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Attraction of *Dibrachys cavus* (*Hymenoptera: Pteromalidae*) to its Host Frass Volatiles

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Abstract The European grapevine moth, *Lobesia botrana* (Lepidoptera: Tortricidae), is a polyphagous insect able to develop on grapes and wild plants. We tested the hypothesis that the parasitoid *Dibrachys cavus* (Hymenoptera: Pteromalidae) uses the larval frass in its host search. A two-armed olfactometer was used to measure the attractiveness of *L. botrana* larvae, their silk, or their frass after larvae were fed on different host plants. Frass of three Lepidoptera (*L. botrana*, *Eupoecillia ambiguella*, *Sphinx ligustri*) and one Orthoptera (*Chorthippus brunneus*) was assayed, but only *L. botrana* was used to test an effect of the larval host plant (two grape cultivars and three other plant species) to *D. cavus* females. Larvae without frass did not attract *D. cavus* whatever their origin, but their frass was attractive at a dose of 2–3 days equivalent of larval frass production. The silk produced by a single larva (*L. botrana*) was not attractive to *D. cavus*. The parasitoid was most attracted to the odor of *S. ligustri*; the frass of *L. botrana* was more attractive than that of *E. ambiguella*, irrespective of the species on which *D. cavus* had been reared. There was no difference in attractiveness of frass collected from *L. botrana* raised on food containing different plants. Chemical extracts using five different polarity solvents (acetone, dichloromethane, hexane, methanol, and water) differed in attractiveness to *D. cavus*. Water and dichloromethane were the most attractive. This suggests that a complex volatile signal made from intermediate to polar volatiles may be involved in attraction. *D. cavus* used frass to discriminate between different potential host species. Our results revealed that the larval food of *L. botrana* did not modify frass attractiveness, but that the moth species did.

Keywords Parasitoids · Tortricids · Vineyard · Host-plant · Tritrophic interactions · Attraction to odors · Olfactometer · *Lobesia botrana* · *Eupoecilia ambiguella* · *Vitis vinifera* · *Daphne gnidium* · *Rosmarinus officinalis* · *Tanacetum vulgare*

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Introduction

Generalist phytophagous insects feed on a wide variety of plant species. However, their host choice is of ecological importance, and the host species on which females oviposit affects the development and fitness of offspring (Jaenike, 1978; Singer, 1983; Courtney et al., 1989). In many herbivorous species, young instars are more vulnerable to natural enemies and are less efficient at escaping natural enemies than imagoes (Nomikou et al., 2003). It would be advantageous for adult herbivores to discriminate among risky and safe host plant species, and thus to select high-quality host plants whatever the risk is when the threat of natural enemies is low (Freitas and Oliveira, 1996). Moreover, natural enemies may exert selection pressure on the host plants used by phytophagous insects (Ohsaki and Sato, 1999; Stireman and Singer, 2003; Singer and Stireman, 2003). For example, a plant that contains defensive allelochemicals or precursors can be chosen by a phytophagous insect for the protection it provides against natural enemies (Stamp, 2001; Shiojiri et al., 2002). Plants can also change phytophagous aspects so that the attractiveness of their by-products (e.g., frass) to the parasitoids is modified (Mondor and Roland, 1997).

Grape berry moths, *Lobesia botrana* (Lepidoptera: Tortricidae) and *Eupoecilia ambiguella* (Lepidoptera: Tortricidae), are among the most serious insect pests in European viticulture. Both are polyphagous and may occur sympatrically in vineyards, but their relative frequency depends on climatic factors (Thiéry, 2005). The larval host plant, including the grape cultivar, modifies several patterns involved in the reproductive output of *L. botrana*, for example, the development time of the larvae (Savopoulou-Soultani et al., 1994; Thiéry and Moreau, 2005; Moreau et al., 2006a) and larval metabolism. As a result, infochemicals produced by larvae may be modified as in other species (Lill and Marquis, 2001; Thorpe and Day, 2002). The host plant ingested by *L. botrana* larvae during its development may also modify parasitism of eggs by the generalist egg parasitoid *Trichogramma cacoeciae* (Thiéry, Pizzol, and Wajnberg, unpublished data).

Female *L. botrana* exhibit preferences among the different grape cultivars (Maher et al., 2001), and larvae feed on the plant on which the eggs are laid, most of the larvae developing close to the oviposition site. Therefore, the chemical cues related to frass are always located close to the larvae themselves, and thus provide pertinent local information for a larval parasitoid. Frass is often a relevant cue for natural enemies during the host location process (Auger et al., 1990; Reddy et al., 2002; Steidle and Van Loon, 2003), and it can be expected to be relevant also to our model/system.

Several studies have shown that parasitoids and predators can be efficient biological control agents against the different grape berry moths. As much as 50–60% of the moth larvae can be naturally controlled (Luciano et al., 1988; Coscolla, 1997; Thiéry et al., 2001; Bagnoli and Lucchi, 2005; Thiéry et al., 2006). The main parasitoids reported in most European vineyards belong either to Hymenoptera (Trichogrammatidae, Ichneumonidae, Braconidae or Pteromalidae) or to Diptera (Tachinidae; Thiéry et al., 2001, 2006). The pteromalid wasp *Dibrachys cavus* is a generalist, gregarious ectoparasitoid of more than 200 species belonging to different families (Peck, 1963, Universal Chalcidoïdea Database, 2003). It has been found on overwintering pupae of *L. botrana* in France (Causse et al., 1984), Italy (Marchesini and Della Monta, 1994), and Spain (Coscolla, 1997). This parasitoid is a multivoltine species that can attack each generation of *L. botrana* (Faure and Zolstarewsky, 1925). *D. cavus* parasitizes fifth instars of *L. botrana* just before pupation and not pupae (Faure and Zolstarewsky, 1925; Chuche, Xuéreb and Thiéry, unpublished observations).

The goal of our study is to determine which components of the host odor attract *D. cavus* from a distance. Thus, we tested the specificity of such an attraction and whether it varied according to the larval food plant. First, we tested the response of *D. cavus* females to host larvae without frass, to silk, and to frass alone, and whether it discriminated among different host species on the basis of their odor. Second, we tested the influence of host larval food and frass for attractiveness.

Methods and Materials

Insects

Our *D. cavus* strain originates from grapes harvested in an experimental vineyard (INRA Bordeaux, La Ferrade). Insects were reared in the laboratory for successive generations on *L. botrana* larvae under a 16:8 (light–dark) photoperiod, at 23 ± 1°C, and 45–50% relative humidity. Under these conditions, adults *D. cavus* emerged ca. 20 days after oviposition on the larval cuticle. Emerging adults were collected daily, except during the weekends, transferred into new boxes containing fifth instars *L. botrana*, and supplied with a 20% honey–water solution. We used a strain of *L. botrana* reared without diapause under the conditions described above on a semisynthetic diet (control medium) as described in Thiéry and Moreau (2005), and a strain of *E. ambiguella* reared in our laboratory (same conditions as for *L. botrana* except 60–70% relative humidity). All experiments were performed in a climate chamber under controlled conditions as described above. *D. cavus* were all 48-hr-old, mated, fed females with no previous oviposition experience. They were tested only once. The frass of four phytophagous insect species was tested: three Lepidoptera—*L. botrana*, *E. ambiguella*, and *Sphinx ligustri* (Sphingidae)—and an Orthoptera selected as a control: *Chorthippus brunneus* (Acrididae). The Sphingidae and the Orthoptera used have never been described as *D. cavus* hosts.

Plants, Insect Diets, Frass Collection, and General Procedure

Grape cultivars supplied as larval food were compared using a standardized procedure adapted from that described by Thiéry and Moreau (2005) and Moreau et al. (2006a). *L. botrana* larvae were reared in enclosed plastic cups (diam: 3 cm on base and 4 cm on top; height: 3 cm) with five larvae per cup, filled with 15 ml of artificial diet. This medium was identical to the two references quoted above. Plant material was freeze dried, and a fine powder was made using a blender as described in Moreau et al. (2006a). A limited range of host plants was tested, two grape cultivars: *Vitis vinifera* (Vitaceae) cv. Pinot noir and Riesling, the presumed ancestral host of *L. botrana*: *Daphne gnidium* (Thymelaeaceae; Maher and Thiéry, 2006), another possible host plant of *L. botrana*: *Rosemary officinalis* (Lamiaceae; Katerinopoulos et al., 2005), and tansy: *Tanacetum vulgare* (Asteraceae) used as a possible repellent source for *D. cavus.* We used bunches of *V. vinifera* harvested in mid-July, *T. vulgare* flowers (β-thujone chemotype, cf. Gabel and Thiéry, 1994), leaves of *R. officinalis*, and flowers, and berry of *D. gnidium*. Plants were all collected on the INRA Bordeaux site.

Box lids were pierced to allow air circulation. Using a fine brush, five newly hatched larvae (age < 24 hr) were transferred into each box: 15 boxes for *R. officinalis* and *D. gnidium* diet, 30 for Pinot noir and *T. vulgare*, 45 for Riesling, and control.

The two grape moths were fed on the control medium and their frass was collected. Sphinx frass was harvested from a natural population of larvae collected from *Catalpa* *bignonioides* (Bignoniaceae) leaves. Larvae of *C. brunneus*, a specialist of Poacea, were harvested from a natural population in the Limoges area, and their frass were collected.

Bioassays

Experiments were conducted by using a T-tube olfactometer made of transparent glass (0.4 cm ID; stem 10 cm, arms 5 cm). Each arm was connected to a small plastic chamber holding the odor source (Fig. 1). To avoid contact with the odor source and to hide the source, small pieces of black glass fiber tissue were placed at the ends of each arm of the olfactometer. Filtered air (0.3 l min^{-1}) was sucked through the olfactometer by a pump connected to a flowmeter. Females were individually introduced into the olfactometer and observed for at least 2 min. Females that did not express a choice after 2 min were discarded. A female that settled at least 10 sec near one of the container was scored.

To avoid a bias due to possible chemical marking of the walking tracks, the glass tube and the glass fiber tissue were changed after each test. The position of the T-tube was turned 180° after each test to avoid effects of any directional bias. The T tubes were washed in hot water (ca. 70°C), rinsed in purified high-performance liquid chromatography (HPLC) quality water, and dried in an oven at 60°C before each experiment. All tests were performed between 09:00 and 18:00. All experiments were conducted under artificial light at 24 ± 1°C. A white circular paperboard arena (diam: 35 cm; height: 21 cm) surrounded the olfactometer to prevent visual perturbations and to create a homogeneous light. *D. cavus* females were offered different dual choices.

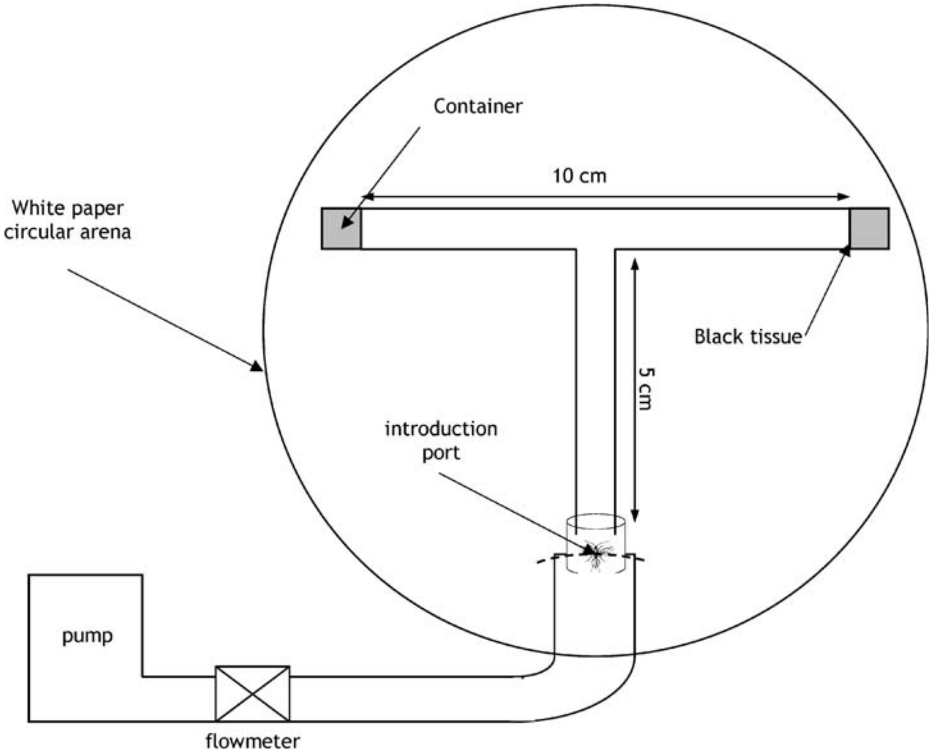

Fig. 1 T-tube olfactometer and set-up used in this study. Details are provided in the text

Responses to Larvae, Silk, and Frass

Attractiveness of fifth instar *L. botrana* or of their by-products (silk and frass) was tested. In this experiment, parasitoids were given the choice between one larva or 0.07 mg of silk, which corresponds to the average mass of a *L. botrana* cocoon, or 0.02 g of frass (i.e., the average production of two to three larvae in 24 hr or the larval production in 2–3 d) and a blank (no odor). Twelve cocoons of larvae reared on control medium were weighed to calculate the average amount of silk produced per larva. The average amount of frass produced per *L. botrana* larva was calculated from 19 fourth instars (L4) reared on control medium and by collecting their frass produced during 24 hr. The average amount collected in this condition was 9.96 ± 4.78 mg. Because of the small number of *E. ambiguella* and *S. ligustri* larvae, their attractiveness could not be tested.

Preferences for *L. botrana* Larvae Reared on Different Foods

The attractiveness of larvae fed on different plants (Pinot noir, Riesling, or *T. vulgare*) was compared with larvae fed on control medium.

Preferences for Frass Produced by Different Species

Frass produced by the three Lepidoptera species was compared at the identical mass mentioned above. To test the influence of the rearing host on the olfactory response of parasitoid females, some *D. cavus* were reared on *E. ambiguella*, as described for *L. botrana*. These parasitoids had the choice between frass produced by the two tortricids.

Preferences for *L. botrana* Frass from Different Larval Foods

Frass collected from larvae fed with different plants (Pinot noir, Riesling, *T. vulgare*, *D. gnidium*, or *R. officinalis*) was compared with those of larvae fed on control medium or on another plant supplemented medium.

Responses to Solvent Extracts

To isolate attractive cues, *L. botrana* frass was extracted by using solvents with different polarities. Three ml of solvent were added to 172.5 mg of dry frass (the production of ca. 300 L4). After 15 min at room temperature, frass was removed. Five different solvents were used: acetone, dichloromethane, hexane, methanol (99–99.80% purity, SDS, Peypin, France), or purified HPLC quality water. Each solvent was tested in the olfactometer, and none was found repellent or attractive. *D. cavus* females were given the choice between an extract and its respective solvent. Extracts and solvents were presented on a piece of Whatman paper (1 cm^2). Different volumes were tested: 10, 30, and 60 μl, corresponding to 1, 3, and 6 larval equivalents, respectively.

Statistical Analysis

Statistical tests were performed using Statistica Software (Version 6.0, Stat Soft, Inc.). Attraction scores were analyzed using the Cochran *Q test*.

Results

Responses to Larval Silk and Frass

Female parasitoids were not attracted to larvae ($N=100$; $Q=0.1$; $P>0.05$) nor to silk ($N=99$; $Q=2.13$; $P>0.05$; Fig. 2). However, *D. cavus* females were attracted to the frass of the three Lepidoptera tested: *L. botrana* ($N=100$; $Q=20.60$; $P<0.001$), *E. ambiguella* ($N=100$; $Q=5.07$; $P=0.02$), and *S. ligustri* ($N=100$; $Q=4.06$; $P=0.04$). The frass produced by the grasshopper, *C. brunneus*, was not attractive ($N=100$; $Q=0.41$; $P>0.05$; Fig. 2).

Preferences for *L. botrana* Larvae Reared on Different Foods

There was no significant difference in the choice of *D. cavus* for larvae fed on control medium or on media supplemented with Pinot, Riesling, or tansy ($N=50$; respectively, $Q=0.53$; $Q=0$ and $Q=0$).

Preferences for Frass Produced by Different Species

The parasitoid was more attracted to the odor of from *S. ligustri* than from *L. botrana* ($N=100$; $Q=25.82$; $P<0.001$), or *E. ambiguella* ($N=100$; $Q=9.04$; $P=0.003$; Fig. 3). *D. cavus* was also more attracted to the frass from *L. botrana* than from *E. ambiguella* ($N=100$; $Q=4.74$; $P=0.03$). This preference was independent of the species on which *D cavus* had been reared; *D. cavus* females reared from *E. ambiguella* also preferred *L. botrana* frass ($N=100$; $Q=7.04$; $P=0.008$).

Preferences for *L. botrana* Frass from Different Larval Foods

There was no significant difference in choice of *D. cavus* for frass from *L. botrana* fed on control medium or fed on supplemented medium ($N=50$; Pinot, $Q=0.35$; Riesling, $Q=3.13$; tansy, $Q=0.82$ and rosemary, $Q=1.39$). There was also no significant difference in choice of *D. cavus* for frass from *L. botrana* fed on different supplemented medium: Riesling vs. Pinot ($Q=1.26$), Pinot vs. tansy ($Q=0.20$), Riesling vs. tansy ($Q=3.27$), Riesling vs. daphne ($Q=1.09$), and Riesling vs. rosemary ($Q=0.09$). For all, $N=50$.

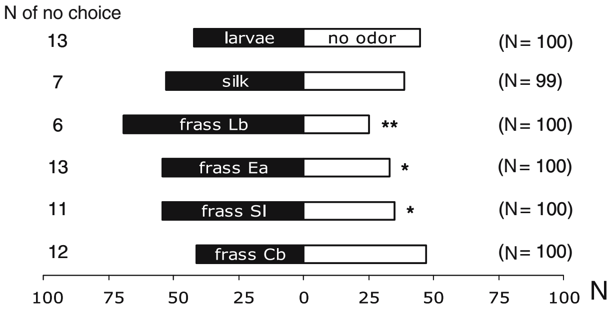

Fig. 2 Responses of *D. cavus* females to larvae, silk of *L. botrana*, or frass of different insect species. Lb: *Lobesia botrana*; Ea: *Eupoecilia ambiguella*; Sl: *Sphinx ligustri*; Cb: *Chorthippus brunneus*. *White bars* = no odor. *$P<0.05$ and **$P<0.01$

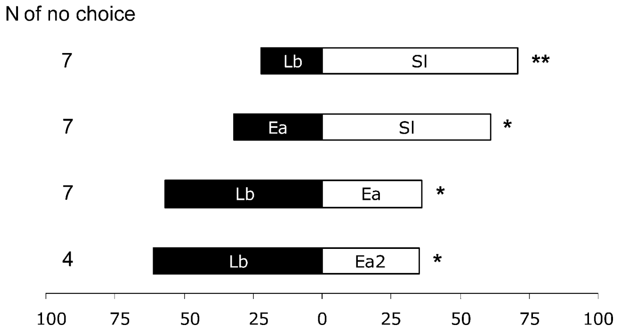

Fig. 3 Choice of *D. cavus* females between the odor of frass produced by caterpillars from different species. Lb: *Lobesia botrana*; SI: *Sphinx ligustri*; Ea: *Eupoecilia ambiguella*. Ea2: choice of females reared on *E. ambiguella*. All results: $N=100$. $^{*}P<0.05$ and $^{**}P<0.01$

Responses to the Solvent Extracts

D. cavus females responded in a dose-related way to extracts. None of the solvent extracts were attractive at the dose of 1 larval equivalent (Fig. 4). However, significant attraction was observed with water, dichloromethane, and methanol extracts applied at 3 larval equivalents ($N=50$; respectively $Q=12.8$; $P<0.001$; $Q=8$; $P=0.005$; $Q=4$; $P=0.045$). At the higher dose of 6 larval equivalents, only dichloromethane and water extracts elicited attractive responses as compared with solvent alone ($N=50$; respectively $Q=8.07$; $P=0.004$ and $Q=6.25$; $P=0.012$). Acetone and hexane extracts were not found to be attractive. Methanol elicited a similar percentage of females attracted, but because of a higher proportion of nonchoosing females, this result was not significant ($Q=3.2$; NS).

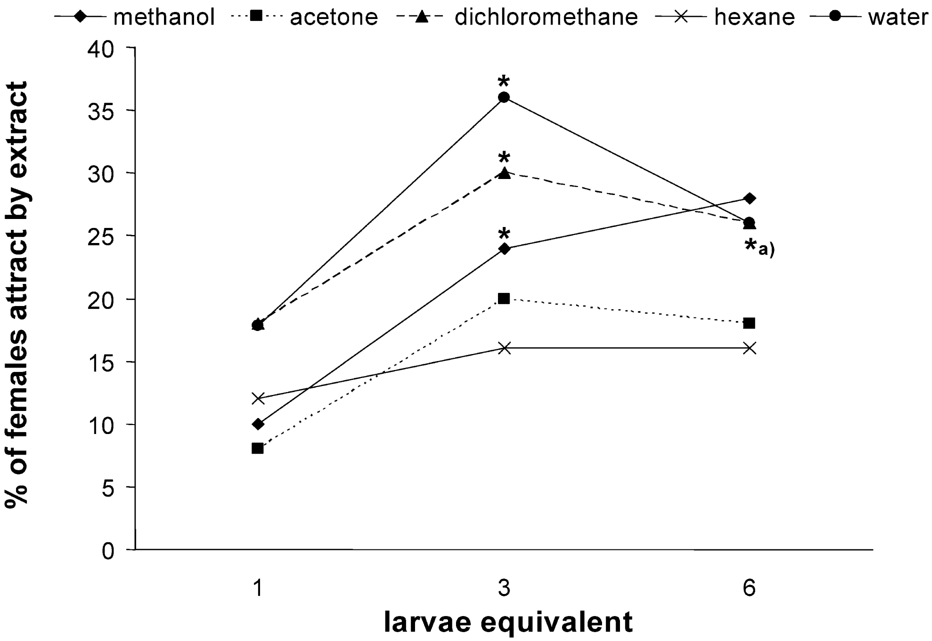

Fig. 4 Choice of *D. cavus* females between extracts of frass of *L. botrana* larvae and the correspondent solvent. All results: $N=50$. $^{*}P<0.05$; *a), concerns the two treatments dichloromethane and water (see Results for details)

Thus, 3 larvae equivalents represented the optimally attractive dose, which corresponds to the amount of frass tested in the other experiments.

Discussion

The experiments demonstrate that *D. cavus* was attracted to frass produced by three species of Lepidoptera, but not by larvae alone. Moreover, *D. cavus* was not attracted to the silk produced by *L. botrana* larvae. Results revealed that larval food did not modify frass attractiveness, but that the moth species did.

Frass is a digestion residue containing nonabsorbed solids, water, scraps, diverse secretions, and microorganisms. Defecation is an essential physiologic process that also plays an important role in the ecology of host–parasitoid interactions (Weiss, 2003, 2006). Defecation behavior can partly be the result of natural selection, including predator/prey interactions, toxins or pathogens exposure, feeding, and social signalization (Weiss, 2003, 2006). For animals living near their feeding site, like *L. botrana*, presence and accumulation of frass can be disadvantageous because this can make prey more obvious to natural enemies. Hence, egestion products like frass can be perceived as an indicator of host presence (Bouchard and Cloutier, 1985; Reddy et al., 2002; Rogers and Potter, 2002).

D. cavus females were not attracted at distance to the different larvae tested or to their silk, but their frass represented an orientation cue. This could be extracted by different solvents, and *D. cavus* responded to these extracts in a dose-dependent way. Thus, frass bears chemical information able to attract this parasitoid. The volatiles extracted by water, dichloromethane, and methanol were attractive; thus, one may expect that a complex volatile signal made from intermediate to polar volatiles is needed to mimic the complete frass odor. Analytical comparisons of the different extracts were not performed in this work. However, such comparisons would be needed to confirm this point.

Although *D. cavus* is a generalist species, it was attracted in varying degree to the frass of the three Lepidoptera tested, and not at all to that of *C. brunneus*, which has not been described as a host. Generalist insects do exhibit preferences among their different hosts (Vinson, 1976; Janz, 2003; Maher and Thiéry, 2006). There is increasing evidence that natal or prenatal experience influences the preferences of the adult insect (Corbet, 1985; Vet et al., 1990; Rojas and Wyatt, 1999; Davis and Stamps, 2004). There are several examples of parasitoids responding to chemicals encountered during their larval or preimaginal instars (Corbet, 1985; Vet et al., 1990; Vet and Groenewold, 1990). The parasitoid *Nemeritis canescens* (Hymenoptera: Ichneumonoidea) reared on the nonhost insect *Meliphora grisella* (Lepidoptera: Pyralidae) develops an olfactory attraction for its rearing host (Alloway, 1972). In *D cavus*, females reared on *L. botrana* were more attracted to *L. botrana* frass, but those reared on *E. ambiguella* were not specifically attracted to their developmental host frass. Therefore, we conclude that preimaginal conditioning to the rearing species did not occur in *D. cavus*.

Host alimentation can strongly influence parasitoid choices (Sauls et al., 1979; Benrey et al., 1997). Gandolfi et al. (2003) showed that rearing *Hyssopus pallidus* (Hymenoptera: Eulophidae) on *Cydia pomonella* (Lepidoptera: Tortricidae), fed on a medium supplemented with apple, enhances the attractiveness of the parasitoid to caterpillar frass. *D. cavus* has been found on numerous phytophagous species that feed on a wide range of host plants. However, none of the plants used in our experiment modified the attractiveness of the frass. Therefore, the plant on which the host feeds may be of minor importance to this parasitoid.

The experiments demonstrate that there is likely a general signal that makes Lepidoptera frass attractive to *D. cavus*. Actually, *D. cavus* is an extreme generalist, and generalists often use nonspecific chemical cues for host location rather than specific ones (Vet and Dicke, 1992; Thiéry and Gabel, 1993; Godfray, 1994; Steidle and van Loon, 2003). The olfactory signal used by this species may include general molecules indicating the occurrence of a wide range of possible hosts (e.g., Lepidoptera) and additional ones giving more specific information to discern among hosts.

This work is a first step toward understanding the relationships between *D. cavus* and two grape moths. We only focused on the responses of the wasp to odors, not considering the complete set of cues used by the wasp in its host recognition and acceptance. Indeed, the larval host plant influences the growth and survival of larvae of several generalist herbivores (Lazarević et al., 1998; Tikkanen et al., 1999; Serrano and Lapointe, 2002). In *L. botrana*, previous work showed that larval food modifies the larval development time (Savopoulou-Soultani et al., 1994; Moreau et al., 2006a,b; Thiéry and Moreau, 2005) and also their size with consequences on adult fitness. *L. botrana* larvae fed on different host plants may offer different food quality for their parasitoids, but *D. cavus* seems not to discriminate between the volatile information corresponding to such larvae.

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