, 161–180.
- Harvey, J. A., & Witjes, L. M. A. (2005). Comparing and contrasting life history and development strategies in the pupal hyperparasitoids *Lysibia nana* and *Gelis agilis* (Hymenoptera: Ichneumonidae). *Applied Entomology and Zoology*, 40, 309–316.
- Haverkamp, A., Hansson, B. S., & Knaden, M. (2018). Combinatorial codes and labeled lines: How insects use olfactory cues to find and judge food, mates, and oviposition sites in complex environments. *Frontiers in Physiology*, 9, 1–8.
- Haverkamp, A., & Smid, H. M. (2020). A neuronal arms race: The role of learning in parasitoid–host interactions. *Current Opinion in Insect Science*, 42, 47–54.
- Hempel de Ibarra, N., Vorobyev, M., & Menzel, R. (2014). Mechanisms, functions and ecology of colour vision in the honeybee. *Journal of Comparative Physiology A*, 200, 411–433.
- Ho, W. W., & Riffell, J. A. (2016). The olfactory neuroecology of herbivory, hostplant selection and plant–pollinator interactions. *Integrative and Comparative Biology*, 56, 856–864.
- Hollis, K. L., & Guillet, L. M. (2015). What associative learning in insects tells us about the evolution of learned and fixed behavior. *International Journal of Comparative Psychology*, 28. <https://doi.org/10.46867/ijcp.2015.28.01.07>
- Hu, X., Su, S., Liu, Q., Jiao, Y., Peng, Y., Li, Y., & Turlings, T. C. J. (2020). Caterpillar-induced rice volatiles provide enemy-free space for the offspring of the brown planthopper. *eLife*, 9, e55421.
- Huber, F. K., Kaiser, R., Sauter, W., & Schiestl, F. P. (2005). Floral scent emission and pollinator attraction in two species of *Gymnadenia* (Orchidaceae). *Oecologia*, 142, 564–575.
- Iizuka, T., & Takasu, K. (1998). Olfactory associative learning of the pupal parasitoid *Pimpla luctuosa* Smith (Hymenoptera: Ichneumonidae). *Journal of Insect Behavior*, 11, 743–760.
- Internicola, A. I., Page, P. A., Bernasconi, G., & Gigord, L. D. B. (2009). Carry-over effects of bumblebee associative learning in changing plant communities leads to increased costs of foraging. *Arthropod-Plant Interactions*, 3, 17–26.
- Jang, E. B., Messing, R. H., Klungness, L. M., & Carvalho, L. A. (2000). Flight tunnel responses of *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) to olfactory and visual stimuli. *Journal of Insect Behavior*, 13, 525–538.
- Janz, N. (2008). Evolutionary ecology of oviposition strategies. In M. Hilker & T. Meiners (Eds.), *Chemoecology of insect eggs and egg deposition* (pp. 349–376). Blackwell.
- Janz, N., Söderlind, L., & Nylin, S. (2009). No effect of larval experience on adult host preferences in *Polygonia c-album* (Lepidoptera:

- Nymphalidae*): On the persistence of Hopkins' host selection principle. *Ecological Entomology*, 34, 50–57.
- Jardine, K., Abrell, L., Kurc, S. A., Huxman, T., Ortega, J., & Guenther, A. (2010). Volatile organic compound emissions from *Larrea tridentata* (creosotebush). *Atmospheric Chemistry and Physics*, 10, 12191–12206.
- Jersáková, J., Johnson, S. D., & Kindlmann, P. (2006). Mechanisms and evolution of deceptive pollination in orchids. *Biological Reviews*, 81, 219–235.
- Jersáková, J., Jürgens, A., Šmilauer, P., & Johnson, S. D. (2012). The evolution of floral mimicry: Identifying traits that visually attract pollinators. *Functional Ecology*, 26, 1381–1389.
- Johnson, S. D. (2000). Batesian mimicry in the non-rewarding orchid *Disa pulchra*, and its consequences for pollinator behaviour. *Biological Journal of the Linnean Society*, 71, 119–132.
- Jones, P. L., & Agrawal, A. A. (2017). Learning in insect pollinators and herbivores. *Annual Review of Entomology*, 62, 53–71.
- Joseph, R. M., Devineni, A. V., King, I. F. G., & Heberlein, U. (2009). Oviposition preference for and positional avoidance of acetic acid provide a model for competing behavioral drives in *Drosophila*. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 11352–11357.
- Juillet, N., & Scopece, G. (2010). Does floral trait variability enhance reproductive success in deceptive orchids? *Perspectives in Plant Ecology, Evolution and Systematics*, 12, 317–322.
- Junker, R. R., & Parachnowitsch, A. L. (2015). Working towards a holistic view on flower traits—How floral scents mediate plant–animal interactions in concert with other floral characters. *Journal of the Indian Institute of Science*, 95, 43–68.
- Jürgens, A., & Bischoff, M. (2017). Changing odour landscapes: The effect of anthropogenic volatile pollutants on plant–pollinator olfactory communication. *Functional Ecology*, 31, 56–64.
- Kandori, I., & Yamaki, T. (2012). Reward and non-reward learning of flower colours in the butterfly *Byasa alcinous* (Lepidoptera: Papilionidae). *Naturwissenschaften*, 99, 705–713.
- Kantsa, A., Raguso, R. A., Lekkas, T., Kalantzi, O.-I., & Petanidou, T. (2019). Floral volatiles and visitors: A meta-network of associations in a natural community. *Journal of Ecology*, 107, 2574–2586.
- Kanwal, J. K., & Parker, J. (2022). The neural basis of interspecies interactions in insects. *Current Opinion in Insect Science*, 50, 100891.
- Kárpáti, Z., Knaden, M., Reinecke, A., & Hansson, B. S. (2013). Intraspecific combinations of flower and leaf volatiles act together in attracting hawkmoth pollinators. *PLoS One*, 8, e72805.
- Keasar, T., Motro, U., & Shmida, A. (2013). Temporal reward variability promotes sampling of a new flower type by bumblebees. *Animal Behaviour*, 86, 747–753.
- Kessler, A., & Halitschke, R. (2009). Testing the potential for conflicting selection on floral chemical traits by pollinators and herbivores: Predictions and case study. *Functional Ecology*, 23, 901–912.
- Kinoshita, M., Stewart, F. J., & Ômura, H. (2017). Multisensory integration in Lepidoptera: Insights into flower–visitor interactions. *BioEssays*, 39, 1600086.
- Klahre, U., Gurba, A., Hermann, K., Saxenhofer, M., Bossolini, E., Guerin, P. M., & Kuhlemeier, C. (2011). Pollinator choice in *petunia* depends on two major genetic loci for floral scent production. *Current Biology*, 21, 730–739.
- Knauer, A., & Schiestl, F. (2015). Bees use honest floral signals as indicators of reward when visiting flowers. *Ecology Letters*, 18, 135–143.
- Knudsen, J. T., Eriksson, R., Gershenzon, J., & Ståhl, B. (2006). Diversity and distribution of floral scent. *The Botanical Review*, 72, 1–120.
- Kobayashi, K., Arai, M., Tanaka, A., Matsuyama, S., Honda, H., & Ohsawa, R. (2012). Variation in floral scent compounds recognized by honeybees in Brassicaceae crop species. *Breeding Science*, 62, 293–302.
- Kunze, J., & Gumbert, A. (2001). The combined effect of color and odor on flower choice behavior of bumble bees in flower mimicry systems. *Behavioral Ecology*, 12, 447–456.
- Kuppler, J., & Kotowska, M. M. (2021). A meta-analysis of responses in floral traits and flower–visitor interactions to water deficit. *Global Change Biology*, 27, 3095–3108.
- Langford, B., Ryalls, J. M. W., Mullinger, N. J., Hayden, P., Nemitz, E., Pfrang, C., Robins, A., Touham, D., Bromfield, L. M., & Girling, R. D. (2023). Mapping the effects of ozone pollution and mixing on floral odour plumes and their impact on plant–pollinator interactions. *Environmental Pollution*, 336, 122336.
- Larsson, S., & Ekblom, B. (1995). Oviposition mistakes in herbivorous insects: Confusion or a step towards a new host plant? *Oikos*, 72, 155–160.
- Lee, J. C., & Heimpel, G. E. (2008). Effect of floral nectar, water, and feeding frequency on *Cotesia glomerata* longevity. *BioControl*, 53, 289–294.
- Leonard, A. S., Dornhaus, A., & Papaj, D. R. (2012). Why are floral signals complex? An outline of functional hypotheses. In S. Patiny (Ed.), *Evolution of plant–pollinator relationships* (pp. 261–282). Cambridge University Press.
- Leonard, A. S., & Masek, P. (2014). Multisensory integration of colors and scents: Insights from bees and flowers. *Journal of Comparative Physiology A*, 200, 463–474.
- Leonard, R. J., Pettit, T. J., Irga, P., McArthur, C., & Hochuli, D. F. (2019). Acute exposure to urban air pollution impairs olfactory learning and memory in honeybees. *Ecotoxicology*, 28, 1056–1062.
- Leonard, R. J., Vergoz, V., Proschogo, N., McArthur, C., & Hochuli, D. F. (2019). Petrol exhaust pollution impairs honey bee learning and memory. *Oikos*, 128, 264–273.
- Leonhardt, S. D. (2017). Chemical ecology of stingless bees. *Journal of Chemical Ecology*, 43, 385–402.
- Leonhardt, S. D., Baumann, A.-M., Wallace, H. M., Brooks, P., & Schmitt, T. (2014). The chemistry of an unusual seed dispersal mutualism: Bees use a complex set of olfactory cues to find their partner. *Animal Behaviour*, 98, 41–51.
- Leonhardt, S. D., Schmitt, T., & Blüthgen, N. (2011). Tree resin composition, collection behavior and selective filters shape chemical profiles of tropical bees (Apidae: Meliponini). *PLoS One*, 6, e23445.
- Levin, R. A., Raguso, R. A., & McDade, L. A. (2001). Fragrance chemistry and pollinator affinities in Nyctaginaceae. *Phytochemistry*, 58, 429–440.
- Levin, S. A., Carpenter, S. R., Godfray, H. C. J., Kinzig, A. P., Loreau, M., Losos, J. B., Walker, B., & Wilcove, D. S. (2009). *The Princeton guide to ecology*. Princeton University Press.
- Lhomme, P., Carrasco, D., Larsson, M., Hansson, B., & Anderson, P. (2018). A context-dependent induction of natal habitat preference in a generalist herbivorous insect. *Behavioral Ecology*, 29, 360–367.
- Lichtenberg, E. M., Heiling, J. M., Bronstein, J. L., & Barker, J. L. (2020). Noisy communities and signal detection: Why do foragers visit rewardless flowers? *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 375, 20190486.
- Linsley, E. G. (1978). Temporal patterns of flower visitation by solitary bees, with particular reference to the southwestern United States. *Journal of the Kansas Entomological Society*, 51, 531–546.
- Linz, J., Baschwitz, A., Strutz, A., Dweck, H. K. M., Sachse, S., Hansson, B. S., & Stensmyr, M. C. (2013). Host plant-driven sensory specialization in *Drosophila erecta*. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20130626.
- Lunau, K. (2000). The ecology and evolution of visual pollen signals. *Plant Systematics and Evolution*, 222, 89–111.
- Martin, J. P., Beyerlein, A., Dacks, A. M., Reisenman, C. E., Riffell, J. A., Lei, H., & Hildebrand, J. G. (2011). The neurobiology of insect olfaction: Sensory processing in a comparative context. *Progress in Neurobiology*, 95, 427–447.
- Mathews, L. (2018). Learning in herbivorous insects: Dispersing aphids spend less time evaluating familiar than novel non-host plant species. *Oecologia*, 188, 1049–1057.

- McCormick, A. C. (2016). Can plant–natural enemy communication withstand disruption by biotic and abiotic factors? *Ecology and Evolution*, 6, 8569–8582.
- Meiners, T., Wäckers, F., & Lewis, W. J. (2002). The effect of molecular structure on olfactory discrimination by the parasitoid *Microplitis croceipes*. *Chemical Senses*, 27, 811–816.
- Mendel, Z., Zegelman, L., Hassner, A., Assael, F., Harel, M., Tam, S., & Dunkelblum, E. (1995). Outdoor attractancy of males of *Matsucoccus josephi* (Homoptera: Matsucoccidae) and *Elatophilus hebraicus* (Hemiptera: Anthocoridae) to synthetic female sex pheromone of *Matsucoccus josephi*. *Journal of Chemical Ecology*, 21, 331–341.
- Milet-Pinheiro, P., Ayasse, M., Dobson, H. E. M., Schlindwein, C., Francke, W., & Dötterl, S. (2013). The chemical basis of host-plant recognition in a specialized bee pollinator. *Journal of Chemical Ecology*, 39, 1347–1360.
- Milet-Pinheiro, P., Herz, K., Dötterl, S., & Ayasse, M. (2016). Host choice in a bivoltine bee: How sensory constraints shape innate foraging behaviors. *BMC Ecology*, 16, 20.
- Morawo, T., Burrows, M., & Fadamiro, H. (2016). Electroantennogram response of the parasitoid, *Microplitis croceipes* to host-related odors: The discrepancy between relative abundance and level of antennal responses to volatile compound. *F1000Research*, 5, 2725.
- Morawo, T., & Fadamiro, H. (2016). Identification of key plant-associated volatiles emitted by *Heliothis virescens* larvae that attract the parasitoid, *Microplitis croceipes*: Implications for parasitoid perception of odor blends. *Journal of Chemical Ecology*, 42, 1112–1121.
- Morehead, S. A., & Feener, D. H. (2000). Visual and chemical cues used in host location and acceptance by a dipteran parasitoid. *Journal of Insect Behavior*, 13, 613–625.
- Moreira, X., Castagneyrol, B., Abdala-Roberts, L., & Traveset, A. (2019). A meta-analysis of herbivore effects on plant attractiveness to pollinators. *Ecology*, 100, e02707.
- Moya, S., & Ackerman, J. D. (1993). Variation in the floral fragrance of *Epidendrum ciliare* (Orchidaceae). *Nordic Journal of Botany*, 13, 41–47.
- Mumm, R., & Dicke, M. (2010). Variation in natural plant products and the attraction of bodyguards involved in indirect plant defense. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 88, 628–667.
- Nicholls, E., & Hempel de Ibarra, N. (2017). Assessment of pollen rewards by foraging bees. *Functional Ecology*, 31, 76–87.
- Nilsson, L. A. (1992). Orchid pollination biology. *Trends in Ecology & Evolution*, 7, 255–259.
- Noriyuki, S., & Osawa, N. (2012). Intrinsic prey suitability in specialist and generalist *Harmonia* ladybirds: A test of the trade-off hypothesis for food specialization. *Entomologia Experimentalis et Applicata*, 144, 279–285.
- Nottingham, S. F. (1988). Host-plant finding for oviposition by adult cabbage root fly, *Delia radicum*. *Journal of Insect Physiology*, 34, 227–234.
- Otieno, M., Karpati, Z., Peters, M. K., Duque, L., Schmitt, T., & Steffan-Dewenter, I. (2023). Elevated ozone and carbon dioxide affects the composition of volatile organic compounds emitted by *Vicia faba* (L.) and visitation by European orchard bee (*Osmia cornuta*). *PLoS One*, 18, e0283480.
- Papaj, D. R., Snellen, H., Swaans, K., & Vet, L. E. M. (1994). Unrewarding experiences and their effect on foraging in the parasitic wasp *Leptopilina heterotoma* (Hymenoptera: Eucolidae). *Journal of Insect Behavior*, 7, 465–481.
- Papini, M. R. (2003). Comparative psychology of surprising nonreward. *Brain, Behavior and Evolution*, 62, 83–95.
- Pichersky, E., & Gershenzon, J. (2002). The formation and function of plant volatiles: Perfumes for pollinator attraction and defense. *Current Opinion in Plant Biology*, 5, 237–243.
- Pickett, J. A., Woodcock, C. M., Midega, C. A. O., & Khan, Z. R. (2014). Push-pull farming systems. *Current Opinion in Biotechnology*, 26, 125–132.
- Poelman, E. H., Bourne, M. E., Croijmans, L., Cuny, M. A. C., Delamore, Z., Joachim, G., Kalisvaart, S. N., Kamps, B. B. J., Longuemare, M., Suijkerbuijk, H. A. C., & Zhang, N. X. (2023). Bringing fundamental insights of induced resistance to agricultural management of herbivore pests. *Journal of Chemical Ecology*, 49, 218–229.
- Poelman, E. H., Bruinsma, M., Zhu, F., Weldegergis, B. T., Boursault, A. E., Jongema, Y., van Loon, J. J. A., Vet, L. E. M., Harvey, J. A., & Dicke, M. (2012). Hyperparasitoids use herbivore-induced plant volatiles to locate their parasitoid host. *PLoS Biology*, 10, e1001435.
- Poelman, E. H., Cusumano, A., & Boer, J. G. D. (2022). The ecology of hyperparasitoids. *Annual Review of Entomology*, 67, 143–161.
- Polidori, C., Jorge, A., & Ornos, C. (2020). Antennal morphology and sensillar equipment vary with pollen diet specialization in *Andrena* bees. *Arthropod Structure & Development*, 57, 100950.
- Possell, M., & Loreto, F. (2013). The role of volatile organic compounds in plant resistance to abiotic stresses: Responses and mechanisms. In Ü. Niinemets & R. K. Monson (Eds.), *Biology, controls and models of tree volatile organic compound emissions* (pp. 209–235). Springer Netherlands.
- Powell, G., Toshi, C. R., & Hardie, J. (2006). Host plant selection by aphids: Behavioral, evolutionary, and applied perspectives. *Annual Review of Entomology*, 51, 309–330.
- Prokopy, R. J., & Owens, E. D. (1983). Visual detection of plants by herbivorous insects. *Annual Review of Entomology*, 28, 337–364.
- Raguso, R. A. (2008). Wake up and smell the roses: The ecology and evolution of floral scent. *Annual Review of Ecology, Evolution, and Systematics*, 39, 549–569.
- Ramírez, G., Fagundez, C., Grosso, J. P., Argibay, P., Arenas, A., & Farina, W. M. (2016). Odor experiences during preimaginal stages cause behavioral and neural plasticity in adult honeybees. *Frontiers in Behavioral Neuroscience*, 10, 105. <https://doi.org/10.3389/fnbeh.2016.00105>
- Reinhard, J., Sinclair, M., Srinivasan, M. V., & Claudianos, C. (2010). Honeybees learn odour mixtures via a selection of key odorants. *PLoS One*, 5, e9110.
- Renou, M. (2014). Pheromones and general odor perception in insects. In C. Mucignat-Caretta (Ed.), *Neurobiology of chemical communication*. CRC Press/Taylor & Francis.
- Riffell, J. A., & Alarcón, R. (2013). Multimodal floral signals and moth foraging decisions. *PLoS One*, 8, e72809.
- Riffell, J. A., Lei, H., Christensen, T. A., & Hildebrand, J. G. (2009). Characterization and coding of behaviorally significant odor mixtures. *Current Biology*, 19, 335–340.
- Riffell, J. A., Shlizerman, E., Sanders, E., Abrell, L., Medina, B., Hinterwirth, A. J., & Kutz, J. N. (2014). Flower discrimination by pollinators in a dynamic chemical environment. *Science*, 344, 1515–1518.
- Rusch, C., Broadhead, G. T., Raguso, R. A., & Riffell, J. A. (2016). Olfaction in context—Sources of nuance in plant–pollinator communication. *Current Opinion in Insect Science*, 15, 53–60.
- Rusman, Q., Lucas-Barbosa, D., Poelman, E. H., & Dicke, M. (2019). Ecology of plastic flowers. *Trends in Plant Science*, 24, 725–740.
- Rusman, Q., Poelman, E. H., Nowrin, F., Polder, G., & Lucas-Barbosa, D. (2019). Floral plasticity: Herbivore-species-specific-induced changes in flower traits with contrasting effects on pollinator visitation. *Plant, Cell & Environment*, 42, 1882–1896.
- Saunier, A., Grof-Tisza, P., & Blande, J. D. (2023). Effect of ozone exposure on the foraging behaviour of *Bombus terrestris*. *Environmental Pollution*, 316, 120573.
- Schäffler, I., Steiner, K. E., Haid, M., van Berkel, S. S., Gerlach, G., Johnson, S. D., Wessjohann, L., & Dötterl, S. (2015). Diacetyl, a reliable cue and private communication channel in a specialized pollination system. *Scientific Reports*, 5, 12779.
- Schiestl, F. P. (2005). On the success of a swindle: Pollination by deception in orchids. *Naturwissenschaften*, 92, 255–264.

- Schiestl, F. P. (2010). The evolution of floral scent and insect chemical communication. *Ecology Letters*, 13, 643–656.
- Schiestl, F. P. (2015). Ecology and evolution of floral volatile-mediated information transfer in plants. *New Phytologist*, 206, 571–577.
- Schiestl, F. P. (2017). Innate receiver bias: Its role in the ecology and evolution of plant–animal interactions. *Annual Review of Ecology, Evolution, and Systematics*, 48, 585–603.
- Schiestl, F. P., Kirk, H., Bigler, L., Cozzolino, S., & Desurmont, G. A. (2014). Herbivory and floral signaling: Phenotypic plasticity and tradeoffs between reproduction and indirect defense. *New Phytologist*, 203, 257–266.
- Schiestl, F. P., Steinebrunner, F., Schulz, C., von Reuß, S., Francke, W., Weymuth, C., & Leuchtman, A. (2006). Evolution of ‘pollinator’-attracting signals in fungi. *Biology Letters*, 2, 401–404.
- Schlaepfer, M. A., Runge, M. C., & Sherman, P. W. (2002). Ecological and evolutionary traps. *Trends in Ecology & Evolution*, 17, 474–480.
- Schoonhoven, L. M., van Loon, J. J. A., & Dicke, M. (2005). *Insect-plant biology*. Oxford University Press.
- Schuman, M. C., Valim, H. A., & Joo, Y. (2016). Temporal dynamics of plant volatiles: Mechanistic bases and functional consequences. In J. D. Blande & R. Glinwood (Eds.), *Deciphering chemical language of plant communication* (pp. 3–34). Springer International Publishing.
- Schwarzkopf, A., Rosenberger, D., Niebergall, M., Gershenson, J., & Kunert, G. (2013). To feed or not to feed: Plant factors located in the epidermis, mesophyll, and sieve elements influence pea aphid's ability to feed on legume species. *PLoS One*, 8, e75298.
- Sheehan, W., & Shelton, A. M. (1989). The role of experience in plant foraging by the aphid parasitoid *Diaeretiella rapae* (Hymenoptera: Aphidiidae). *Journal of Insect Behavior*, 2, 743–759.
- Shelton, A. M., & Badenes-Perez, F. R. (2006). Concepts and applications of trap cropping in pest management. *Annual Review of Entomology*, 51, 285–308.
- Shelton, A. M., & Nault, B. A. (2004). Dead-end trap cropping: A technique to improve management of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Crop Protection*, 23, 497–503.
- Siekmann, G., & Hommes, M. (2007). Yellow rocket (*Barbarea vulgaris*) as a trap crop in cole crops? *IOBC WPRS Bulletin*, 30, 101.
- Silva, R., & Clarke, A. R. (2020). The “sequential cues hypothesis”: A conceptual model to explain host location and ranking by polyphagous herbivores. *Insect Science*, 27, 1136–1147.
- Singer, M. C., & Parmesan, C. (2018). Lethal trap created by adaptive evolutionary response to an exotic resource. *Nature*, 557, 238–241.
- Smid, H. M., & Vet, L. E. M. (2016). The complexity of learning, memory and neural processes in an evolutionary ecological context. *Current Opinion in Insect Science*, 15, 61–69.
- Sobhy, I. S., Goelen, T., Herrera-Malaver, B., Verstrepen, K. J., Wäckers, F., Jacquemyn, H., & Lievens, B. (2019). Associative learning and memory retention of nectar yeast volatiles in a generalist parasitoid. *Animal Behaviour*, 153, 137–146.
- Sobhy, I. S., Tamiru, A., Chiriboga Morales, X., Nyagol, D., Cheruiyot, D., Chidawanyika, F., Subramanian, S., Midega, C. A. O., Bruce, T. J. A., & Khan, Z. R. (2022). Bioactive volatiles from push-pull companion crops repel fall armyworm and attract its parasitoids. *Frontiers in Ecology and Evolution*, 10. <https://doi.org/10.3389/fevo.2022.883020>
- Spiesman, B. J., Bennett, A., Isaacs, R., & Gratton, C. (2017). Bumble bee colony growth and reproduction depend on local flower dominance and natural habitat area in the surrounding landscape. *Biological Conservation*, 206, 217–223.
- Stephens, D. W. (1991). Change, regularity, and value in the evolution of animal learning. *Behavioral Ecology*, 2, 77–89.
- Stephens, D. W. (1993). Learning and behavioral ecology: Incomplete information and environmental predictability. In D. R. Papaj & A. C. Lewis (Eds.), *Insect learning: Ecology and evolutionary perspectives* (pp. 195–218). Springer US.
- Steward, R. A. (2019). The persistent maladaptation of *Pieris macdunnoughii*: Constraints on adaptation to an evolutionary trap. Doctoral dissertation.
- Steward, R. A., & Boggs, C. L. (2020). Experience may outweigh cue similarity in maintaining a persistent host-plant-based evolutionary trap. *Ecological Monographs*, 90, e01412.
- Storeck, A., Poppy, G. M., van Emden, H. F., & Powell, W. (2000). The role of plant chemical cues in determining host preference in the generalist aphid parasitoid *Aphidius colemani*. *Entomologia Experimentalis et Applicata*, 97, 41–46.
- Takasu, K., & Lewis, W. J. (2003). Learning of host searching cues by the larval parasitoid *Microplitis croceipes*. *Entomologia Experimentalis et Applicata*, 108, 77–86.
- Takemoto, H. (2016). Cross-modal effect of natal habitat experience increases receptivity to non-natal habitat cues in generalist parasitic wasps. *Arthropod-Plant Interactions*, 10, 303–310.
- Takemoto, H., & Yoshimura, J. (2020). Unrewarding experience with a novel environment modulates olfactory response in the host-searching behavior of parasitic wasps. *Arthropod-Plant Interactions*, 14, 433–440.
- Talsma, D., Senkowski, D., Soto-Faraco, S., & Woldorff, M. G. (2010). The multifaceted interplay between attention and multisensory integration. *Trends in Cognitive Sciences*, 14, 400–410.
- Thomas, G., Rusman, Q., Morrison, W. R., Magalhães, D. M., Dowell, J. A., Ngumbi, E., Osei-Owusu, J., Kansman, J., Gaffke, A., Pagadala Damodaram, K. J., Kim, S. J., & Tabanca, N. (2023). Deciphering plant-insect-microorganism signals for sustainable crop production. *Biomolecules*, 13, 997.
- Thompson, J. N. (1988). Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia Experimentalis et Applicata*, 47, 3–14.
- Thompson, J. N., & Pellmyr, O. (1991). Evolution of oviposition behavior and host preference in Lepidoptera. *Annual Review of Entomology*, 36, 65–89.
- Thorpe, W. H. (1956). *Learning and instinct in animals*. Harvard University Press.
- Townsend-Mehler, J. M., & Dyer, F. C. (2012). An integrated look at decision-making in bees as they abandon a depleted food source. *Behavioral Ecology and Sociobiology*, 66, 275–286.
- Turlings, T. C. J., McCall, P. J., Alborn, H. T., & Tumlinson, J. H. (1993). An elicitor in caterpillar oral secretions that induces corn seedlings to emit chemical signals attractive to parasitic wasps. *Journal of Chemical Ecology*, 19, 411–425.
- Turlings, T. J. C., & Erb, M. (2018). Tritrophic interactions mediated by herbivore-induced plant volatiles: Mechanisms, ecological relevance, and application potential. *Annual Review of Entomology*, 63, 433–452.
- Vanderplanck, M., Lapeyre, B., Brondani, M., Opsommer, M., Dufay, M., Hossaert-McKey, M., & Proffit, M. (2021). Ozone pollution alters olfaction and behavior of pollinators. *Antioxidants*, 10, 636.
- Veromann, E., Kaasik, R., Kovács, G., Metspalu, L., Williams, I. H., & Mänd, M. (2014). Fatal attraction: Search for a dead-end trap crop for the pollen beetle (*Meligethes aeneus*). *Arthropod-Plant Interactions*, 8, 373–381.
- Vet, L. E. M., & Dicke, M. (1992). Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology*, 37, 141–172.
- Vinson, S. B. (1998). The general host selection behavior of parasitoid hymenoptera and a comparison of initial strategies utilized by larviphagous and oophagous species. *Biological Control*, 11, 79–96.
- Visser, M. E., van Alphen, J. J. M., & Nell, H. W. (1992). Adaptive superparasitism and patch time allocation in solitary parasitoids: The influence of pre-patch experience. *Behavioral Ecology and Sociobiology*, 31, 163–171.
- Vosteen, I., van den Meiracker, N., & Poelman, E. H. (2019). Getting confused: Learning reduces parasitoid foraging efficiency in some environments with non-host-infested plants. *Oecologia*, 189, 919–930.
- Vosteen, I., van den Meiracker, N., & Poelman, E. H. (2020). Gone with the wind: Low availability of volatile information limits foraging efficiency in downwind-flying parasitoids. *Animal Behaviour*, 165, 59–70.
- Wardle, A. R., & Borden, J. H. (1989). Learning of an olfactory stimulus associated with a host microhabitat by *Exeristes roborator*. *Entomologia Experimentalis et Applicata*, 52, 271–279.

- Webster, B., Bruce, T., Pickett, J., & Hardie, J. (2010). Volatiles functioning as host cues in a blend become nonhost cues when presented alone to the black bean aphid. *Animal Behaviour*, 79, 451–457.
- Webster, B., & Cardé, R. T. (2017). Use of habitat odour by host-seeking insects. *Biological Reviews*, 92, 1241–1249.
- Webster, B., Gezan, S., Bruce, T., Hardie, J., & Pickett, J. (2010). Between plant and diurnal variation in quantities and ratios of volatile compounds emitted by *Vicia faba* plants. *Phytochemistry*, 71, 81–89.
- Webster, B., Qvarfordt, E., Olsson, U., & Glinwood, R. (2013). Different roles for innate and learnt behavioral responses to odors in insect host location. *Behavioral Ecology*, 24, 366–372.
- Williams, N. H., & Dodson, C. H. (1972). Selective attraction of male euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. *Evolution*, 26, 84–95.
- Williams, N. M. (2003). Use of novel pollen species by specialist and generalist solitary bees (Hymenoptera: Megachilidae). *Oecologia*, 134, 228–237.
- Wright, G. A., Kottcamp, S. M., & Thomson, M. G. A. (2008). Generalization mediates sensitivity to complex odor features in the honeybee. *PLoS One*, 3, e1704.
- Wright, G. A., & Schiestl, F. P. (2009). The evolution of floral scent: The influence of olfactory learning by insect pollinators on the honest signalling of floral rewards. *Functional Ecology*, 23, 841–851.
- Wright, G. A., Thomson, M. G. A., & Smith, B. H. (2005). Odour concentration affects odour identity in honeybees. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2417–2422.
- Zhang, P.-J., Liu, S.-S., Wang, H., & Zalucki, M. P. (2007). The influence of early adult experience and larval food restriction on responses toward nonhost plants in moths. *Journal of Chemical Ecology*, 33, 1528–1541.
- Zhao, Z., & McBride, C. S. (2020). Evolution of olfactory circuits in insects. *Journal of Comparative Physiology A*, 206, 353–367.
- Zito, P., Tavella, F., Pacifico, D., Campanella, V., Sajeve, M., Carimi, F., Ebmer, A. W., & Dötterl, S. (2019). Interspecific variation of inflorescence scents and insect visitors in *Allium* (Amaryllidaceae: Allioideae). *Plant Systematics and Evolution*, 305, 727–741.
- Zuk, M., & Kolluru, G. R. (1998). Exploitation of sexual signals by predators and parasitoids. *The Quarterly Review of Biology*, 73, 415–438.

How to cite this article: Rusman, Q., Cusumano, A., & Vosteen, I. (2024). En route to resources: Foraging strategies of plant-associated insects to identify resources in complex dynamic environments. *Functional Ecology*, 00, 1–19. <https://doi.org/10.1111/1365-2435.14606>