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Specificity of odour-mediated avoidance of competition in *Drosophila* parasitoids

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Abstract Although there are many examples of the role of volatile infochemicals in interactions between trophic levels of insect communities, surprisingly little is known of volatile interactions between species within the third trophic level. Recently it was found that *Leptopilina heterotoma*, an endoparasitoid that attacks *Drosophila* larvae, avoids one type of patches (decaying stinkhorn mushrooms) when parasitoids of another species (*L. clavipes*) are present on these patches. *L. heterotoma* is able to smell the presence of *L. clavipes* from a distance (Fig. 1). In this paper we investigate the source of the odour that induces avoidance behaviour, by varying the host species and parasitoid species present on stinkhorn mushrooms, and by using another type of patch (sap-fluxes of wounded trees). *L. heterotoma* was found to avoid stinkhorn patches with conspecific as well as heterospecific parasitoids (Fig. 2). Hosts had to be present in the patch to elicit avoidance, but avoidance behaviour was also found with another host species present in the patch (Fig. 3). No avoidance behaviour was found with sap-flux patches with hosts and parasitoids on them (Fig. 4). Avoidance of stinkhorn patches only occurred when the parasitoids present on the patch were able to contact hosts (Figs. 5 and 6). The exact source of the odour that elicits avoidance is still unclear, so that one can only speculate on the function of the signal. However, there is a clear benefit to the receiver, because it is able to avoid superior competitors. Avoidance can lead to non-aggregated parasitoid distributions. The importance of avoidance behaviour for population dynamics and stability of parasitoid-host systems is discussed.

Key words Semiochemicals · Parasitoids · Avoidance · Interspecific competition · Olfactory searching

Introduction

Since the appearance of two papers by Price and coworkers (Price et al. 1980; Price 1981), a number of studies have focused on the role of volatile compounds in interactions between members of simple tritrophic food chains consisting of a plant, one species of herbivore and one natural enemy of this herbivore (see Dicke et al. 1993; Tumlinson et al. 1993; Dicke 1994 for review). These studies specifically consider the role of volatiles in the interactions between host plant and natural enemy.

Interspecific interactions involving volatiles *within* trophic levels have received little attention. A few examples of such interactions within the second trophic level come from studies of bark beetles (Wood 1982; Byers 1993; and references in Price 1981). Within the third trophic level, the study of Price (1970) is the first and only example of infochemicals (*sensu* Dicke and Sabelis 1988) that mediate interspecific interactions. He found that ichneumonid parasitoids avoided areas that had previously been searched by conspecific and heterospecific wasps. Price concluded that his parasitoids produced trail odours, and showed that this odour is recognised by parasitoids that enter the presearched area. It is not clear whether the signals from the trails were actually volatile and could have been perceived from a distance.

A recent example of the role of volatiles in interactions between species of the third trophic level concerns *Leptopilina heterotoma* Thompson (Hymenoptera: Eucoilidae) (Janssen et al. 1991; Janssen et al. in press). This parasitoid attacks *Drosophila* larvae in several types of patches. Three patch types predominate in mid-summer, a period of high parasitoid activity:

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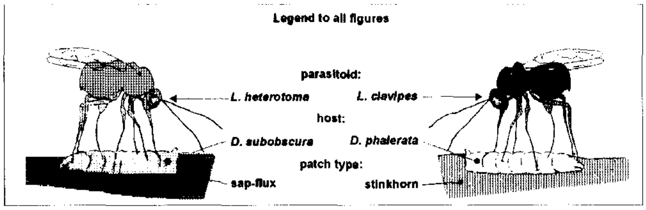
sap-fluxes of wounded trees and two types of rotting and fermenting fungi (Janssen et al. 1988). *L. heterotoma* females are rarely found on stinkhorns (*Phallus impudicus* Pers.), one of the fungus species, although host-infested stinkhorns are very attractive in olfactometer experiments in the laboratory (Fig. 1, top bar) and offspring of *L. heterotoma* survive quite well in the host species present in stinkhorns in the field (Janssen 1989).

The reason that *L. heterotoma* avoids visiting stinkhorn patches in the field seems to be that most stinkhorns in the field are occupied by *L. clavipes* (Hartig), a closely related parasitoid. Olfactometer experiments showed that *L. heterotoma* females prefer the odours of stinkhorn with hosts to odours of stinkhorn, hosts, and searching *L. clavipes* parasitoids (Fig. 1, lower bar). Furthermore, *L. heterotoma* females that were released 0.7 m downwind from stinkhorn patches with hosts and searching *L. clavipes* avoided visiting these patches and flew away (Janssen et al. in press). Competition between offspring of both parasitoids within hosts is strongly asymmetric, and in favour of *L. clavipes*. Hence, *L. heterotoma* is able to smell odours associated with the presence of searching *L. clavipes* parasitoids, and it uses the odours to avoid patches with these parasitoids. This leads to a reduction in interspecific competition for hosts.

It is not yet known whether this avoidance behaviour is specific for the presence of *L. clavipes* on stinkhorns, or whether avoidance behaviour also occurs with other types of patches, other host species, or other parasitoids. This paper describes experiments that were done to further investigate the conditions under which avoidance behaviour occurs, by offering *L. heterotoma* odours of stinkhorn with two different host and parasitoid species, and odours from sap-fluxes with hosts and parasitoids.



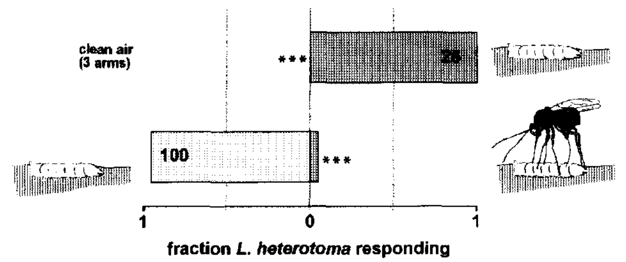


Fig. 1 The fraction of *Leptopilina heterotoma* female parasitoids responding to several combinations of odour sources in a Pettersson olfactometer. The fractions responding to either odour source are shown. *Upper bar*: the odour of 5 g of stinkhorn (*Phallus impudicus*) with 20 *Drosophila phalerata* larvae (*right*) was led through one arm of the olfactometer, whereas clean air was lead to the remaining three arms (*left*). *Lower bar*: stinkhorn infested with *D. phalerata* hosts in one arm (*left*), tested against stinkhorn with *D. phalerata* plus searching *L. clavipes* parasitoids in another arm (*right*). Clean air was led through the other two arms. *Numbers inside bars* indicate the number of females tested. *** $P < 10^{-6}$, two-tailed binomial test. See Materials and methods for experimental set-up

Materials and methods

The procedures for rearing *Drosophila* and parasitoids were described earlier (Janssen 1989; Driessen et al. 1991). The host species used were *Drosophila phalerata* Meigen, the predominant species in stinkhorn, and *D. subobscura* Collin, a species that often breeds in sap-fluxes (Janssen et al. 1988; Driessen et al. 1990). Parasitoids used were *L. heterotoma* Thompson and *L. clavipes* (Hartig). *L. heterotoma* females were reared on second stage *D. subobscura* larvae, whereas *L. clavipes* was reared on *D. phalerata*. Upon emergence from their host, parasitoids were stored at 20°C in a vial with an agar bottom to humidify the air, and a piece of filter paper dipped in a honey solution to provide food. Parasitoids used for experiments were c. 7 days of age, and had never searched or oviposited. Second-instar host larvae were used in all experiments.

Samples of patches (i.e. stinkhorn mushrooms) were collected in summer in the field (Janssen et al. 1988; Janssen 1989). Care was taken that samples contained host larvae and/or eggs, because such samples contain an aggregation pheromone deposited by adult *Drosophila* that oviposit on a patch. This pheromone is strongly attractive for parasitoids (Wiskerke et al. 1992). Upon collection, samples were stored in a freezer (−20°C). Samples were defrosted the day prior to experiments. Because host and parasitoid larvae do not survive the low temperature of the freezer, samples were re-infested with second instar host larvae. Care was taken to use equal amounts of sample material (c. 5 g) for all odour sources and the same numbers of hosts were added to each sample. In experiments where both odour sources consisted of stinkhorn, we used the halves of a single stinkhorn, split lengthways, to produce odour sources that were as similar as possible.

A Pettersson olfactometer (Vet et al. 1982) was used to test attractiveness of patches in the laboratory. It consists of a flat, diamond-shaped perspex chamber, where odours enter through inlets in the four corners, and air is sucked through a hole in the centre of the bottom. A series of three vials was connected to each of the four inlets. The vial closest to the olfactometer was empty and served to collect parasitoids that left the olfactometer, the second contained the odour source, and the third contained demineralized water to humidify the air. The series of vials was connected to a flow meter with a needle valve to measure and adjust wind speed. With the proper speed, four separated odour fields are obtained in the chamber (Vet et al. 1982). In all experiments, the odour sources were put in vials connected to adjacent odour inlets, resulting in two neighbouring odour fields in the olfactometer. Clean air was led through the other two odour inlets. The odour sources were connected to another arm of the olfactometer after testing ten parasitoids to correct for unforeseen asymmetries in the experimental set-up.

When a parasitoid is introduced through the central outlet in the bottom, it can choose between the odours, and walk in the direction of one of the odour inlets. Upon introduction, each female parasitoid was observed for 10 min, or until she left the olfactometer through the odour inlet of one of the arms, to end up in the collecting vial. Only the numbers of females that left the chamber in this way were used for subsequent analysis. Few parasitoids chose for an empty odour field in all experiments. For clarity, these numbers are not presented in this paper. Each individual was tested only once.

When odour sources had to contain searching parasitoids, three to five adult female parasitoids were added to the source 1 h prior to the olfactometer experiment. The searching activity of these females, defined as the rhythmical probing in the substrate with their ovipositor, was checked regularly before and during experiments, and individuals that did not search were replaced. Parasitoids tested in the olfactometer were prevented to see the odour sources or the parasitoids searching thereon to rule out any effect of visual cues. When a significant difference in attraction between odour sources with and without searching adult females was found, the adult females were transferred from their odour source to the alternative source, and both sources were subsequently used for another replicate of the same experiment. This was done to ensure that differences in attractiveness were not due to differences between patches, but to the presence of searching parasitoids on the patches.

The patch type used as an odour source and the species of host and parasitoid present in the odours source were varied separately or in combinations to elucidate the specificity of the odour that invokes avoidance behaviour.

The parasitoid species

To test whether *L. heterotoma* also avoids patches with parasitoids other than *L. clavipes*, we offered *L. heterotoma* females a choice between odours emanating from two equal quantities of stinkhorn with equal numbers of *D. phalerata* hosts, but with five searching *L. heterotoma* parasitoids added to one, and five searching *L. clavipes* females added to the other stinkhorn.

The host species

Several experiments were done to test whether avoidance behaviour occurs specifically when *D. phalerata* hosts are present. First, *L. heterotoma* was given a choice between the odours of two equal parts of stinkhorn with searching *L. clavipes* parasitoids, one with the host species *D. phalerata,* and the other with *D. subobscura* hosts. To test the combined effect of changing host and parasitoid species, *L. heterotoma* parasitoids were offered the odours of stinkhorn with *D. subobscura* hosts and stinkhorn with *D. subobscura* hosts and searching *L. heterotoma.*

To test whether the presence of hosts was necessary at all for avoidance, *L. heterotoma* parasitoids were offered a choice between the odours of stinkhorn without hosts or parasitoids and a similar piece of stinkhorn with *D. phalerata* hosts and searching *L. clavipes* parasitoids, and between the odours of stinkhorn without hosts and parasitoids and stinkhorn without hosts but with searching *L. clavipes* parasitoids.

The patch type

The effect of the type of patch on avoidance behaviour was tested by offering *L. heterotoma* a choice between the odours of 5 g of sap-flux infested with *D. subobscura* hosts and a similar sample of sap-flux with an equal amount of hosts and five searching *L. heterotoma* parasitoids.

Separating hosts from parasitoids

To investigate whether actual interactions between the hosts and parasitoids present on a patch are necessary to elicit avoidance behaviour an additional vial was connected to one of the arms of the olfactometer. After passing through the vial with demineralised water, the air was passed through a vial with *L. heterotoma* parasitoids only, then through a vial with stinkhorn with *D. subobscura* hosts, and subsequently through an empty vial into the olfactometer. In this way, the odours of parasitoids, hosts and stinkhorn were combined, without the possibility of physical contact between parasitoids and hosts. A series of three vials was connected to the three other arms. The middle vial connected to one of the arms next to the arm with four vials contained stinkhorn with *D. subobscura* hosts. Because the extra vial with parasitoids did not contain any stinkhorn or other substrate, parasitoids in this vial did not show any of their typical searching behaviour. To investigate the possibility that odours responsible for avoidance behaviour are specifically produced by *searching* parasitoids, we did a series of similar experiments with combined odour sources, but now 5 g of stinkhorn without hosts was added to the vial containing parasitoids. The parasitoids readily searched on the piece of stinkhorn without hosts. To compensate for the extra 5 g of stinkhorn added to one odour source, we also added an extra vial with an equal amount of stinkhorn without hosts to the other odour source. With this set-up, a series of experiments were done with the vial with parasitoids and stinkhorn connected upwind from the vial with stinkhorn and hosts, and another series with the vial with parasitoids downwind. In the latter case, the parasitoids in the vial were able to perceive odours from the vial with hosts. The parasitoid species *L. clavipes* and host species *D. phalerata* were used in these experiments.

Results

The parasitoid species

When *L. heterotoma* was offered a choice between the odours of stinkhorn with *D. phalerata* hosts and searching *L. heterotoma* parasitoids and a similar piece of stinkhorn with an equal number of *D. phalerata* hosts and searching *L. clavipes* parasitoids, no preference for either of the two arms was found (Fig. 2). This suggests that avoidance behaviour is elicited by the presence of *L. heterotoma* as well as *L. clavipes* parasitoids.

The host species

Leptopilina heterotoma females were offered a choice between the odours of stinkhorn infested with *D. phalerata* hosts plus searching *L. clavipes* parasitoids and stinkhorn infested with *D. subobscura* hosts and similar parasitoids. Figure 3 (upper bar) shows that there may be a slight difference in preference between the two odour sources, but this difference is not significant.

Avoidance behaviour was found when *L. heterotoma* could choose between the odours of stinkhorn with *D. subobscura* hosts and stinkhorn with similar hosts and searching *L. heterotoma* (Fig. 3, second bar) Compared to the original experiment, both host and parasitoid species were now different. Hence, avoidance behaviour is not only elicited through the presence of a specific host (Fig. 3, upper bar) or parasitoid species (Fig. 2) or a combination of the two (Fig. 3, second bar).

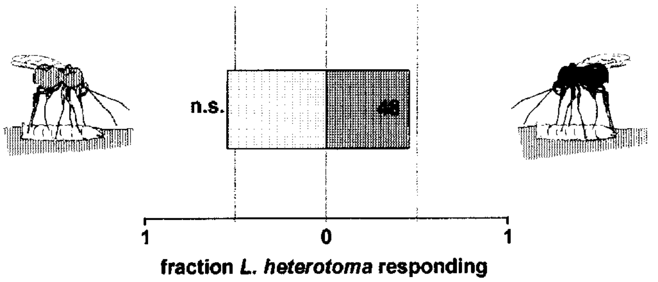


Fig. 2 The effect of parasitoid species on avoidance behaviour of *L. heterotoma* parasitoids in an olfactometer. *L. heterotoma* females could choose between the odour of stinkhorn with *D. phalerata* hosts and searching *L. heterotoma* parasitoids (*left*) and the odour of stinkhorn with similar hosts and searching *L. clavipes* parasitoids (*right*). See Fig. 1 for further explanation. *n.s.* not significant (two-tailed binomial test)

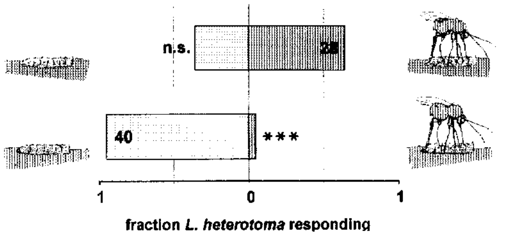


Fig. 4 The effect of patch type on avoidance behaviour of *L. heterotoma* females in an olfactometer. *Upper bar*: *L. heterotoma* parasitoids could choose between odours of sap-flux with *D. subobscura* hosts (*left*) and odours of sap-flux with similar hosts and searching *L. heterotoma* (*right*). *Lower bar*: odour sources were stinkhorn with *D. subobscura* (*left*) and stinkhorn with similar hosts and searching *L. heterotoma* parasitoids (*right*). This bar is equal to the second bar of Fig. 3, and is added for comparison. See Fig. 1 for further explanation. ***$P < 10^{-6}$; *n.s.* not significant (two-tailed binomial test)

The third bar of Fig. 3 shows that *L. heterotoma* parasitoids actually prefer the odour of stinkhorn without hosts and searching competitors to the odour of stinkhorn with both hosts and competitors present, and the lower bar shows that this effect is absent when the hosts are removed from the stinkhorn with competitors as well. Thus, there is a distinct effect of the presence of hosts on the occurrence of avoidance behaviour, but this effect is not host species specific. It can also be concluded that the presence of parasitoids without hosts does not elicit avoidance (lower bar of Fig. 3).

Patch type

The effect of patch type on avoidance behaviour was tested by offering *L. heterotoma* a choice between odours of host-infested sap-fluxes with and without searching conspecifics (Fig. 4, upper bar). For comparison, we included results of a similar experiment with stinkhorn (lower bar of Fig. 4 = second bar of Fig. 3). Contrary to results with stinkhorn, no avoidance was found with sap-fluxes. Hence, there is a clear effect of patch type on avoidance behaviour.

Separating hosts from parasitoids

When *L. heterotoma* could choose between odours of two equal pieces of stinkhorn infested with equal numbers of *D. subobscura*, but with an extra vial with *L. heterotoma* parasitoids added to one of the two, no avoidance behaviour was observed (Fig. 5, lower bar). For comparison, results from an earlier experiment where parasitoids in the odour source were able to contact hosts, are presented (upper bar of Fig. 5 = second bar of Fig. 3). Apparently, parasitoids need to search and/or oviposit in order to cause an odour source to become less attractive.

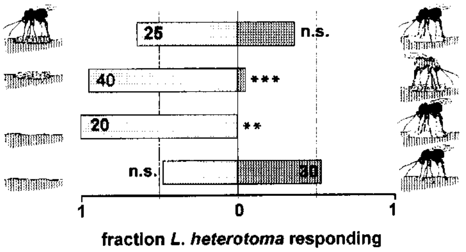


Fig. 3 The effect of hosts on avoidance behaviour of *L. heterotoma* females in an olfactometer. *Upper bar*: *L. heterotoma* parasitoids could choose between odours of stinkhorn with *D. subobscura* hosts and searching *L. clavipes* parasitoids (*left*) and odours of stinkhorn with *D. phalerata* hosts and similar parasitoids (*right*). *Second bar*: odour sources were stinkhorn with *D. subobscura* hosts (*left*) and stinkhorn with similar hosts and searching *L. heterotoma* parasitoids (*right*). *Third bar*: odour sources were stinkhorn without hosts or parasitoids (*left*) and stinkhorn with *D. phalerata* hosts and searching *L. clavipes* parasitoids (*right*). *Lowest bar*: stinkhorn without hosts or parasitoids (*left*) versus stinkhorn without hosts but with searching *L. clavipes* parasitoids (*right*). See Fig. 1 for further explanation. **$P < 10^{-5}$; ***$P < 10^{-6}$; *n.s.* not significant (two-tailed binomial test)

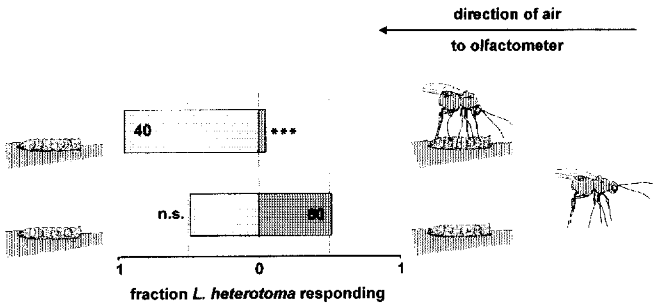


Fig. 5 The effect of separating hosts and parasitoids in an odour source on avoidance behaviour of *L. heterotoma* females in an olfactometer. *Upper bar*: *L. heterotoma* could choose between the odour of stinkhorn infested with *D. subobscura* hosts (*left*) and the odour of stinkhorn with similar hosts and searching *L. heterotoma* parasitoids (*right*). This bar is equal to the second bar of Fig. 3, and is added for comparison. The *lower bar* shows the response of *L. heterotoma* to odours of stinkhorn infested with *D. subobscura* (*left*) tested against odours of stinkhorn with similar hosts plus an extra vial with *L. heterotoma* parasitoids positioned upwind from the stinkhorn (*right*). See Fig. 1 for further explanation. ***$P < 10^{-6}$; *n.s.* not significant (two-tailed binomial test)

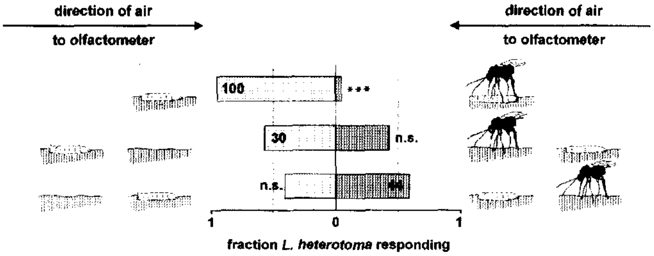


Fig. 6 Further effects of separating hosts and parasitoids in an odour source on avoidance behaviour of *L. heterotoma* parasitoids in an olfactometer. *Upper bar*: *L. heterotoma* females could choose between the odours of stinkhorn infested with *D. phalerata* hosts (*left*) and odour of stinkhorn infested with similar hosts and searching *L. clavipes* parasitoids (*right*). This bar is equal to the lower bar of Fig. 1, and is added for comparison. *Middle bar*: response of *L. heterotoma* to the combined odour of stinkhorn with *D. phalerata* hosts and stinkhorn without hosts (*left*) vs. stinkhorn with similar hosts and stinkhorn with searching *L. clavipes* parasitoids (*right*). The *L. clavipes* parasitoids were placed in a vial separate from the stinkhorn with hosts and were thus unable to contact the hosts. *Lowest bar*: similar to *middle bar*, but with the vial with searching *L. clavipes* parasitoids positioned upwind of the stinkhorn with hosts

When parasitoids were again separated from hosts, but were able to search on a piece of stinkhorn without hosts, again no avoidance was elicited (Fig. 6, lower two bars). For comparison, results from experiments with *L. clavipes* and hosts present in the same vial are also presented (upper bar of Fig. 6 = lower bar of Fig. 1). There was no difference in response of *L. heterotoma* in experiments with parasitoids upwind or downwind from the infested stinkhorn (lower two bars, $\chi^2 = 1.2$, $P = 0.27$). It can be concluded that contact of parasitoids with hosts is necessary to elicit avoidance behaviour.

Discussion

L. heterotoma is able to smell odours associated with the presence of conspecific and heterospecific parasitoids on host patches, and it avoids patches with these competitors. This avoidance only occurs when both hosts and parasitoids are present on the same patch. Both species of hosts and parasitoids tested here elicit avoidance behaviour. This is the first example of a truly volatile signal that causes interspecific interactions between members of the third trophic level. It remains to be investigated whether *L. clavipes* can also avoid patches with con- and heterospecific parasitoids.

Price (1970) attributed the avoidance reaction that he found with ichneumonid parasitoids to the pungent odour produced by ichneumonids in general. Adult *Leptopilina* females also produce a pungent odour, but this odour alone cannot be responsible for the avoidance behaviour observed here, since it is also produced in the absence of hosts (personal observations), and parasitoids without hosts did not elicit avoidance behaviour in the receiver (Figs. 5 and 6). Hence, the circumstances under which the signal is produced seem more specific than those of the system studied by Price (1970).

Recently, it was found that an aphid primary parasitoid avoided patches with hyperparasitoids (Höller et al. 1994). This is an example of the role of volatiles in interspecific interactions between the third and fourth trophic level. However, to show avoidance behaviour at a distance, Höller and co-authors added 200 mated adult female hyperparasitoids to the odour source. This seems an unrealistically high density of hyperparasitoids, and it is still unclear whether avoidance behaviour would have been found had more natural densities of hyperparasitoids been used. The numbers of parasitoids used in our study are well within the range of densities found in the field (Driessen et al. 1990). Moreover, *L. heterotoma* do seem to avoid patches with *L. clavipes* in the field.

It seems strange that *L. heterotoma* actually prefers stinkhorn patches without hosts to stinkhorns with hosts and parasitoids (Fig. 3, third bar). As mentioned earlier, this parasitoid responds to an aggregation pheromone deposited by adult *Drosophila* females (Wiskerke et al. 1992). Since the stinkhorns used here did contain *Drosophila* eggs and larvae when collected in the field, it is likely that the stinkhorn patches used in the olfactometer still elicited these pheromones, causing the attractiveness of the patches without hosts.

Production and evolution of the signal

Although it is clear that *L. heterotoma* females avoid stinkhorns with con- and heterospecific parasitoids, the exact source of the odour remains unknown. The odour could be produced by parasitoids searching for hosts. It could then serve two goals:

A. The volatile serves as a pheromone to mark parasitised hosts or area already searched. This is an unlikely scenario because a volatile marker would quickly diffuse into the environment, leaving the host or area without a mark, or marking unparasitised hosts or unsearched areas.

B. The volatile serves to warn other parasitoids. In such a case, the pay-off to the emitter would strongly depend on the reaction of the receivers, and this reaction is likely to depend on habitat quality: it is expected that parasitoids will refrain from visiting oviposition sites already occupied by others when unoccupied sites are available. When occupied patches are scarce, however, parasitoids searching for patches will also accept patches with competitors. In this case the emitter would not benefit from producing the signal. Evolution of the signal would thus depend on the costs associated with producing the signal and the benefit of the signal to the receiver (see Nagelkerke et al. in press, for a similar discussion).

The volatile signal could also be produced by host larvae that are being attacked. Again, it is difficult to envisage a direct benefit to the producer, because host larvae have a low probability of surviving parasitism (Janssen 1989). An alternative explanation would be that the signal is produced to alarm related host larvae. Since individual *Drosophila* females deposit clutches of eggs at one breeding site, there is a distinct possibility that some of the other host larvae present are related to the larva that is being attacked. Nothing is known about the olfactory apparatus of *Drosophila* larvae. In fact, it is difficult to imagine how they could perceive any odour at all, because they spend most of their time buried in the substrate.

The volatile signal may also be produced as a side-effect of the oviposition behaviour of the parasitoid. Volatiles may for example escape from hosts through the wound produced by the parasitoid's attack, and parasitoids that are able to perceive this odour may experience a selective advantage because they can avoid competition. However, the leaking of volatiles from hosts would not explain the effect of patch type on avoidance (Fig. 4).

To summarise, it is not yet clear who produces the avoidance-invoking odour. Identification of the odour could help in determining the exact odour source. However, this will be very difficult, because the odour will be mixed with the numerous volatiles emitted by stinkhorns and their associated micro-organisms.

Avoidance behaviour and population dynamics

Theoretical studies of population dynamics of parasitoid-host systems have shown that aggregation of parasitoids on certain host patches can determine stability or instability of host-parasitoid systems (Hassell and May 1973, 1974, 1988; Murdoch and Steward-Oaten 1989; Hassell et al. 1991; Pacala and Hassell 1991; Murdoch et al. 1992). These studies are based on the intuitively appealing notion that parasitoids and predators should search longer in patches with higher prey densities. However, mechanisms *causing* the distribution of parasitoids over host patches have received relatively little attention. Here we show that parasitoids use odours to avoid patches where conspecifics or heterospecifics are present. This mechanism may prevent the formation of aggregations and promote the occurrence of ideal free distributions of parasitoids over host patches. Ideal free distributions have been shown to have a significant impact on host-parasitoid interactions; they reduce the parameter space where stable dynamics are found (van Baalen and Sabelis 1993). Future theoretical and empirical studies of host-parasitoid dynamics should therefore consider avoidance behaviour.

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