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The Role of Olfactory Cues for the Search Behavior of a Specialist and Generalist Butterfly

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Abstract Searching for resources is often a challenging task, especially for small organisms such as insects. Complex stimuli have to be extracted from the environment and translated into a relevant behavioral output. A first step in this process is to investigate the relative roles of the different senses during search for various resources. While the role of olfaction is well documented in nocturnal moths, the olfactory abilities of the closely related diurnal butterflies are poorly explored. Here we investigated how olfactory information is used in the search for host plants and asked if these abilities varied with levels of stimulus complexity. Thus, we tested two nymphalid butterfly species with divergent host plant range in a two-choice olfactometer testing different combinations of host and non-host plants. The experiments show both the monophagous *Aglais urticae* and the polyphagous *Polygonia c-album* could navigate towards an odor source, but this ability varied with context. While mated females exhibited a preference for their host plant, unmated females of both species did not show a preference for host plant cues. Furthermore, both species showed inabilities to make fine-tuned decisions between hosts. We conclude that olfactory cues are important for butterflies to navigate towards targets. We argue that there are limitations on how much information can be extracted from host volatiles. These results are discussed in the light of neural processing limitations and degree of host plant specialization, suggesting the necessity of other sensory modalities to sharpen the decision process and facilitate the final oviposition event.

Keywords Olfaction · Lepidoptera · search behavior · information processing hypothesis · host plant specialization

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Introduction

For an insect, locating and evaluating the various resources required for feeding, mating and oviposition can be a formidable task. Not only are these resources often dispersed on a large scale relative to the size of the insect, but the different resource types are also likely to require unique sets of recognition cues. As a consequence, insect search behavior is a complex behavioral process mediated by a multitude of sensory inputs (Bergman and Wiklund 2009; Byers 1996; Finch and Collier 2000; Papaj and Vet 1990) and although search behavior has been studied extensively it is still very much unclear how different search modalities function in an ecological context and contribute to the decision process that allows the insect to find its target of search.

In order to resolve the mechanisms behind this search- and evaluation behavior we need to disentangle the different stimuli and understand their role in different stages of the search process. For example, when a female is searching for oviposition sites, a suitable habitat, assessing a potential host before alighting and on-plant evaluation all require different sets of evaluation tools. Visual (Goyret et al. 2008; Kelber 1999), olfactory (Cardé and Willis 2008; Visser 1986), gustatory (Chapman 2003; Ômura et al. 2008) and mechano-sensory (Foster and Howard 1998; Goyret and Raguso 2006) cues can by themselves or in combination with each other enhance or facilitate behaviors to find and assess a potential mate, host or food source. The combinations of cues used as well as the extent to which different sensory modalities are employed are thus likely to vary not only between species, but also with search context.

Again in the case of searching for oviposition sites, chemical and tactile cues have been identified in a number of herbivores as instrumental in evaluating plants after alighting, rendering them as crucial for post-alighting decision making (Feeny et al. 1989; Städler and Reifenrath 2009; van Loon et al. 1992). Pre-alighting mechanisms have not been studied to the same extent, but beetles (Ninkovic et al. 2001), hymenopterans (Steidle and Schöller 1997), flies (Dweck et al. 2013) and moths (e.g. Finch and Kienegger 1997) have been shown to possess these abilities. Even though visual cues can play a role for moths in the foraging context (Kelber 2002; Raguso and Willis 2002) their typical nocturnal or crepuscular lifestyle necessitates them to mainly rely on olfactory cues. In several studies, moths have been shown to be able to learn with help of odors and to track targets aided by odor cues alone (e.g. Cunningham et al. 1999; Mozuraitis et al. 2002; Pivnick et al. 1994; Willis and Arbas 1991). In contrast, for the day active butterflies, there is ample evidence that visual cues are important in host-searching as well as in foraging and mating contexts (e.g. Goulson and Cory 1993; Kelber 1999; Rutowski 2003; Snell-Rood et al. 2009).

Even though butterflies may be depicted as “visual animals” it is hard to believe that they do not take advantage of olfactory cues, considering that butterflies have a well developed, functional olfactory system (Carlsson et al. 2011, 2013). There are a handful of studies that have investigated responses to odorants in butterflies, but the majority examined antennal reactions to food or host plant volatiles (Andersson 2003; Honda et al. 1998; Ômura et al. 1999). Others tested olfactory cues in combination with other stimuli (Andersson and Dobson 2003; Heinz 2008) and only a single study (in *Pieris rapae*) unequivocally showed female preference to a host plant odor (Ikeura et al. 2010). Hence, even though volatile chemicals are sources of information clearly available for butterflies, relatively little is known about the importance of olfactory cues for food and host plant search, especially how this information is used in an ecological context, as for example in connection to host plant range or to distinguish between host plants of different preference rank.

Although there are several potential advantages of a broad host range, such as a greater flexibility towards variation in the environment (Agosta et al. 2010; Agosta and Klemens 2008; Murphy 2004), a number of both experimental and theoretical studies suggest that specialization can improve the effectiveness of the decision-making during oviposition (e.g. Bernays 1998; Egan and Funk 2006; Janz and Nylin 1997; Tosh et al. 2009). This idea has come to be known as the information processing hypothesis. The gist of this hypothesis is that species with a relatively more specialized resource use should be more efficient in finding and evaluating potential resources, since they only have to distinguish between a small subset of plants. A broader diet infers costs that are twofold: (i) an increased risk of oviposition on non-hosts or hosts of inferior quality and (ii) an increased host-plant evaluation time (Bernays 2001; Egan and Funk 2006; Janz 2003; Janz and Nylin 1997; Nylin et al. 2000).

If decision-making in relative host-plant generalists is believed to be constrained by neural processing capacity, this should be represented as a limitation in the quantity or quality of olfactory or other information that can be handled at a time. Using a conceptual model of the insect olfactory system, Cunningham (2012) suggested that the need to obtain sharp and unique coding in the antennal lobe can limit the number of host species that can be successfully recognized. By extension, because the perception of every plant odor is interrelated, the need to identify a multitude of potential hosts should potentially blur the clear line between hosts and non-hosts, making decisions more error-prone.

All else being equal, search context for a relative generalist will then be perceived as more complex, because it needs to be attentive to more of the available stimuli in the environment. In contrast, for the relative specialist the search task should be less complex; because it can focus on fewer stimuli the signal to noise ratio should typically be higher. For the same reason, individuals should also be expected to focus on one task at a time, as the stimuli required to elicit different behaviors are likely to differ and may well be in conflict (Bernays 2001). The internal state of the organism should then determine if she should focus on stimuli that can guide her towards food, oviposition sites or mates.

To approach these questions, we tested the two closely related nymphalid butterfly species *Aglais urticae* and *Polygonia c-album*, which differ in their degree of host-plant specialization. In a series of behavioral assays of olfactory choice we investigated (i) if these butterfly species oriented towards host plant-related olfactory cues, (ii) if responses varied with mating state, (iii) with different levels of stimulus complexity or (iv) if responses differed between the species.

Material and Methods

Experimental Animals

The monophagous butterfly *Aglais urticae* (small tortoiseshell) oviposits clutches of eggs on its host-plant, *Urtica dioica* (stinging nettle). *Polygonia c-album* (the comma butterfly), is polyphagous placing its eggs singly on a variety of host-plants from different plant families; among those are the highly preferred host *U. dioica* (Urticaceae) and the medium-ranked hosts *Salix caprea* (Salicaceae), and *Ribes uva-crispa* (Grossulariaceae) (Janz et al. 2009; Nylin 1988).

The butterflies used in the experiments were from a broad sample bred between 1 and 6 generations in the lab, originating from a stock of over 20 females per species caught during spring 2011 and 2012 at several non-protected, public sites in the greater Stockholm area. Catching the adults did not require any permit due to the principle of public access to the wilderness. Animals were reared under long daylength at around 23 °C on *U. dioica* – from previous studies we know that larval host-plant does not affect female adult host preference in *P. c-album* (Janz et al. 2009). Larvae were reared in plastic jars until pupation. After emergence they were put into cages for mating (50*50*50 cm) at L:D 18:6 around 26 °C. They were provided with sugar solution (15 %) ad libitum and, occasionally, with fresh flowers. Mating individuals were collected while *in copula*, however sometimes matings could go unnoticed. Therefore, fresh cut shoots of *U. dioica* were temporarily placed into the cages to attract mated individuals. After performing typical evaluation behaviors such as bending of the antenna, tarsal drumming, abdomen curling or even oviposition of an egg, females were caught and used in the experiments as soon as possible, but at the latest after 3 h. Tested butterflies were between 3 and 19 days old. Experiments were conducted during spring/summer 2011 and 2012. We observed that especially females of *P. c-album* could lay eggs even when unmated, so after the experiment females were dissected to verify mating status.

Experimental Setup

Adult butterflies were tested in a Y-tube olfactometer (Analytical Research Systems Inc., Gainesville, Florida, USA) with 43 mm inner diameter. Charcoal-filtered, compressed air was regulated to 0.3 l/min airflow, humidified and then directed to glass flasks that contained fresh, cut plant shoots. From the flasks air was led into the two arms of the Y-tube, where odors of the tested plants were clearly detectable to a human. Plants were replaced frequently and cut into a size so that leaf area of each shoot was roughly similar. Sides were switched regularly to avoid possible position-effects and individuals were tested one at a time. A decision line was located in each side of the Y-tube, and an individual crossing the line within 3 min from release with at least half the body was counted as a response. If no line was crossed after the experimental time had run out, the experiment was counted as “no response”. Increasing the experimental time did not increase the number of responding animals, indicating that 3 min of exposure to an odor was long enough to elicit a maximal number of responding animals. To eliminate traces from previous trials, the tube was cleaned with 95 % ethanol and dried before a new individual was tested. Except for the variation in odor cues, the experimental conditions followed the same standardized protocol described above. Since it was not always easy to obtain mated females, some females were used in several different trials, but no difference between females that have been used several times and those that only have been used only once could be detected. Testing order was randomized to control for a potential effect from previous trials. In butterflies, the extension of the proboscis is a behavioral reaction that signals that the individual is motivated to feed

(Ômura et al. 1999). Hence, if tested individuals performed a proboscis extension in the host plant setup, the trial was stopped, the individuals fed and re-tested to ensure that their behavioral choice was not based on food searching behavior.

Pre-Trials

To verify that the butterflies were able to discriminate between the arms of the Y-tube based on odor, both males and virgin females of each species were tested with an odor from a preferred food source against an empty side. As *A. urticae* is mainly a nectar feeder, it was presented to fresh inflorescences of *Syringa vulgaris* (common lilac). *P.c-album*, on the other hand, mainly prefers fermented sugar in the form of tree sap or fallen fruit, and was instead presented with the odor of a fermented sugar solution.

Experimental Trials

Only vegetative parts of all plants were used. To investigate the role of host plant odors for the monophagous *A. urticae*, several combinations were tested. Mated and unmated *A. urticae* females were given a choice between the host *U. dioica* and non-host *S. caprea*. To check whether the presence of non-host odors influenced the host search, a single shoot of U. dioica was tested against several shoots, one each from *U. dioica* and the non-hosts *S. caprea* and *R. uva-crispa*. In addition, mated females were given a choice between a shoot of "high" and "low" quality *U. dioica*. Shoots with fresh, green leaves from the top of an immature plant are referred to as "high" quality, whereas leaves, usually from lower parts of the shoot, that show yellow or brown spots without being wilted are referred to as "low" quality shoots (see also Janz and Nylin 1997).

We further tested the olfactory abilities of *P. c-album* in a series of combinations: the host *U. dioica* was offered against the non-host *C. arvense* for unmated and mated females. After that we investigated whether mated females could discriminate between the preferred host *U. dioica* and the medium-ranked host *S. caprea*, several hosts (*U. dioica*, *S. caprea*, *R. uva-crispa*) against a single host (*U. dioica*) and shoots of high vs. low quality *U. dioica*, as described above, were tested against each other as a further investigation of the ability to handle the increased complexity of additional synergistic or conflicting information. Graphs were produced in Adobe Illustrator CS4. All data was analyzed with binomial tests in R, version 3.1.1 (R Core Team 2014).

Results

Our Y-tube setup allowed for appropriate behavioral responses in our butterflies, as verified by the pre-trials with the food-related odors. Both species showed a clear preference for their food source over an empty vial (*A. urticae*: $n=20$, $p=0.003$; *P. c-album*: $n=22$, $p=0.017$).

Host Odor Trials

In the simple setup, where the host-plant was presented against a non-host (Fig. 1, Treatment A), unmated *A. urticae* females did not exhibit any side preference ($n=36$,

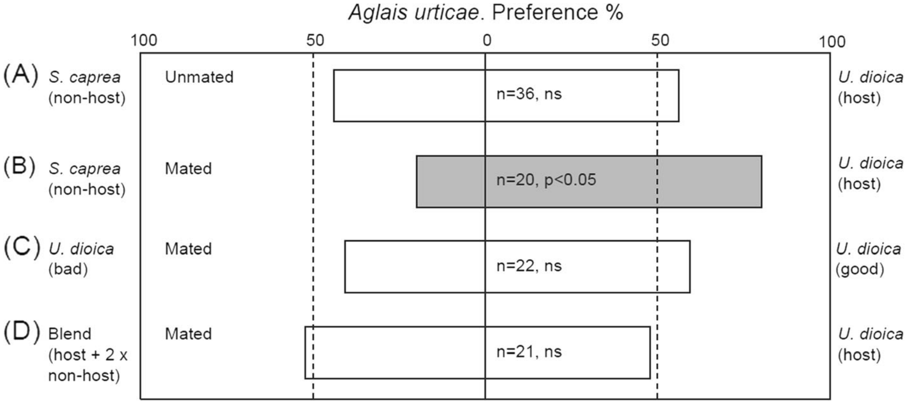

Fig. 1 Preference ratios (%) of the specialist *Aglais urticae* for either side of the two-way olfactometer. Sample size and α-levels are written within the respective bar, treatment letters in brackets. "n" denotes the total number of responding individuals. Host *Urtica dioica* vs. non-host *Salix caprea* in unmated (**a**) and mated (**b**) females; **c** shoots of "high" vs. "poor" quality host *U. dioica*; **d** host *U. dioica* in a blend with the two non-hosts *S. caprea* and *Ribes uva-crispa* vs. the host *U. dioica*

p=0.618, Fig. 1), whereas mated females entered the side with the host odor more often (n=20, p=0.012, Fig. 1, Treatment B). Interestingly, the females made no distinction between "high" and "poor" quality host plant (n=22, p=0.524, Fig. 1, Treatment C). Neither did they differentiate when the host plant was presented with two non-hosts and contrasted against the host plant odor alone (n=21, p=1, Fig. 1, Treatment D).

Just as with *A. urticae*, unmated *P. c-album* females showed no preference when given a choice between a host and a non-host (n=22, p=1, Fig. 2, Treatment A), while mated females showed a preference for the host plant (n=32, p= 0.050, Fig. 2, Treatment B). Also like *A. urticae*, *P. c-album* females showed no preference for either the "high" or "poor" quality nettle (n=10, p=0.754, Fig. 2, Treatment C). Females showed no ability to distinguish between odors of a high- and medium-ranked host (n=12, p=1, Fig. 2, Treatment D), or between a single high-ranked host (*U. dioica*) and a combination of several host plants (n=34, p=0.229, Fig. 2, Treatment E).

Discussion

Our results confirmed our assumption that both butterfly species are able to use olfactory cues in food and host plant context to navigate towards targets. Even though such findings are often assumed and discussed, unequivocal evidence for olfactory navigation in butterflies has so far been scarce. This ability was found in both the generalist and specialist butterfly; however, there seems to be variation in this ability along with the investigated parameters. Whereas mated females of both species were attracted to a host plant odor, virgin females did not show any preference. This finding conforms to a study on the moth *Spodoptera littoralis*, where females shifted their preference from food in an unmated state to a preference for host plant odors after mating (Saveer et al. 2012). Assuming limited processing capacity of the neural machinery (Bernays 2001; Cunningham 2012), sensitivity to host plant odors is not

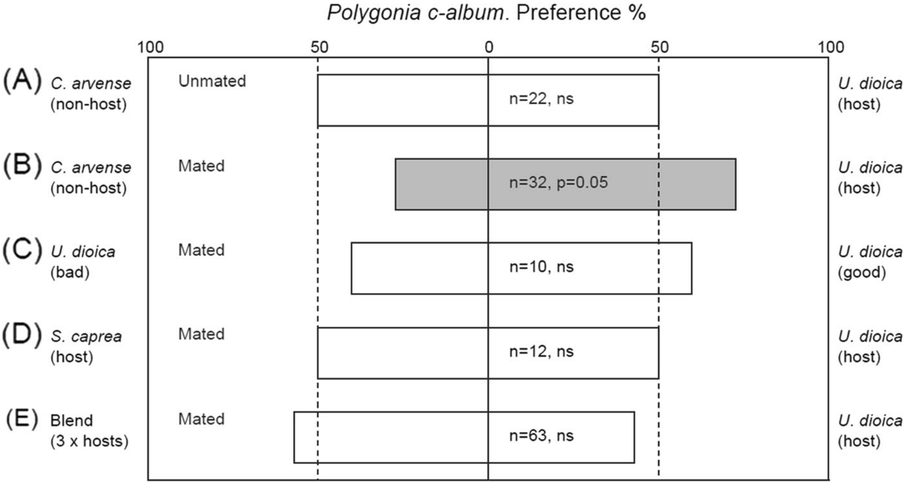

Fig. 2 Preference ratios (%) of the generalist *P. c-album* for either side of the two-way olfactometer. Sample size and α-levels are written within the respective bar, treatment letters in brackets. "n" denotes the total number of responding individuals. Non-host *Cirsium arvense* vs. host *Urtica dioica* in unmated (**a**) and mated (**b**) females; **c** "high" vs. "poor" quality host *U. dioica*; **d** medium-ranked host *Salix caprea* vs. high ranked host *U. dioica*; **e** blend of three hosts (*U. dioica*, *S. caprea*, *Ribes uva-crispa*) vs. the host *U. dioica*

as important in an unmated state. On the other hand, it would be advantageous to simply up-regulate the sensitivity to host plant related odors after mating.

Due to its host specificity and the fact that *A. urticae* lays eggs in batches on its host plant, one should expect a good ability to distinguish between non-hosts and hosts, and even between individuals of the same host plants. As we found in the experiments, mated females showed preferences for odors emitted by host plants and were not distracted when the host was presented together with non-hosts. *Aglais io* and *A. urticae* were found in oviposition assays conducted by Janz and Nylin (1997) and Schäpers et al. (unpublished) respectively, to clearly differentiate between nettles of varying quality. In this light it is interesting to see that females do not differentiate between these categories of plants based on pre-alighting odor cues alone.

Females of *P. c-album* also failed to distinguish between intraspecific host plants of different quality, which is less surprising since females of this species do not appear to be able to make this distinction at all during oviposition (Janz and Nylin 1997). They do, however, show a clear interspecific rank order of plants during oviposition (Janz et al. 1994; Nylin 1988), yet in this study females showed no ability to make this distinction based on olfactory cues alone.

When the relative generalist was presented with three host plants together against a single host, the combined odor of several hosts could potentially either be perceived as conflicting or as reinforcing (additive) signals. The latter alternative could be a possible advantage of having a broader diet if several available hosts in an area could facilitate host location. Our results support neither alternative. Instead, the females made no distinction beyond the simple presence or absence of a host odor in the airstream.

Somewhat to our surprise, this was mostly true also for the specialist. The odor of a host plant seems to be sufficient for both for the generalist and the specialist to be able to navigate towards a patch of host plants, but despite physiological and morphological differences between the generalist *P. c-album* and the specialist *A. urticae* (Carlsson et al. 2011, 2013), it seems that the last piece of host plant evaluation is performed at a later stage in the search process, irrespective of host plant range. A previous study has indeed found that the generalist *P. c-album* can distinguish between different host plants based on contact chemicals (Mozuraitis et al. 2012).

Our results, then suggest that, first, butterflies can use olfactory information alone to navigate towards food or host plant targets; second, both species seem to have limitations in how much information that can efficiently be obtained and used at this stage of the search. Both species seem to be able to distinguish a host from non-hosts, but any further resolution appears to require approaching the plant for further evaluation.

In a wider context this suggests that the quality of the host plant stimulus in combination with the way information is processed set a limit to the resolution an insect can extract from volatile information. The pattern we observed in our experiment could be expected either if the butterflies do not discriminate between host compounds or if they actually contain the same cue compound. This inability to differentiate between the presented alternatives, may result from a modulation of the olfactory information, that simplifies the stimulus and therewith allows the insect to cope with neural processing limitations, as stated by the information processing hypothesis. When detecting a plant-related odor, the possible information may be relayed as a binary signal: either (0) “no host” or (1) “host”. This offers an explanation for why both species failed to make beneficial fine-tuned decisions when comparing the smell of host plants against each other – they perceived a similar presence of a “host” on both sides of the olfactometer. In nature, it is likely that upon detection of host plant-related olfactory cues, butterflies follow these volatiles towards the source, as demonstrated in our experiments. However, the females then need additional cues, such as vision or contact-chemosensation, to assess the plant to reach the decision to land and lay an egg or to reject the plant as host. A previous study found a higher correlation between physiological responses to odorants from different host species in the neurological response of *P. c-album* as compared with *A. urticae* for the same species (Carlsson et al. 2011). This indicates that the reliance of such common host cues would also by necessity make more fine-grained decisions more difficult.

Host location is a complicated process. Females must employ several different sensory modalities on several different levels of resolution to find a potential oviposition site. Hence, the final oviposition event is the result of a process with many steps, where signal processing in each step can lead to the termination and re-setting of the search process. In addition to these female decisions, many larval stages possess the ability to extract sensory information from their environment (Carlsson et al. 1999; Tanaka et al. 2009; van Loon 1990) and locate feeding sites (Holliday 1977; Nylin et al. 2000; Nylin and Janz 1996). These larval capacities further complicate the impact of female evaluation abilities. A high larval capacity to locate feeding sites on their own could relax the pressure on females to find an optimal oviposition site, allowing for less precise female oviposition behavior. For example, Perkins and co-workers (2013) demonstrated differences in behavior of generalist and specialist larvae to induced plant defenses. Thus, it would be highly interesting to delve deeper into investigating larval navigational and dispersal skills and to link such abilities to female oviposition behavior.

In summary, this study investigated how olfactory information is used in two nymphalid butterfly species and how they can be interpreted in an ecological and behavioral context. It demonstrates that butterflies can use olfactory information alone to navigate towards targets, which is especially interesting, as a large body of evidence supports the importance of visual cues for butterflies. Further, we found that this ability is limited to distinguishing between host plants and non-hosts, as females of both the generalist and specialist species did not display preferences in any setup when confronted with a more complex choice. We assume a trade-off between host plant perception and neural processing limitations to be the underlying reason for this incapability. Thus, additional sensory input is required to reach a decision of oviposition or rejection. It will be of high interest to direct future studies both towards how female perception functions in more detail as well as how this oviposition decision interacts with host location and acceptance behavior in other life stages.

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