



Kairomones from scarabaeid grubs and their frass as cues in below-ground host location by the parasitoids *Tiphia vernalis* and *Tiphia pygidialis*

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Abstract

Cues used in below-ground host-searching behaviour and host discrimination were examined for *Tiphia vernalis* Rohwer and *Tiphia pygidialis* Allen (Hymenoptera: Tiphidae), ecto-parasitoids of root-feeding larvae of the Japanese beetle, *Popillia japonica* Newman, and masked chafers, *Cyclocephala* spp. (Coleoptera: Scarabaeidae), respectively. Response to potential stimuli was compared in dual choice tests in an observation chamber filled with soil. Each wasp showed species-specific, directed movement along residual body odor trails made by dragging its respective host through the soil. Presence of a grub was not necessary for wasps to follow such trails. Frass from either host- or non-host grubs elicited trail-following, but each *Tiphia* species followed frass trails from its respective host when a choice was presented. Frass trails elicited stronger responses than body odor trails. The combination of host frass and body odor elicited the strongest trail-following responses. Our results suggest that once in the soil, *Tiphia* spp. locate their hosts using contact kairomones present in grub body odor trails and frass.

Introduction

The process of host location has been studied for many parasitic insects (Vet & Dicke, 1992), yet relatively little is known about the behaviour of those species that exploit soil-dwelling hosts. Parasitoids whose victims feed on, or within, above-ground plant tissues may use visual cues (Sandlan, 1980; Glas & Vet, 1983), host kairomones (Klomp, 1981; Dicke et al., 1985; Vet & Dicke, 1992), host feces (Auger et al., 1990; Turlings et al., 1991; Steinberg et al., 1993; Agelopoulos & Keller, 1994), substrate-borne vibrational cues (Glas & Vet, 1983; Meyhofer & Casas, 1999), or combinations thereof to locate their hosts. Such parasitoids may also eavesdrop on volatile allelochemicals produced by insect-damaged plants (Turlings et al., 1991, 1993; Potting et al., 1995; De Moraes et al., 1998). In subterranean habitats, however, soil properties such as pore size, continuity of voids, as well as gradients in moisture and gas

diffusion may confound the task of host location (Vilani et al., 1999). Here, we report on cues used by two species of *Tiphia* wasps (Hymenoptera: Tiphidae) to locate soil-dwelling scarabaeid larvae, and to discriminate between host and non-host species.

Solitary wasps in the genus *Tiphia* are the predominant parasitoids of scarabaeid larvae (Clausen, 1940). More than 80 species of *Tiphia* occur in North America (Krombein et al., 1979). Insofar as is known, most *Tiphia* are host specific, although some species may attack several congeneric host species (Jaynes & Gardner, 1924).

Two species of *Tiphia* commonly attack turf-infesting scarabaeid larvae, commonly referred to as white grubs, in Kentucky. *Tiphia vernalis* Rohwer, which is native to Japan, Korea, and China, was first released in the United States in the 1920's for biological control of the Japanese beetle, *Popillia japonica* Newman (Fleming, 1968). Although data concerning

its present distribution are limited, the wasp appears to be established across much of the range of *P. japonica* in the eastern United States (Fleming, 1968). In Kentucky, adults of *T. vernalis* are active in May and June, ovipositing on overwintered third-instar grubs. *Tiphia pygidialis* Allen is a native wasp which we recently determined attacks third-instar masked chafer (*Cyclocephala* spp.) grubs from late August through early October. Both *Tiphia* species can be locally abundant, parasitizing 15–30% or more of their respective host grubs in a given stand of turf (M. E. Rogers, unpubl.).

During the initial stage of host-searching, a female *Tiphia* wasp flies over turf or pasture, drops down, and burrows into the soil. Upon encountering a suitable host, the wasp stings the grub, causing temporary paralysis. It then deposits an egg on the host in a location that is specific for that particular *Tiphia* species (Clausen & King, 1927). The *Tiphia* larva feeds externally, killing its victim within a few weeks. It then spins a silken cocoon, overwinters, and emerges the following year. Limited, past observations of *Tiphia* behavior implied that host location involves random, undirected searching while in the soil (Rivers et al., 1979). Given their purported host specificity, we hypothesized that female wasps use species-specific cues, such as grub body odor trails and frass, in the below-ground phase of host location.

Materials and methods

Collection and handling of wasps. Female *T. pygidialis* and *T. vernalis* were collected from golf courses in central Kentucky. *Tiphia pygidialis* were collected during late August by spraying 1 m² plots of turfgrass with a 10% sugar water solution to thoroughly wet the grass blades. A hand-held vacuum (BioQuip Products Inc., Gardena, CA) was used to collect wasps attracted to the sprays. *Tiphia vernalis*, which feeds on honeydew secretions of aphids, scale insects, and other homopterans (Clausen & King, 1927), were collected during May in a similar manner except that sugar sprays were applied to the foliage of trees bordering areas of turf. Wasps were separated by sex and females were placed individually into 118 ml plastic cups (Solo, Highland Park, IL) half-filled with moist autoclaved soil. A film canister lid containing a piece of dental wick soaked in a 10% sugar water solution was placed on the surface of the soil as a food source. Containers with wasps were held at room temperature (22–24 °C) and light regime L14:D10. One

third-instar host was provided each day to allow the opportunity for oviposition. Wasps were deprived of hosts for 24 h before being used in experiments.

Collection of grubs and frass. Together with *P. japonica*, two native species, *Cyclocephala lurida* Bland and *Cyclocephala borealis* Arrow, are the predominant turf-infesting scarabs in Kentucky. All three species are univoltine, and *Cyclocephala* spp. and *P. japonica* grubs often co-occur in the same stand of grass. Eggs are laid from mid-June until late July. Eggs hatch in about two weeks, and the grubs develop through three instars, becoming nearly full-sized by autumn. They overwinter as third instars, resume feeding in the spring, and pupate in late May or June. *Cyclocephala lurida* and *C. borealis* are closely related and they share the same sex pheromone (Potter, 1980; Haynes et al., 1992). Because their larvae cannot be separated by known morphological characteristics, we refer to them as *Cyclocephala* spp. grubs.

Third instar *Cyclocephala* spp. and *P. japonica* were collected from stands of predominantly Kentucky bluegrass, *Poa pratensis* L., on golf courses and sod farms in central Kentucky. For experiments with *T. vernalis*, post-overwintered third instars were collected during wasp flight in early May. For tests with *T. pygidialis*, third instars were collected in late August and September. *Cyclocephala* spp. and *P. japonica* grubs were separated and placed into plastic containers (26.5 × 19.5 × 10 cm) containing a 1:1 mixture of autoclaved soil and peat moss. After one week, frass was collected by sifting the contents of the containers using a sieve. Frass pellets were individually removed from the soil remaining in the sieve using forceps and stored in sealed 30-ml diet cups until use. Frass used in experiments was 1–6 days old, with about 2% moisture content.

Observation chamber. Response of female wasps to potential host-location cues was tested in an observation chamber intended to simulate below-ground conditions. Two panes of glass (bottom, 27 × 30 cm; top, 20 × 20 cm), positioned horizontally, were separated by an outline of modeling clay. The gap between the glass panes, measuring 0.75 cm which is slightly more than the width of the grubs being tested, was filled with autoclaved, moist sifted soil. A 10-cm long piece of flexible plastic tubing was inserted through a break in the modeling clay at one end of the observation chamber to allow for introduction of wasps.

To conduct a run in this chamber, the top pane of glass was removed. Then, at the point where the tube entered the chamber, a Y-trail (0.5 cm wide) was made by dragging a piece of dental wick (2 cm long, 0.5 cm diam.) through the soil. The base of the Y was 8 cm long with each arm extending at a 45° angle for 8 cm. Proper trail width was important in order to direct wasp movement but still require them to burrow through the soil while antennating their surroundings. In this setup, potential host-location cues were presented to wasps in dual choice tests on opposite arms of the Y-trail. When response to grub body odor trails or grub frass was tested, the potential cues were extended to the juncture of the arms. After the treatments had been prepared, the upper glass pane was replaced.

Experiments were carried out at 28 °C in near-dark conditions with a red light bulb (40 W) positioned 1 m above the observation chamber. One female wasp was placed into the tube leading to the chamber and allowed to enter the Y-trail. The wasp was observed as it burrowed through the loose soil of the base and then chose between the arms containing treatments. Choice was determined when a wasp had traveled 6 cm down one arm. Depending upon the experiment, each comparison was replicated 30 or 40 times using a different wasp for each run. In a few cases (< five runs per comparison) wasps remained stationary on the trail without committing to either arm, or else burrowed through the soil away from the trail. These wasps were removed from the chamber, held for at least 1 h, and then re-tested. Between runs with individual wasps, the observation chamber was disassembled and cleaned, new soil was added and a new Y-trail made, and the treatments were switched to opposite arms. Wasps were used only once in each set of comparisons. Some wasps were tested in more than one set of comparisons. In such cases, they were held without grubs for at least 24 h before being used again.

Ability of wasps to locate a host from a distance. We first sought to determine if female *Tiphia* use cues from their hosts to perform a directed search while below ground. Each wasp species was tested with its normal host; i.e., *P. japonica* for *T. vernalis*, and *Cyclocephala* for *T. pygidialis*. A grub was dragged down one arm of the Y-trail and left at the end of that arm. A 2-cm long piece of dental wick (0.5 cm diam) was dragged down the opposite arm to create a similar physical disturbance and left at the end of that arm. Care was taken to ensure that both arms of the trail were the same width.

Response to grub body odor trails. This set of trials tested the hypothesis that each *Tiphia* species uses host-specific body odor trails to locate grubs in the soil. In the first trial, a host grub was placed at the end of both arms of the Y-trail. In one arm, the grub was dragged through the soil to potentially leave a scent trail, whereas in the other arm, a dental wick was dragged to produce a physically-similar, inert trail to the host grub. In a second trial, both arms of the Y-trail were provisioned with body odor trails of their host grubs, but only one arm was provided with a grub. This trial was intended to determine whether the presence of a living grub, which would produce movement, vibrations, and possibly other cues, would elicit a stronger response than a scent trail alone. In a third trial, the ability of wasps to distinguish between odor trails of host versus non-host grubs was tested.

Use of grub frass in host location. Three trials were conducted to evaluate potential use of grub frass in host searching behavior. In the first trial, one arm of the Y-trail contained frass from host grubs while the other arm was empty. Frass (about 0.3 g or 30 pellets) was sprinkled along the entire length of the arm to simulate the amount of frass we have observed around grubs feeding on turfgrass roots. This amount of frass was used in the following comparisons as well. In a second trial, frass from non-host grubs was present on one arm while the opposite arm was empty. In a third trial, the ability of wasps to distinguish between frass from host and non-host grubs was determined by placing frass from *Cyclocephala* and *P. japonica* grubs on opposite arms. Based upon the results from these trials, two additional trials were conducted to determine the relative strength of wasps' response to different host cues. First, we compared response to a grub body odor trail versus a trail with frass, and then a combination of frass and body odor versus frass alone was tested.

Statistical analysis. Within each trial, the number of wasps responding to each choice was analyzed by a chi-square test against the null hypothesis of a 1:1 ratio (Snedecor & Cochran, 1991). Separate analyses were conducted for responses of *T. vernalis* and *T. pygidialis*.

Table 1. Response of *Tiphia vernalis* and *T. pygidialis* to their normal hosts (*Popillia japonica* and *Cyclocephala* spp. respectively) versus a non-host object

Species tested	Trail selected ^a		χ^2
<i>T. vernalis</i>	<i>P. japonica</i> with scent trail	Dental wick trail with dental wick	10.8**
	24	6	
<i>T. pygidialis</i>	<i>Cyclocephala</i> spp. with scent trail	Dental wick trail with dental wick	16.1***
	26	4	

^aResponse of 30 wasps when given a choice between two trails.

P < 0.01, *P < 0.001.

Results

Ability of wasps to locate a host from a distance. Each *Tiphia* species showed significantly greater response to a trail made by dragging its host through the soil and leaving the grub at the end, than to a physically-similar trail made with a dental wick (Table 1). This confirms the wasps' ability to perform a directed search for hosts while in the soil.

Response to grub body odor trails. Each *Tiphia* species was able to detect and follow the scent trail of a host in the soil as well as discriminate between scent trails of host and non-host grubs (Table 2). When both arms of the Y-trail contained a host but only one arm had a scent trail leading to the grub, both *T. vernalis* and *T. pygidialis* showed significant preference for the arm with the scent trail. When both arms of the Y-trail had a host scent trail but only one trail led to a grub, the wasps chose the two trails with equal probability. Thus, grub body odor trails in the soil are a stronger stimulus than the mere presence of a grub at a distance. Wasps also were able to distinguish between scent trails produced by different grub species, each *Tiphia* species showing significant preference for the residual odor of its respective host (Table 2).

Use of grub frass in host location. Frass from grubs elicited a strong response from wasps, usually resulting in immediate burrowing into and antennating the soil where frass was present. When presented with a choice between an empty trail or a trail containing frass from their host grub, each *Tiphia* species showed a significant response to the trail containing frass (Table 3). When presented alone, frass from non-host grubs also was attractive to the wasps. However, when provided a choice of frass from either host or non-host

grubs, both wasp species preferred the trail containing frass from their hosts.

Presence of frass elicited stronger response than grub body odor trails (Table 4). Each *Tiphia* species responded more strongly to the combination of host body odor and frass than to host frass alone.

Discussion

Grub body odor trails, as well as frass from host grubs, elicited strong response from both *T. pygidialis* and *T. vernalis* females. Wasps burrowed slowly, continuously antennating the soil, when following a trail with host odor. Often a wasp would begin to burrow away from the physical trail losing contact with the host scent trail. When this occurred, she would quickly quit burrowing and begin an intensive antennating of the surrounding soil. Once the scent was found again, the wasp would resume following the trail. In experiments where a host was present, once the wasp reached the end of the scent trail it would begin to antennate and then attack the host. In trials where wasps were following body odor trails that did not lead to a host, upon reaching the end of the scent trail the female would turn around and re-examine the trail, eventually abandoning the unsuccessful search by burrowing away. If a female *Tiphia* encounters a non-host grub while burrowing through the soil, once antennal contact is made, the grub is rejected and abandoned (M.E. Rogers, unpubl.).

Wasps showed equal response to host scent trails regardless of whether or not they led to a grub. Based on these experiments, female *Tiphia* seem less likely to use cues such as volatile body odors emanating from hosts, host-created vibrations, CO₂, or body heat to locate grubs in the soil. Studies of above-ground par-

Table 2. Response of *Tiphia vernalis* and *T. pygidialis* to their normal hosts (*Popillia japonica* and *Cyclocephala* spp. respectively) and to cues from non-host grubs

Species tested	Trail selected ^a		χ^2
<i>T. vernalis</i>	<i>P. japonica</i> with scent trail	<i>P. japonica</i> no scent trail	16.1***
	26	4	
	<i>P. japonica</i> scent trail with grub	<i>P. japonica</i> scent trail no grub	0.1
	16	14	
<i>T. pygidialis</i>	<i>P. japonica</i> with scent trail	<i>Cyclocephala</i> spp. with scent trail	19.2***
	27	3	
	<i>Cyclocephala</i> spp. with scent trail	<i>Cyclocephala</i> spp. no scent trail	13.3***
	25	5	
<i>Cyclocephala</i> spp. scent trail with grub	<i>Cyclocephala</i> sp. scent trail no grub	1.2	
	18	12	
	<i>Cyclocephala</i> spp. with scent trail	<i>P. japonica</i> with scent trail	6.5*
	22	8	

^aResponse of 30 wasps when given a choice between two trails.

*P < 0.05, ***P < 0.001.

Table 3. Response of *Tiphia vernalis* and *T. pygidialis* to frass from their normal hosts (*Popillia japonica* and *Cyclocephala* spp. respectively) and to frass from non-host grubs

Species tested	Trail selected ^a		χ^2
<i>T. vernalis</i>	<i>P. japonica</i> frass	Empty	36.1***
	39	1	
	<i>Cyclocephala</i> frass	Empty	16.9***
	33	7	
	<i>P. japonica</i> frass	<i>Cyclocephala</i> frass	16.2***
	38	2	
<i>T. pygidialis</i>	<i>Cyclocephala</i> frass	Empty	25.6***
	36	4	
	<i>P. japonica</i> frass	Empty	6.4*
	28	12	
	<i>Cyclocephala</i> frass	<i>P. japonica</i> frass	14.4***
	32	8	

^aResponse of 40 wasps when given a choice between two trails.

*P < 0.05, ***P < 0.001.

Table 4. Preference of *Tiphia vernalis* and *T. pygidialis* for host body odor trails or host frass

Species tested	Trail Selected ^a	χ^2	
<i>T. vernalis</i>	<i>P. japonica</i> scent trail	<i>P. japonica</i> frass	10.0**
	10	30	
	<i>P. japonica</i> scent trail + frass	<i>P. japonica</i> frass	10.0**
	30	10	
<i>T. pygidialis</i>	<i>Cyclocephala</i> scent trail	<i>Cyclocephala</i> frass	19.6***
	6	34	
	<i>Cyclocephala</i> scent trail + frass	<i>Cyclocephala</i> frass	4.9*
	27	13	

^aResponse of 40 wasps when given a choice between two trails.

*P < 0.05, **P < 0.01, ***P < 0.001.

asitoids have shown that plant damage and host frass, rather than volatile host odors, are the primary cues used in host location (Turlings et al., 1991; Steinberg et al., 1993; Agelopoulos & Keller, 1994).

It is possible that vibrations in the soil may play some role in host location by *Tiphia* that was not determined in this study. Predators can use vibrations transmitted through sand to direct movement towards their prey (Brownell & Farley, 1979; Hetherington, 1989). In non-sandy soils, however, differences in composition and compaction affect the frequency and distance a sound is transmitted (Mankin et al., 2000). This might confound the use of vibrational cues for host location. Nevertheless, depending on soil parameters, feeding and movement of white grubs produces vibrations that can be detected up to 30 cm away using acoustic detection systems (Mankin et al., 2000). In our study, vibrational cues may have been reduced due to the loose packing of the soil in the observation chamber.

The presence of host frass elicited a strong response from both species of wasps. When a female encountered frass, she thoroughly antennated it and then continued a much slower progression along the frass trail, examining the surrounding soil. Upon reaching the end of a frass trail, wasps often moved halfway back down the trail and then attempted to burrow downward into the soil, as if searching deeper for a nearby host. Wasps continued to dig and search the area surrounding the frass, never abandoning that

area during the short observation periods. These observations, coupled with choice tests where wasps chose frass trails over host body odor trails, show that frass elicits a stronger response than host body odor.

Both *T. pygidialis* and *T. vernalis* were able to distinguish between body odor trails and frass from host and non-host grubs. This indicates use of species-specific kairomones in below-ground host location. Although wasps preferred frass from their host grub species when given a choice, they also responded to frass from non-host grubs when no other cues were present. In the field, such a response could lead to inefficient foraging because both grub species often co-occur. Those physical and chemical properties of frass that are common to both *Cyclocephala* spp. and *P. japonica* grubs probably play some role in this response. Parasitoids may be attracted to frass from hosts and non-hosts feeding on the same plant because of similarities in their plant-derived volatiles (Auger et al., 1990; Agelopoulos & Keller, 1994; Agelopoulos et al., 1995). This may account for attraction of *Tiphia* to frass from non-host grubs in no-choice tests.

The condition of the frass used in our study may also have influenced the wasps' response to non-host frass in no-choice tests. Moisture content can affect the types and quantity of volatile compounds released from frass (Agelopoulos et al., 1995). The frass we used was several days old and drier (about 2% moisture content) than what would normally be found under field conditions. It may be difficult for wasps in

no-choice situations to recognize and reject non-host frass that is dry. Nevertheless, frass from each wasp's respective host species elicited a relatively stronger response, suggesting that species-specific kairomones in frass also are involved.

Our experiments indicate that as grubs move through the soil, some residual cuticular substance is deposited on soil particles, leaving a scent trail for *Tiphia* wasps to follow. Some parasitoids respond to species-specific properties of a host's cuticular hydrocarbons (W.J. Lewis et al., 1976; Howard et al., 1998). While not highly volatile, cuticular hydrocarbons have enough vapor pressure to contaminate the surrounding substrate, allowing their use as a contact cue in host finding and recognition (Howard, 1992). Host frass, which may contain some of the same cuticular hydrocarbons (W.J. Lewis et al., 1976), may serve to reinforce the presence of a host through both its chemical and physical properties. Whether or not cuticular hydrocarbons from grubs are involved in trail-following by *Tiphia* wasps is presently unknown.

Some parasitoids exploit sex or aggregation pheromones of their hosts as kairomones in host location (Noldus et al., 1991; Wiskerke et al., 1993). Interestingly, an unidentified volatile sex pheromone that attracts adult males of both *C. lurida* and *C. borealis* is present on the cuticle of *Cyclocephala* spp. grubs (Haynes et al., 1992). The pheromone is present in both male and female larvae, but lost by males between the pupal stage and the adult (Haynes & Potter, 1995). Whether or not the *Cyclocephala* sex pheromone is involved in host-seeking or recognition by *T. pygidialis* is presently unknown. Notably, bioassays with *P. japonica* and several other species of scarab larvae that are parasitized by *Tiphia* spp. have indicated absence of sex pheromones in the larval stage (Haynes & Potter, 1995; Leal, 1998).

Scarabaeid grubs tend to be patchily-distributed in turf (Dalthorp et al., 2000). While it seems unlikely that *Tiphia* females search randomly for such patches, the cues that the flying wasps may use to guide them to areas where their below-ground hosts are abundant are presently unknown. Potential intermediate- and long-range signals include visual cues from grub-damaged grasses, volatile odors from grubs and their frass, or synomones emitted by above-ground plant tissues in response to root damage.

The present study indicates that after they have entered the soil, female *T. vernalis* and *T. pygidialis* locate their hosts by following species-specific grub body odor trails that are deposited on soil par-

ticles, as well as kairomones present in grub frass. We are aware of no previous studies of host location by parasitoids that attack soil-dwelling insects; however, entomopathogenic nematodes have been shown to exploit host odors and frass to locate and recognize their scarabaeid hosts (E.E. Lewis et al., 1992, 1993; Grewal et al., 1993). Thus, these distinctly different taxa seem to exploit some of the same cues to locate patchily-distributed hosts in the soil. Additional studies are needed to determine the extent to which other natural enemies that attack edaphic insects have evolved similar host-location strategies.

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