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Understanding insect foraging in complex habitats by comparing trophic levels: insights from specialist host-parasitoid-hyperparasitoid systems

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Insects typically forage in complex habitats in which their resources are surrounded by non-resources. For herbivores, pollinators, parasitoids, and higher level predators research has focused on how specific trophic levels filter and integrate information from cues in their habitat to locate resources. However, these insights frequently build specific theory per trophic level and seldom across trophic levels. Here, we synthesize advances in understanding of insect foraging behavior in complex habitats by comparing trophic levels in specialist host-parasitoid-hyperparasitoid systems. We argue that resources may become less apparent to foraging insects when they are member of higher trophic levels and hypothesize that higher trophic level organisms require a larger number of steps in their foraging decisions. We identify important knowledge gaps of information integration strategies by insects that belong to higher trophic levels.

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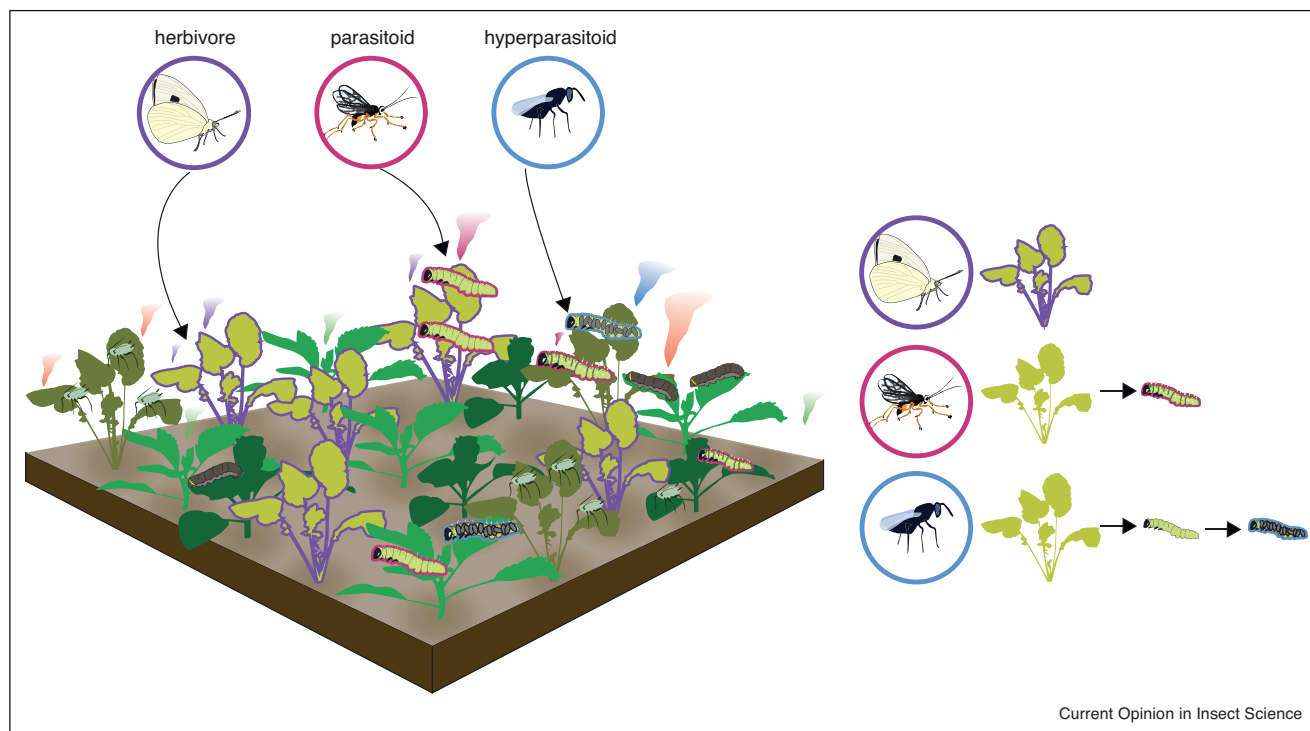
Introduction

Insects forage in complex environments where their resources are found among non-resources. Non-resource organisms contribute to complexity in cues out of which the foraging insect needs to filter information about its desired resource [1^{**}]. Most (if not all) cues have multiple sources of variation (e.g. spatial, temporal, due to (a) biotic factors), and this variation leads to an enormous amount of information an insect has to handle [2]. Moreover,

information on a food source may differ in reliability as well as detectability due to differences in evolutionary pressure on conspicuousness of organisms as well as similarity in cues of resources and non-resources [3–7]. In specialist host-parasitoid-hyperparasitoid systems, each of the trophic levels ranging from herbivore, parasitoid to hyperparasitoid forages in the same complex environment (Figure 1). However, information on the presence and location of their resources may be more sparse or indirect for different organisms in the food chain. In their search for suitable food plants in plant communities, herbivores can rely on direct cues associated with their food plant and require relatively few behavioral steps to reach their food plant [1^{**},8]. Parasitoids associated with these herbivores need to be able to locate their hosts hidden among non-host insects which are feeding in speciose plant communities [9]. Because herbivores are inconspicuous, parasitoids use indirect information of herbivore induced plant volatiles (HIPVs) that are a detectable source of information of herbivore presence. However, other non-host herbivores feeding on the same food plant species may induce similar volatile blends which may result in reduced reliability of the information [9,10,11^{**}]. Parasitoids may therefore need to go through multiple foraging steps to not only locate food plants with potential hosts, but to also locate the host on these plants [9,10,11^{**}]. Hyperparasitoids that parasitize the larvae or pupae of these parasitoids even need to be able to locate parasitized herbivores in these plant-insect communities [12^{**}], which may require a longer series of foraging steps to reach the resource (Figure 1). We thus argue that the apparency of resources to foraging organisms in complex environments decreases when organisms belong to higher trophic levels in specialist host-parasitoid-hyperparasitoid systems. Comparing how each of these organisms in the trophic chain deals with the complexity of the environment may increase our understanding of search strategies and information integration in insect foraging.

In this review, we discuss whether trophic levels differ in their i) search template of cues used as information source, ii) sensory systems used to filter information, and iii) how the integration of information is structured. We connect literature from different trophic levels to gain

Figure 1



Foraging of insects of different trophic levels (herbivores, parasitoids, hyperparasitoids) in a complex environment. The different trophic levels are exposed to the same complex environment, but are foraging for different resource types (indicated with arrows and resources inside the patch are outlined with the same color as circle around the insect). Herbivores (purple) search for preferred food plants and use plant-derived cues. Parasitoids search for suitable hosts which might be on different food plants and in different densities, occurring near non-host insects and can use plant-derived cues and host-derived cues. Hyperparasitoids (blue) encounter a situation similar to parasitoids, but have to select caterpillars which are parasitized by their host, using plant-derived cues, caterpillar-derived cues and host-derived cues. Cues presented by other organisms in the patch can cause noise during foraging. Odor cues are represented by small plumes: different colors indicate different blend compositions and length indicating the relative strength of the cue.

insight in differences among trophic levels in their foraging strategies. We identify important knowledge gaps in how higher trophic levels filter and integrate information and argue that insights gained in research on pollinator foraging and information use enrich our understanding of information use by higher trophic levels.

Search templates to filter information

Insects in different trophic levels all have a common strategy to deal with the enormous complexity of information they encounter: they do not follow random cues, but a subset of stimuli that are likely correlated with the occurrence of the desired resource. We will refer to this subset of stimuli a foraging insect is focusing on as a search template. This term includes an innate or learned preference for certain stimuli that may be fine-tuned or broadened with additional foraging experience. The template is thus constantly updated. The term thereby differs from the term search image that is a temporal specialization on certain stimuli caused by selective attention to a particular set of stimuli as a strategy to recognize

abundant resources [13–16]. In fact, a search image can be seen as a specific type of transient search template.

Insects are known to use a variety of different stimuli in foraging, which can be classified as olfactory, visual, acoustic, tactile and gustatory cues and a search template can be based on a combination of any of these cues. The use of olfactory cues during long-range foraging is widely distributed across all trophic levels [1^{••},7,17–21] and all trophic levels seem to use gustatory cues to evaluate resource identity and quality after resource contact. As the same cue encompasses different information for different trophic levels, trophic levels likely differ in their cue use and thus search template.

The search template of herbivorous insects is dominated by the use of plant volatiles and colors during long-range foraging [7,18, 22,23,24,25[•]] while tactile and gustatory cues influence host plant selection after contact [26[•],27]. For generalist insects, several ubiquitous primary metabolites stimulate feeding, and the plant will only be

rejected if it has a high concentration of a specific deterrent, while specialist herbivores often use taxonomically characteristic compounds to accept a food plant [28,29].

Higher trophic levels such as parasitoids in the third trophic level, predominantly use herbivore-induced plant volatiles (HIPVs) in long-range foraging [17,30]. The induction of plant volatiles by herbivores results in a well detectable source of information [3] and can even contain information on the identity of the herbivore [31,32,33]. However, non-host herbivores may also affect the reliability of the information by inducing similar volatiles while feeding on other plants in the community, and by masking or altering volatiles induced by the host when feeding on the same plant as the host herbivore [10]. After arrival at the herbivore-infested plant, the employed search template is broadened with gustatory cues, visual cues (like color, shape and size e.g. [34–39]), as well as olfactory cues emitted from the host or prey itself [40]. It has further been reported that some parasitoids and predators use sound and vibrations generated by prey movement and feeding to detect their prey/host on the plant [41–43]. The number of foraging steps to reach the resource may be larger for parasitoids than for herbivores, and in each step the search template may include different sensory systems (Figure 2).

Fourth and higher trophic level organisms have been understudied for their cue-use in foraging. Caterpillar-associated hyperparasitoids can use HIPVs to discriminate between plants with parasitized and non-parasitized caterpillars [12]. During foraging at close range, caterpillar body-odors can be used to distinguish parasitized and non-parasitized individuals [44]. In aphid-associated hyperparasitoids however, there is so far no evidence for the use of HIPVs [45], but support for direct responses to aphid associated cues [46,47]. Although each trophic level may adopt the search template and use different sets of stimuli in each foraging step, we hypothesize that higher trophic level organisms have longer behavioral sequences to reach the resource and have fewer stimuli available in early foraging steps. This is because only in later foraging steps of higher trophic level organisms information is available from different sensory systems and that may come directly from the resource. However, we lack information for higher trophic levels on in particular, the range at which visual and acoustic stimuli are used in search templates.

Perception of complex information

Trophic levels may differ in cue use because of differences in the perception of cues. The sensory systems of insects in different trophic levels likely evolved to perceive the most reliable information to find the resource, and may thus predict the search template that these organisms use.

In all trophic levels, olfaction is a dominant stimulus in the search template. Interestingly, the organization of the olfactory system is highly conserved in different trophic levels, but the olfactory receptors may differ among species [48]. The olfactory receptors (ORs) located on the antennae (and the palps) detect volatile chemicals. Most insects have ORs that detect volatiles that are characteristic for the host (or unsuitable host), and ORs that detect more general cues [49,50]. For their visual system, insect species differ in the number of color receptor types, their spatial distribution across the retina, and their wavelength sensitivity [51]. Research on the color sensory system is heavily biased to Lepidoptera and bees, and we have limited knowledge on the visual sensory system of higher trophic levels. How vision is incorporated in the search template by different trophic levels remains to be explored.

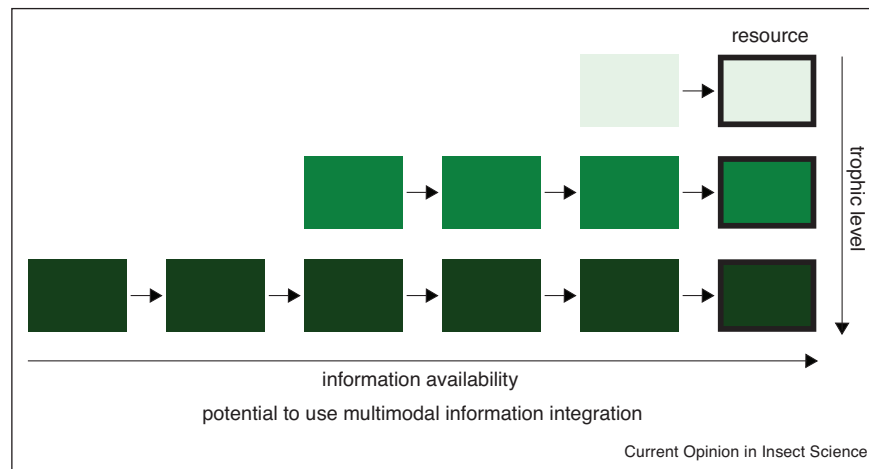
Gustatory receptors (GRs) are highly divergent among different insect species and do not seem to correspond with trophic position [26]. Some GRs probably detect a broad range of compounds, while other might be highly-specific [26]. For herbivores, closely related species might diverge considerably in GRs, and generalist species might contain more GRs than specialist species [26]. This might indicate that the gustatory sensory system is an important filter for some trophic levels like herbivores. Unfortunately, we know little about the gustatory sensory systems of higher trophic levels [but see 52,53].

Predicting differences in foraging strategies between trophic levels in specialist host-parasitoid systems, requires more research on sensory systems of higher trophic levels to gain a more complete picture of their search template.

Integration of complex information

Because higher trophic level organisms in specialist host-parasitoid-hyperparasitoid systems require multiple foraging steps to reach their resource in complex environments, and direct cues associated with their resource are not apparent, they may differ in how they integrate information compared to lower trophic levels. In all trophic levels, foraging steps may use a hierarchical organization of which cues dominate each foraging step [1,29,54]. For herbivores, distinct hierarchical decisions in foraging may include resource habitat and location of the food plant after which the herbivore enters quality assessment of the food source. Already in the first steps, herbivores may make use of different sensory systems, because odor, color and shape of their resource may be available and detected from a longer distance. This allows herbivores to use a multimodal integration of information [55,56]. With multimodal integration, the search template is composed of more than one major cue type (visual, odor, gustatory, or tactile). Multimodal integration is well known for pollinators that use multiple cues such as visual

Figure 2



The number of foraging steps a species makes, corresponds with information availability or apparency of the resource. We predict that longer chains of foraging steps start with multiple unimodal steps and the closer the foraging species gets to its resource the larger the potential for multimodal information integration due to the availability of new cues picked up by different sensory systems. Because lower trophic levels more frequently have smaller number of foraging steps and their information is less sparse than for higher trophic levels, we hypothesize that they may use multimodal information integration earlier in foraging decisions than higher trophic levels.

and odor cues, which might be supplemented by other cues, such as humidity, thermal cues, and electric fields before a resource is successfully located [57^{**},58^{**},59]. Moreover, functional hypotheses have been developed for pollinators that clearly show the benefits of multimodal integration [59–61]. Similar to pollinators, herbivores may be strongly selected for using a multimodal integration of cues. A set of cues as compared to individual cues might reveal both presence and quality of a resource, and increases the accuracy and/or reliability of the information [60–62]. Therefore multimodal integration of information directly optimizes foraging efficiency [60–62]. For multiple herbivore species, multimodal integration in resource location has been identified [54,55].

Higher trophic levels often find themselves in more complex situations when locating their resources and may not be able to use information to identify resource presence and quality at the same distance from the resource, simply because this information is not available to them early in their foraging steps. The first foraging steps in the hierarchy of host searching by parasitoids and hyperparasitoids is known to rely on unimodal use of volatile information [63–65]. Decisions on location of suitable habitat and host-infested patches are dominated by plant volatiles [63,65]. When arriving on a plant, parasitoids and hyperparasitoids may be able to use visual, gustatory and tactile cues to locate their resource. At this stage in their foraging steps, higher trophic level organisms may use a multimodal integration of information. However, multimodal information use has only recently gained attention in higher trophic level arthropods [66]

and to our knowledge has not been studied for parasitoids and hyperparasitoids. Interestingly, the brain structures responsible for multimodal integration such as the mushroom body calyces are highly developed in parasitoids [67,68] and predict similar capacities of multimodal information use as known for Hymenopteran pollinators such as honeybees and bumblebees [59,61].

Conclusion and future perspectives

Differences in information availability may underlie that the number of steps in foraging decisions corresponds with the potential to use unimodal versus multimodal information integration, and may cause trophic levels to differ in information use in the same complex environment. Important knowledge gaps are to explore whether higher trophic levels use multimodal integration of cues [65] and how each trophic levels uses a hierarchical structure of unimodal or multimodal information [58^{**},62,69,70]. Moreover, how foraging experience modulates search templates and integration of information is understudied in especially herbivores and hyperparasitoids. Recent studies suggest that for all trophic levels, search templates for patch and resource location are especially plastic, while habitat location and resource acceptance templates seem more fixed [1^{**},71]. Here, we focused on specialist host-parasitoid systems. A broader comparison between generalist and specialist species within trophic levels may further reveal which search templates and information integration strategies correspond with foraging strategies. Direct experimental comparison of how different trophic levels deal with the same complex environment will provide us with

understanding how organisms deal with habitat complexity on different scales. This is important in fundamental understanding of how habitat complexity alters the strength of trophic interactions and can be applied to design cropping systems in which foraging efficiency of desired organisms is enhanced and that of undesired organisms decreased.

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