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Original article

Response of the small hive beetle (*Aethina tumida*) to honey bee (*Apis mellifera*) and beehive-produced volatiles

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Abstract – The response of male and female Small Hive Beetle (SHB), *Aethina tumida*, to air-borne volatiles from adult worker bees, (*Apis mellifera*), pollen, unripe honey, beeswax, wax by-products ("slumgum"), and bee brood, was investigated in olfactometric and flight-tunnel choice bioassays. In both bioassay systems, males and females responded strongly to the volatiles from worker bees, freshly collected pollen and slumgum but not to those from commercially available pollen, beeswax and bee brood. The response to pollen volatiles was dose dependent, while response to volatiles from worker bees increased with both the number and age of the bees. Females were more responsive than males to the different volatile sources, with greater response in tests with unripe honey. In flight-tunnel choice tests, Super Q-trapped volatiles from worker bees elicited a response comparable to the response to living workers, while trapped volatiles from other sources were not attractive.

small hive beetle / *Aethina tumida* / hive volatiles / olfactometer / flight-tunnel

1. INTRODUCTION

The small hive beetle (SHB, *Aethina tumida* Murray; Coleoptera: Nitidulidae), a newly introduced pest of honey bees in the United States, was first reported in 1998 in Florida (Thomas, 1998). Since then, it has spread throughout most of the eastern and mid-western United States, causing considerable damage to honey bee colonies and negatively impacting the beekeeping industry (Morse and Calderone, 2000). In sub-Saharan Africa, the beetle's native home, they are not considered a major pest of honey bees (Lundie, 1940). SHB attack primarily weak and/or small colonies (Lundie, 1940), but in strong colonies, worker honey bees encapsulate groups of SHB with propolis (Neumann et al., 2001). However, in the United States, where honey bee colonies are predominantly of European origin, SHBs have been reported to damage both weak and strong colonies (Sanford, 1998). Defense mechanisms have yet to be demonstrated in European bees. Damage to honey bee colonies is caused mainly by beetle larvae, which feed on honey, pollen, and brood. In addition, larval excrement tends to ferment honey, rendering it unsuitable for human consumption. In highly infested colonies, where larval feeding is extensive, bees generally abscond.

The available literature on the biology of the SHB is scanty and is based primarily on work carried out several decades ago on the life cycle of the beetle in Africa (Lundie, 1940; Schmolke, 1974). The paucity of biological information for SHB in the United States has hindered its management there. It has also limited the understanding of factors mediating attraction of the beetle to honey bee colonies. In recent field trapping studies conducted in

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Florida, Elzen et al. (1999) reported that SHBs are attracted to a combination of honey, pollen and adult bees. Elzen et al. (1999) also reported that small numbers of beetles were captured in traps baited with adult bees, but not in traps baited with honey and pollen, or brood alone. Thus far, there has been no attempt to identify the cues attracting SHBs to honey bee hives. Therefore, we initiated a comprehensive investigation of the chemical ecology of the SHB. Here, we describe behavioral responses of adult, male and female beetles to volatiles from adult worker bees, pollen, unripe honey, beeswax, wax by-product ("slumgum"), and bee brood.

2. MATERIALS AND METHODS

2.1. Beetles

A colony of SHB was started from beetles that were collected in the field in Umatilla, Florida during November, 1999. The beetles were maintained in Plexiglas cages (25 × 25 × 25 cm) at room temperature (25 °C) with 14L: 10D photoperiod. Beetles were fed on a mixture of pollen and honey (referred to in this paper as pollen dough). Two microscope slides separated by 1mm provided oviposition sites for females. The slides were placed inside the cages and left overnight, allowing female beetles to lay their eggs in the spaces created. Slides with eggs were incubated at 28 °C in 6 cm plastic petri dishes containing 20 g of pollen dough. Food was provided as needed to ensure a constant supply during larval development. After seven to ten days, wandering larvae were transferred into plastic containers (35 × 25 × 10 cm), containing humidified sand as pupation medium. Newly emerged adult beetles were sexed based on observations of their genitalia under a stereoscope. The genitalia were exposed by applying slight pressure to the ventral side of the abdomen. After sexing and prior to bioassays, male and female beetles were kept in separate cages.

2.2. Odor sources

Eight honey bee colonies were maintained at the USDA-ARS facilities in Gainesville, Florida and used as sources of honey bees, fresh pollen, wax, brood, honey and slumgum. Colonies were managed without pesticides to avoid contamination of the volatile sources.

2.3. Olfactometer bioassays

Bioassays were conducted in a four-arm olfactometer (Fig. 1A) (Vet et al., 1983). Charcoal-filtered, humidified air was delivered into the olfactometer at a rate of 0.25 L/min/quadrant. The air was drawn from the center of the olfactometer (vacuum line) at approximately 1 L/min and was adjusted until a well-defined odor zone was formed in each quadrant, as indicated by ammonium chloride smoke (HCl and NH_4OH). Beetles were released one at a time at the center of the olfactometer and their behavior recorded for 1 min using a hand-held computer. For each beetle, the time spent in each odor zone was recorded. The total time spent in each zone was obtained for all the beetles in each replicate and was expressed as a percentage of time spent in each zone. Data were recorded and analyzed with a computer software package (THE OBSERVER ver 3.0, Noldus, Wageningen, The Netherlands). Responses to the different volatile sources (treatments) were tested with male and female beetles in separate tests (20 SHBs per replicate). Each treatment was replicated three times. To minimize positional bias, the olfactometer was rotated 90° after five beetles had been tested. Tests were conducted to compare beetle response when a 40-watt fluorescent or red light bulb was used. The light source was placed 0.3 m above the center of the olfactometer to provide uniform illumination.

Odor sources included adult honey bee workers (200 foragers collected from the hive entrance or frames in supers), freshly collected pollen (5 g), unripe honey (15 mL), honey bee pupae (10 g), wax and slumgum (10 g). Pollen was collected daily from the hive entrance using standard pollen traps (Brushy Mountain Bee Farm, Morovian Falls, NC) and stored at –70 °C until use. Unripe honey was extracted by gently shaking uncapped honey combs over a sheet of household aluminum foil. Wax and slumgum were obtained from honey cappings and old combs, and were separated using a solar wax melter. The wax by-product commonly referred to as "slumgum" by beekeepers is a waste product obtained from the processing of honey, wax, and old combs. Small hive beetle attraction to honey bees was also tested using adult workers that emerged from sealed brood frames held in an incubator at 34 °C and fed with sugar candy (confectioner's sugar and water) and water. This eliminated the possibility that attraction to adult bees might be the result of pollen picked up by bees as they forage. Olfactometric dose response tests were conducted using adult honey bee workers and freshly collected pollen. One, 10, 25, 100 and 200 bees, and 0.1, 1.0, 5.0 and 10.0 g of freshly collected pollen were used.

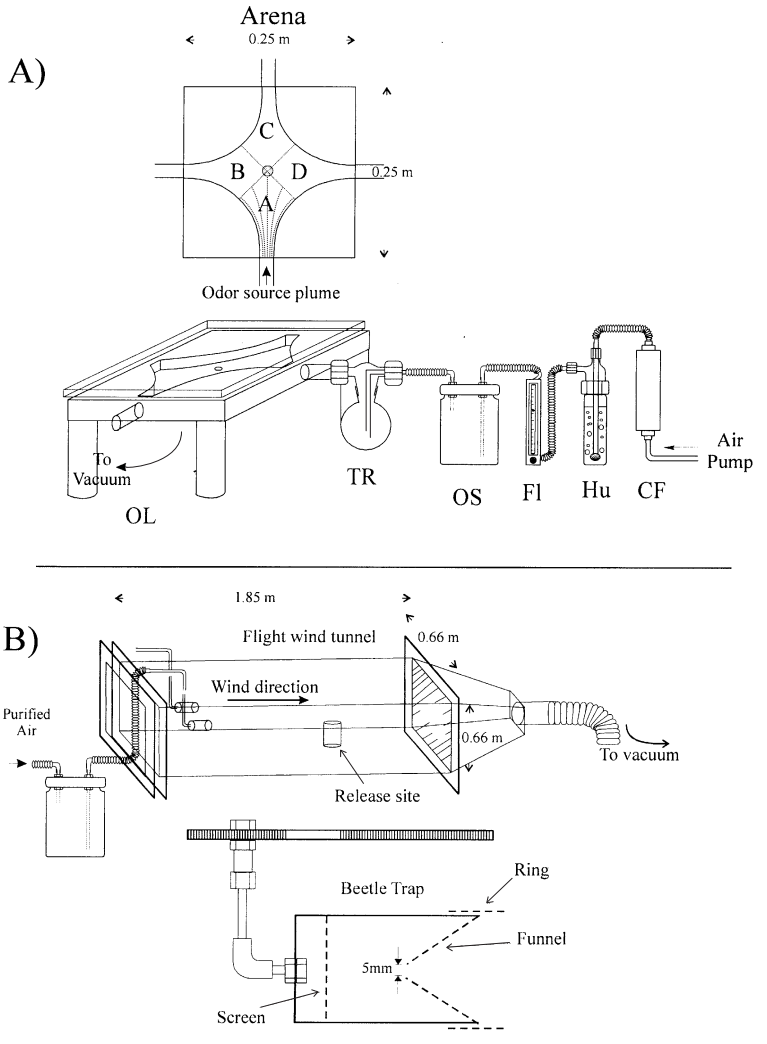

Figure 1. Diagrams of bioassay systems. (A) Four-arm olfactometer. The main arena of the olfactometer consisted of four odor zones. Odor sources to test were in zone "A". OL = Olfactometer, TR = insect trap, OS = odor source, Fl = flowmeter, Hu = humidifier, and CF = Charcoal filter. Air flow was calibrated with ammonium chloride smoke. (B) Flight wind tunnel and beetle trap.

2.4. Flight tunnel bioassays

Behavioral assays were conducted in a horizontal, dual choice flight-tunnel (1.85 × 0.66 × 0.66 m), with a design similar to that reported by Heath et al. (1993). Responding beetles were captured in traps made out of plastic vials (25 dram, BioQuip, Gardena, CA), fitted with a screen cone with a 5 mm opening. The opening allowed beetles to enter the vial but not to exit it (Fig. 1B). A screen was also placed 1 cm from the air tube to prevent beetles from clogging the air port; and a screen ring was fitted to the outside and border of the vial to provide a landing platform (Fig. 1B). Two traps, one for each odor source, were placed upwind, 0.3 m above the floor and separated by 0.3 m from each other. Odor sources were placed in glass chambers (3 litre mason jars) outside the flight-tunnel and a stream of purified air passed through each chamber at a flow rate of 0.5 L/min. Wind speed was set at 0.2 m/s inside the flight-tunnel. Light was provided with 2, 4 foot, 34-watt fluorescent tubes placed 0.2 m above the flight tunnel. The temperature was maintained at 27 °C and the relative humidity between 40 and 60%. Dual choice tests were conducted by releasing

50 beetles (7–10 day old virgins) simultaneously from a holding vial placed at a distance of 1.5 m away from the trap for each replicate. Treatments were replicated three to four times. The position of odor sources was switched between replicates to minimize bias. Flight tunnel bioassays were conducted at peak beetle activity (between 19:00 and 24:00 h). For each replicate, the number of beetles entering the trap was recorded for 15 min. Beetles were used only once and were deprived of food and water for one day prior to the bioassay.

2.5. Volatile collections

Volatiles from adult honey bees, fresh pollen, slumgum and honey were collected by passing purified air over the odor source and collecting the volatiles on filters packed with 30 mg of Super-Q adsorbent (Alltech, Nicholasville, KY) (Loughrin et al., 1995) for two days. Each filter was eluted with 200 µL of dichloromethane (Loughrin et al., 1995). Volatiles were collected from 500–600 adult honey bee workers placed in brass screen canisters and provided with 50 g of sugar candy and water. The canisters were placed in cylindrical glass containers (0.55×0.14 m) through which charcoal-filtered and humidified air was drawn at 0.5 L/min and then through a filter trap. Fresh pollen volatiles were collected from 50 g of pollen in glass collection chambers with the same parameters used to collect bee volatiles. Volatiles were also collected from glass chambers filled with 100 mL of honey and 100 g of slumgum.

2.6. Response to Super-Q trapped volatiles

Volatiles trapped on Super-Q filters and extracted with dichloromethane were tested in flight tunnel assays. Volatiles trapped from bees were expressed as bee day equivalents (1 BDE = volatiles emitted by one bee in a day). Dose response tests were conducted using 50, 100, 200, and 400 BDE. The extracts in dichloromethane (200 µL) were loaded on rubber septa (11 mm sleeve stopper, Wheaton Scientific, Millville, NJ). Dichloromethane was removed by allowing the septa to air dry (Heath et al., 1991) for 3–4 hours prior to each bioassay. One septum was used in each replicate. Septa loaded only with dichloromethane were used as controls. Volatiles from pollen and slumgum were expressed as gram day equivalent (GDE) and those of honey as ml day equivalent (MDE).

2.7. Data analyses

Proportion of time spent per odor zone was arcsin $\sqrt{p}$ transformed (p = proportion) and subjected to two-way analysis of variance to test for differences in response in the odor zones. Means were compared using Duncan's multiple range tests. Male and female responses for each treatment were tested for statistical significance using a Wilcoxon's test (SAS Institute, 1998).

3. RESULTS

3.1. Olfactometer bioassays

The number of male and female SHB entering the odor source (quadrant) was not significantly different ($P > 0.05$, Wilcoxon's test) when adult honey bee workers were used as odor source under fluorescent or red light conditions. However, fluorescent light conditions stimulated beetles to fly, requiring longer bioassay times. Under red light, beetles responded faster by walking to the odor source, thus, requiring shorter bioassay times. Therefore, bioassays using the olfactometer were conducted in the dark using a 40-watt red light bulb. Responses of male and female SHB to honey bees and fresh pollen volatiles were significantly different from controls (Fig. 2, Tab. I). Females spent a significantly greater proportion of time in the zone with odors from unprocessed honey and slumgum. No significant responses were observed between males and females to volatiles from wax and bee brood (Fig. 2, Tab. I). No significant differences between male and female responses were found with honey bee volatiles ($P > 0.05$). A significant increase in response was observed as the bees aged, ranging from 15.7% of time spent in the odor zone source when bees of one to two days were used, to 86.1% when 4 to 7 day old bees were used (Fig. 3, $F_{(2;9)} = 34.38$; $P < 0.0001$). Results of the dose response tests for male and female SHB to honey bees and pollen respectively are shown in Figure 4. Beetle response increased with increasing dose. Males were more responsive than females at the 100 bee level. At higher levels, differences were not significant ($P > 0.05$). Fresh pollen odors also evoked a positive response in both males and females but, unlike honeybee odors, female SHB response to the volatiles was greater than that of males. Maximal responses to fresh pollen volatiles were reached with 1.0 g for males and females followed by a decrease when 5.0 and 10 g were used.

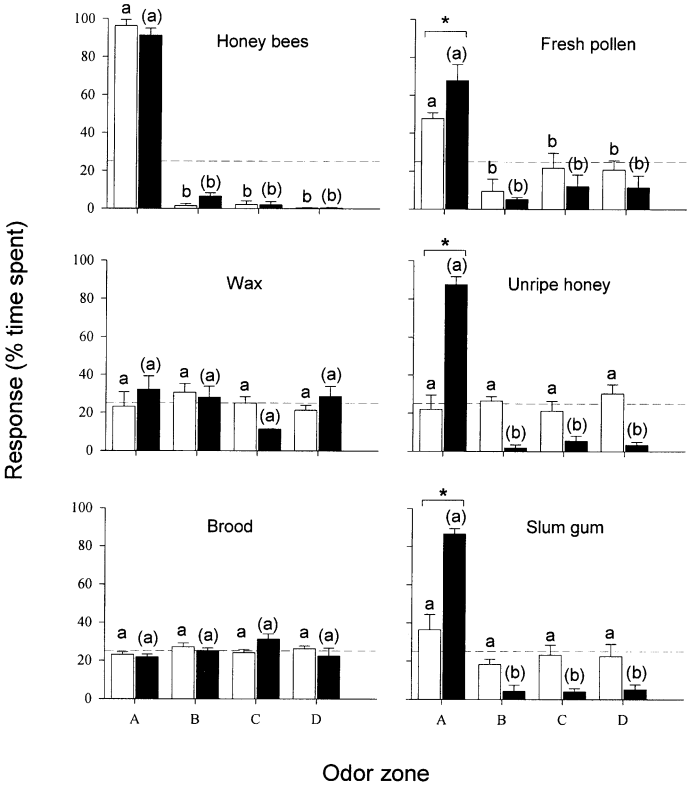

Figure 2. Olfactometer responses of male and female SHB to hive-produced volatiles. Male (open bars) and female (filled bars) responses to each odor zone (indicated as A, B, C and D) are expressed as the percentage of time spent in each zone of the olfactometer. The zone in which the odor source was placed is designated as "A" for all treatments. Mean comparisons of responses by males to odors, among zones within each treatment, are indicated by lowercase letters; mean comparisons of responses by females are indicated by lowercase letters within parentheses. Means with the same letter are not significantly different. The amount of time males and females spent in the zone with the odor source was significantly different ($P < 0.05$) if the bars are capped with an asterisk (fresh pollen, unripe honey and slumgum).

Table I. Analysis of variance results of four-arm olfactometer responses of male and female SHB to different odor sources.

Odor source	Sex	df (model; error)	F-value	*P*-value
Honey bees	Male	3;8	116.26	<0.0001
	Female	3;8	124.09	<0.0001
Fresh pollen	Male	3;8	5.79	0.0210
	Female	3;8	12.08	0.0024
Unripe honey	Male	3;8	0.71	0.5714
	Female	3;8	70.85	<0.0001
Slumgum	Male	3;8	1.61	0.2624
	Female	3;8	62.65	<0.0001
Beeswax	Male	3;8	0.65	0.6047
	Female	3;8	3.86	0.0561
Bee brood	Male	3;8	2.71	0.1147
	Female	3;8	2.64	0.1205

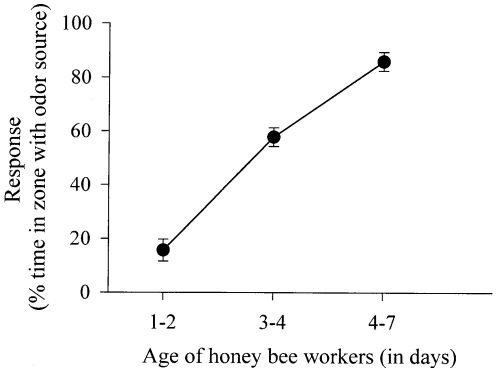

Figure 3. Responses of SHB to volatiles produced by adult honey bee workers of different ages in olfactometer studies. Response is expressed as percentage of time spent in zone with odor source. Each data point corresponds to four replicates and twenty beetles per replicate. Male and female SHBs were used in equal numbers (two male and two female replicates per data point).

3.2. Flight tunnel bioassays

Flight response of males and females to volatiles produced by honeybees, fresh pollen, unprocessed honey and slumgum are presented in Figure 5. Significant differences were found in the response of males and females to the different treatments compared to the control, which captured no beetles in any of the tests. Comparisons between male and female responses within each treatment were also significantly different with females being more responsive than the males to the naturally produced volatiles (Fig. 5, $P < 0.05$, Wilcoxon's test).

3.3. Response to Super-Q trapped volatiles

The responses of male and female SHB to Super-Q extracts of volatiles collected from the different sources are presented in Table II. Only the Super-Q extract from honeybee volatiles evoked a positive response, which led to captures of both male and female beetles. In dose response tests, females responded significantly more to the volatiles than males when 200 BDE or more were assayed (Fig. 6, $P < 0.05$, Wilcoxon's test).

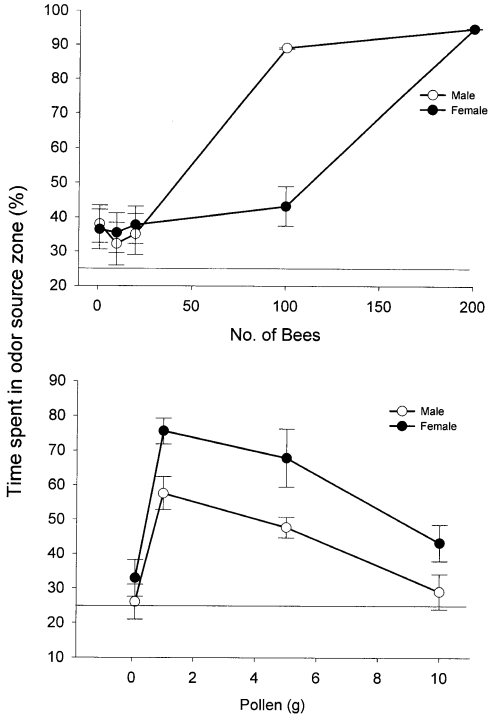

Figure 4. Olfactometric dose response of male and female SHBs to honey bee and pollen volatiles. Male (open circles) and female (closed circles) responses are expressed as time spent in the zone with the odor source. For each sex, each data point corresponds to three replicates and twenty beetles per replicate.

4. DISCUSSION

Volatiles from adult worker bees, freshly collected pollen, unripe honey and slumgum attracted SHBs in olfactometric and flight-tunnel bioassays. Female beetles were generally more responsive than males, however, in olfactometer assays, males were more responsive than females to bee volatiles at certain levels. The significance of these differences in response is not clear, but they may be due to the relatively low numbers of SHBs used in this study compared to natural populations occurring in a beehive. The strong response of both males and females to bee volatiles suggests that the beetles may associate bee volatiles with the presence of food resources in the hive. This is consistent with the fact that the

Table II. Responses in a flight wind tunnel of male and female SHB to Super-Q extracts of hive components. Values are expressed as percentage of beetles trapped in 15 min (mean ± s.e.).

Volatile source	Dose[a]	Male (N = 3; n = 50)	Female (N = 3; n = 50)
Adult honey bees	400 BDE [b]	25.00 ± 4.41*	42.00 ± 0.00*
Fresh pollen	2, 10, 20, 100, 200 GDE [c]	0.00 ± 0.00	0.00 ± 0.00
Wax byproducts ("slumgum")	2, 10, 20, 100, 200 GDE [c]	0.00 ± 0.00	0.00 ± 0.00
Honey	10, 50, 100, 200 MDE [c]	0.00 ± 0.00	0.00 ± 0.00

[a]: BDE = bee day equivalent; GDE = gram day equivalent; MDE = mL day equivalent. [b]: Representative dose. See Figure 6 for dose response curve. [c]: Doses tested with three replicates per dose and 50 beetles per replicate. (*): Significantly different ($P < 0.05$) from the controls. N = number of replicates; n = number of insects per replicate.

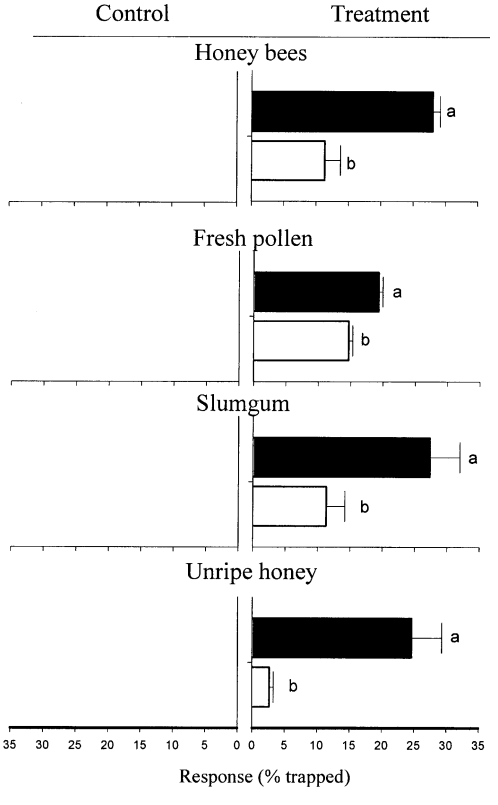

Figure 5. Flight-tunnel bioassay responses of male (open bars) and female (filled bars) SHBs to honey bees, pollen, unripe honey and slumgum volatiles. Responses of male and female within each treatment were all significantly higher than their respective controls ($P < 0.05$). Bars with different letters indicate significant differences between responses of males and females within each treatment ($P < 0.05$).

beetles do not feed on adult honey bees, but rather on pollen, honey and bee brood (Elzen et al., 1999; Elzen et al., 2000).

In the present study, only Super Q-trapped volatiles from worker bees evoked responses similar to those obtained from living bees in flight-tunnel bioassays, confirming the involvement of bee volatiles mediating host location by beetles. In contrast, volatiles collected from freshly collected pollen, unripe honey and slumgum, and loaded separately on rubber septa dispensers, failed to replicate similar responses to the natural sources, although strong upwind flight by beetles to the treated port was observed. In preliminary experiments using rubber septa impregnated volatiles, the presence of residual levels of dichloromethane in the airstream did affect responses of beetles. Optimum responses were obtained from beetles after dichloromethane was allowed to evaporate for 3–4 h. Therefore, the failure of responding beetles to enter the treated port using dichloromethane extracts of some of the natural volatile sources warrants further investigation.

The similar pattern of responses by males and females to volatiles from honey bees and slumgum is noteworthy. Slumgum is composed of a mixture of dead bees, cocoons, honey, beeswax and propolis (Tew, 1992). Perhaps, the emissions, enriched with the volatiles of these hive components, and probably released via a slow release mechanism from the gum, may explain the large populations of beetles found in wax and honey processing

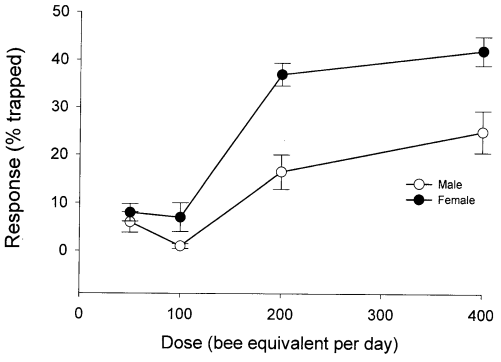

Figure 6. Flight-tunnel response of male (open circles) and female (closed circles) SHBs to different doses (expressed as bee day equivalent) of honey bee volatiles trapped on filters with Super-Q adsorbent and released from rubber septa. Each data point represents four replicates with fifty beetles per replicate.

plants, where feeding larvae are reported to contaminate honey (Sanford, 1998). Although little is known about the feeding preferences of the beetle, the results of the present study suggest that the beetle is probably a more generalist insect, with a wider host range, which may include other insect pollinators such as bumble bees living in colonies (Stanghellini et al., 2000). Thus much more work needs to be done to understand host location by SHB.

Future research in our laboratory is currently directed to identifying the chemical attractants from these volatile sources and development of lures and traps for use in the field.

ACKNOWLEDGMENTS

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Résumé – Réaction du Petit Coléoptère des ruches (*Aethina tumida*) aux substances volatiles émises par les abeilles domestiques (*Apis mellifera*) et la ruche. Le Petit Coléoptère des ruches (PCR), *Aethina tumida* Murray (Coleoptera, Nitidulidae), originaire de l'Afrique sub-saharienne, est un parasite des abeilles domestiques signalé pour la première fois en Floride en 1998. Depuis, il s'est répandu à travers la plupart des États de l'est et du Midwest des USA, provoquant des dégâts considérables aux colonies d'abeilles. Sa présence affecte négativement l'industrie apicole. Les dégâts aux colonies sont causés principalement par les larves du coléoptère qui se nourrissent de miel, de pollen et de couvain. En outre, les excréments des larves ont tendance à faire fermenter le miel, le rendant impropre à la consommation humaine. En général, les abeilles désertent les colonies fortement infestées. Le but de cette étude était d'analyser les réactions comportementales des PCR adultes mâles et femelles aux substances volatiles associées aux abeilles et aux produits du rucher et de déterminer les substances volatiles qui attirent les PCR ou affectent d'une manière quelconque leur comportement.
Un olfactomètre à quatre voies et un tunnel de vol horizontal à double choix (Fig. 1) ont été utilisés pour les tests biologiques. Les odeurs testées provenaient des ouvrières adultes (a), du pollen fraîchement récolté (b), du miel non mûr (c), des nymphes d'abeilles (d), de la cire (e) et du résidu de la fonte des rayons (f). Les substances volatiles a, b c et f ont été obtenues en faisant passer de l'air purifié sur la source odorante et en les récupérant sur des filtres contenant 30 mg d'adsorbant Super-Q. Lors des tests biologiques dans l'olfactomètre et le tunnel de vol, ces substances ont attiré les PCR. En général, les femelles répondaient mieux que les mâles. La forte réaction des mâles et des femelles aux substances volatiles des abeilles (Fig. 5) suggère que les PCR peuvent associer ces substances à la présence de réserves de nourriture dans la ruche. Dans notre étude, seules les substances volatiles des ouvrières piégées par le Super-Q ont déclenché des réactions semblables à celles obtenues avec des abeilles vivantes dans le tunnel de vol (Tab. II). Ceci confirme que les substances volatiles des abeilles sont impliquées dans la localisation de l'hôte par le PCR.

***Aethina tumida* / substance volatile / abeille / olfactométrie / tunnel de vol**

Zusammenfassung – Reaktionen des kleinen Beutenkäfers (*Aethina tumida*) auf Duftstoffe von Honigbienen (*Apis mellifera*) und ihre Produkte. Der kleine Beutenkäfer, *Aethina tumida* Murray (Coleoptera: Nitidulidae), der aus dem Gebiet der Sub-Sahara in Afrika stammt, ist eine kürzlich eingeschleppte Krankheit der Honigbienen in den Vereinigten Staaten. Der erste Bericht stammt aus Florida im Jahr 1998. Seitdem hat sich der Käfer fast überall in den Staaten im Osten und mittleren Westen verbreitet, verursacht erhebliche Schäden in den Bienenvölkern und hat einen negativen Einfluss auf die Imkereiindustrie. Die Schäden in den Völkern werden hauptsächlich von den Käferlarven hervorgerufen, diese ernähren sich von Honig, Pollen und Brut. Zusätzlich führen die Exkremente der Larven zu einer Fermentierung des Honigs, sodass er nicht mehr zum menschlichen Verzehr geeignet ist. Sind die Völker stark befallen und liegt ein starker Fraß der Käferlarven vor,

verlassen die Bienen den Stock. Die geringen biologischen Kenntnisse vom Beutenkäfer in den USA war ein Hindernis beim Umgang mit dem Käfer. Ziel dieser Untersuchung war die Erfassung der Verhaltensreaktionen von adulten Männchen und Weibchen auf die bei Bienen und ihren Bienenprodukten vorkommenden Duftstoffe und eine Identifizierung von flüchtigen chemischen Substanzen, die die Käfer anlocken oder das Verhalten auf andere Weise beeinflussen. Die Biotests wurden in einem 4-armigen Olfaktometer und in einem horizontalen Flugtunnel mit zwei Wahlmöglichkeiten durchgeführt. Die Duftquellen bestanden aus adulten Arbeiterinnen, frisch gesammelten Pollen, unreifem Honig, Bienenpuppen, Wachs und Abfallresten nach dem Schleudern, bestehend aus Honig, Wachs und Waben. Duftstoffe von adulten Honigbienen, frischem Pollen, Abfall und Honig wurden gewonnen, indem gereinigte Luft über die Duftquelle geleitet wurde und die Duftstoffe anschließend mit Filtern aus 30 mg des Super-Q Adsorbenz gebunden wurden. Die Duftstoffe von adulten Arbeiterinnen, frisch gesammeltem Pollen, unreifem Honig und Schleuderresten lockte die kleinen Beutenkäfer im Biotest im Olfaktometer und im Flugtunnel an. Weibliche Käfer reagierten im allgemeinen stärker als Männchen. Die starke Reaktion von beiden, Männchen und Weibchen auf Duftstoffe der Bienen lässt vermuten, dass die Käfer Bienenduftstoffe mit der Präsenz von Futterquellen im Bienenstock verbinden. In der jetzigen Untersuchung riefen nur die Super Q-gebundene Duftstoffe von Arbeiterinnen eine Reaktion hervor, die denen von lebenden Bienen im Flugtunnel Test ähnlich war. Das bestätigt, dass Bienenduftstoffe an der Auffindung von Wirtsvölkern durch die Käfer beteiligt sind.

kleiner Beutenkäfer / *Aethina tumida* / Honigbienen / Olfaktometer / Flugtunnel

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