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Biological Control

Response of *Torymus sinensis*, a parasitoid of the gallforming *Dryocosmus kuriphilus*, to olfactory and visual cues

Ignazio Graziosi, Lynne K. Rieske *

Department of Entomology, University of Kentucky, S225 Ag North, Lexington, KY 40546-0091, USA

HIGHLIGHTS

- *T. sinensis* is a parasite used for biological control of *D. kuriphilus*.
- Behavior of *T. sinensis* adult females was tested in a Y-tube olfactometer.
- Insects were not attracted to gall odor presented alone.
- *T. sinensis* responded negatively to a gall image presented alone.
- Wasps responded positively to olfactory and visual cues when presented together.

GRAPHICAL ABSTRACT
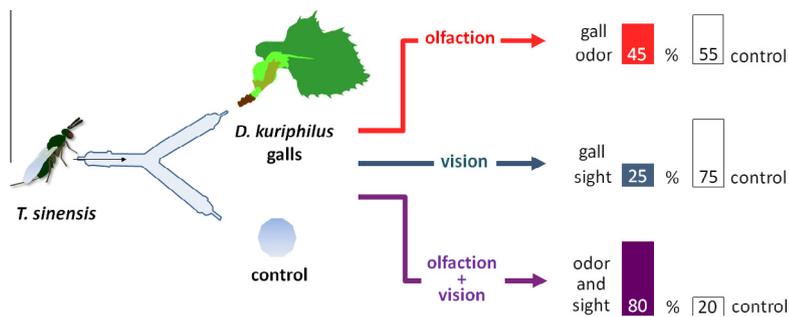
ARTICLE INFO

ABSTRACT

Torymus sinensis (Hymenoptera: Torymidae) has been manipulated extensively in biological control programs targeting the globally invasive Asian chestnut gall wasp, *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae). The life cycle of *T. sinensis* is synchronized with gall wasp larval development to allow effective gall wasp population suppression and a reduction in gall formation. In spite of its extensive use for biological control, relatively little is known about its host location and host acceptance behavior. We investigated *T. sinensis* host location behavior using a Y-tube olfactometer. Adult females were tested for their response to olfactory and visual cues associated with *D. kuriphilus* galls and chestnut foliage. Adult parasitoids were not attracted by the odor of fresh galls alone, and had a negative response to the visual cues of galls and chestnut foliage when odor cues were not provided. However, the combination of olfactory and visual stimuli provided by a fresh gall coupled with chestnut foliage elicited a strongly positive response. This positive response persisted even when the fresh gall was replaced by an inert surrogate gall, provided the visual stimulus remained and the olfactory cues from fresh galls were available. Our results indicate that both visual and olfactory cues are required to enable *T. sinensis* to successfully find suitable hosts. These findings improve our understanding of the stimuli that influence *T. sinensis* host location behaviors leading to successful gall wasp parasitization, and may enhance our ability to manipulate *T. sinensis* for gall wasp management.

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1. Introduction

Non-native species often become invasive due in part to a lack of population regulators in invaded territories (Elton, 1958; Lockwood et al., 2007; Davis, 2009). Biotic factors contributing to invasiveness include such things as host plant susceptibility and distribution (Griffin, 2000; Orwig, 2002), altered competitive interactions (Elton, 1958; Ricciardi et al., 1997; Green et al., 2004), and perhaps most importantly, a lack of natural enemies. Enemy free space is often considered a major determinant of invasiveness of a non-native species (Crawley, 1987; Keane and Crawley, 2002), and is the basis for biological control. Despite criticisms of being oversimplistic (Colautti et al., 2004; Levine et al., 2004) and case-specific

* Corresponding author.
    E-mail addresses: i.graziosi@uky.edu (I. Graziosi), Lrieske@uky.edu (L.K. Rieske).

(Berdegue et al., 1996), the enemy free space hypothesis remains a standard explanation for invasion success.

Several attributes are essential when considering the effectiveness of a natural enemy for pest population regulation, including synchrony with the target pest's life cycle (Hassell, 1985) and the ability to disperse into invaded territory with expanding pest populations (Wright et al., 2005). The ability of a biological control organism to locate suitable host material and disperse is especially important when considering population regulation of an invasive herbivore found on a sporadically occurring host plant across a broad geographic region.

Parasitoid searching and host location is influenced by external stimuli such as olfactory, visual, and tactile cues (Laing, 1937, 1938; Vinson, 1976, 1998; Broad and Quicke, 2000). Olfactory cues include odors emanating from both the host insect, and from host associated plants (Price et al., 1980; Vet and Groenewold, 1990; Whitman and Eller, 1990). The importance of olfactory cues in parasitoid host location behavior is well studied (Weseloh, 1981), but the importance of visual cues is less understood (Turlings et al., 1993). Visual cues may function as a primary stimulus for host location behavior in some parasitoids, whereas in others vision appears to function synergistically with additional environmental cues.

Torymus sinensis Kamijo (Hymenoptera: Torymidae) is a hymenopteran parasitoid utilized for biological control of the Asian chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae), a globally invasive pest of chestnut, *Castanea* spp. *T. sinensis* is the dominant parasitoid reared from *D. kuriphilus* galls in its native China (Kamijo, 1982), and has been introduced to additional regions of Asia, North America, and Europe for management of Asian chestnut gall wasp populations (Moriya et al., 2003; Cooper and Rieske, 2007; Gibbs et al., 2011). *T. sinensis* is a univoltine ectoparasitoid that is phenologically synchronized with *D. kuriphilus*, making it a particularly effective biological control agent (Murakami et al., 1995; Moriya et al., 2003; Cooper and Rieske, 2007, 2011). Adults emerge from vacated galls in early spring and mate. Females locate newly forming galls, insert their ovipositor, and lay eggs internally on chamber walls or on the surface of the *D. kuriphilus* host larvae (Piao and Moriya, 1999; Quacchia et al., 2008).

Long distance dispersal of the gall wasp host occurs through anthropogenic movement of infested plant material, and *T. sinensis* moves with expanding gall wasp populations via infested host material (Cooper and Rieske, 2007; Rieske, 2007). On a localized scale, gall wasp dispersal occurs by adult flight (Graziosi and Rieske, 2012), but localized movement of *T. sinensis* has not been thoroughly evaluated. Although its oviposition behavior has been described (Piao and Moriya, 1999), the environmental cues and behaviors used in host location prior to female oviposition are unknown.

We evaluated olfactory and visual cues contributing to host location behavior of *T. sinensis,* to assess how dispersal of the parasitoid with expanding gall wasp populations is occurring, and to ultimately gain a more complete understanding of the parasitoids' role in gall wasp population regulation. We hypothesized that *T. sinensis* uses host plant cues to detect and orient to galled chestnut shoots.

2. Materials and methods

Parasitoid responses to olfactory and visual cues were evaluated in the laboratory using a Y-tube olfactometer and excised plant material (Yang et al., 2008). The movement and behavior of parasitoids was observed for the duration of each trial, and grooming behavior, flight attempts, and oviposition attempts were noted.

2.1. Parasitoids

Previous year's *D. kuriphilus* galls were collected in March 2012 from *Castanea* hybrids in Meadowview, VA and Mercer, PA, from established populations of *D. kuriphilus* heavily parasitized by *T. sinensis*. These vacated *D. kuriphilus* galls contain overwintering populations of *T. sinensis* (Cooper and Rieske, 2007). Galls were stored in darkened containers at 4 °C until needed. In the laboratory excised galls were placed in darkened boxes (26 × 19 × 9.5 cm) with clear cylindrical collection containers (20 × 1.5 cm diameter) inserted on the upper side to collect emerging *T. sinensis* adults. Parasitoids were collected daily, held in 12 ml glass vials plugged with cotton (N = 4 insects per vial, approximately 1:1 sex ratio), and fed drops of honey water. Emergence boxes and vials were maintained at 20 ± 3 °C under ambient lighting for 2–3 d prior to use in assays. Mating was observed in each vial; only mated females were used in assays.

2.2. Olfactometer

The glass olfactometer (Fig. 1) consisted of a Y-tube with a 115 mm long central stem (internal diameter 19 mm) and two 135 mm arms set at a 65° angle (internal diameter 25 mm). Air was pumped through silicon tubing (Fig. 1a and b), purified by passing through an activated charcoal filter and dust filter, humidified by bubbling through distilled water (Fig. 1c–e) and then passed through a flow meter (Fig. 1f). Air flow (flow rate 10 ml sec^{-1}, wind speed 3 cm sec^{-1}) was split with a glass Y-connector and passed through two 20 ml flasks (Fig. 1g), each containing an odor source or blank, and then through the arms of the Y-tube (Fig. 1h) and the central stem (Fig. 1i).

The olfactometer was isolated from external stimuli by enclosing it horizontally in a box with the top and internal walls covered with white paper. A hole in the top of the holding box allowed even illumination by two 15 W (47 cm) fluorescent bulbs. Light intensity at the Y-tube level was measured with a light meter (Auto-lumi L-158, Sekonic Japan) and was 12,000 Lux. Ambient temperature was 20 ± 3 °C, and assays were conducted between 0800 and 1800 h EDT, 5 April–23 May.

Parasitoids were introduced into the olfactometer through an entrance in the central stem (Fig. 1i) and behavioral responses to selected stimuli were monitored. Parasitoids were scored as having made a "choice" when the insect traveled 3 cm up a Y-tube arm, and the time elapsed was recorded. If parasitoids did not make a choice in 20 min the insect was removed and the trial was recorded as "no choice." Each insect was used only once. The Y-tube and connectors were washed with acetone and dried at room temperature for 20 min after each trial, and stimuli were switched between arms of the olfactometer every five trials.

2.3. Olfactory cues

Fresh *D. kuriphilus* galls served as our olfactory stimulus, and were collected during the period of larval development and rapid gall expansion (April 2012) from mature Chinese chestnut trees (*Castanea mollissima*) located in Lexington, KY. Galls were excised, placed in sealed plastic bags, and transported immediately to the laboratory, where they were maintained at 4 °C until use in assays. Galls were collected each morning for use in assays the same day.

2.4. Visual cues

Visual stimuli included (1) *C. mollisima* shoots containing developing galls, (2) *C. mollisima* shoots free of galls but with expanded leaves, and (3) a 'gall surrogate', consisting of an inert, 16 mm diameter, surface-sterilized green marble. Plant material was collected from the same trees and at the same time as described above.
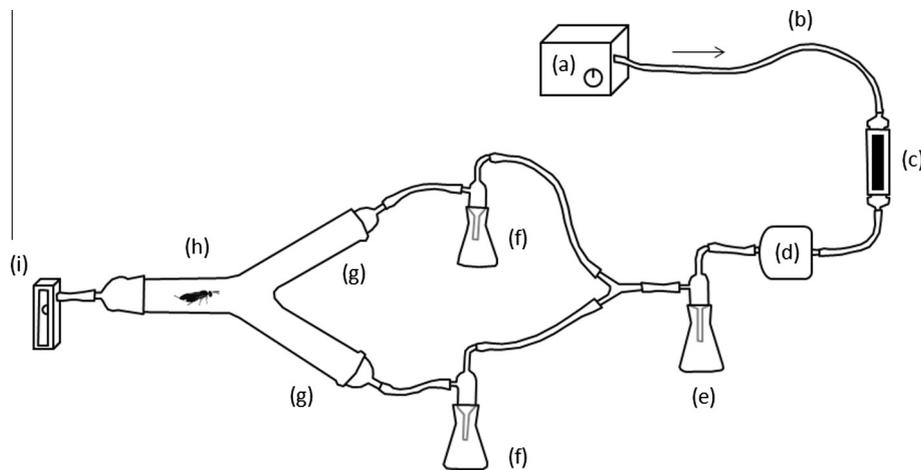
Fig. 1. Olfactometer configuration consists of (a) air source (pump), (b) silicon tubing, (c) charcoal activated filter, (d) dust filter, (e) distilled water, (f) flasks containing odor source or control, (g) side arms, (h) central arm, and (i) flow meter.

2.5. Dual choice experiments

Olfactory and visual stimuli were manipulated in four dual choice experiments to evaluate female *T. sinensis* response. Each set of stimuli were tested in a series of trials consisting of 20 *T. sinensis* females making a choice.

Experiment 1. Olfactory stimulus. We evaluated the response of *T. sinensis* to host odor by comparing fresh *D. kuriphilus* galls to a blank control (air). A single excised gall was placed in one of the odor source flasks, not visible to the insect, and the second source flask remained empty.

Experiment 2. Visual stimuli. To separate visual and olfactory stimuli to evaluate only visual response, we used a gall surrogate (green marble) inserted into the Y-tube arm 3 cm from the central stem, coupled with a chestnut shoot containing 3–5 fully expanded leaves positioned outside the same arm. The opposite arm contained no visual stimulus, and no odor was involved in either arm.

Experiment 3. Olfactory + visual stimuli with fresh gall. A newly excised *D. kuriphilus* gall was inserted in the Y-tube arm and a chestnut shoot with leaves was placed externally next to the same arm as described above.

Experiment 4. Olfactory + visual stimuli with gall surrogate. A visual cue was provided by a surrogate gall coupled with externally placed foliage, and an olfactory stimulus was provided by a fresh gall contained in the flask of the same Y-tube arm, but obscured from the parasitoids' vision.

2.6. Statistical analysis

Preference of *T. sinensis* females for selected stimuli versus blank controls was assessed using a chi-square analysis (Hare, 1998). Analysis of variance was used to evaluate differences in the time elapsed for female wasps to choose (olfactory, visual, olfactory + visual stimuli versus blank control), using SAS v. 9.1 (SAS Institute Inc, 2001).

3. Results

Across all experiments, 91% of the parasitoids assayed (80 out of 88) made a choice (traveled >3 cm into one arm of the olfactometer) within 20 min., demonstrating that they were readily able to respond to stimuli. There were no differences in overall response times across the four experiments. The majority of the wasps began grooming immediately after introduction into the olfactometer; the

duration of this behavior was highly variable. We did not observe any flight attempts inside the olfactometer.

Experiment 1. Olfactory stimulus. There were no differences in olfactory response of *T. sinensis* between *D. kuriphilus* gall volatiles and air (Fig. 2a), nor were there differences in the time required for wasps to make a choice (Fig. 2b).

Experiment 2. Visual stimuli. Only 25% of the *T. sinensis* evaluated responded positively to the visual stimulus of the inert gall surrogate with chestnut leaves, while 75% chose the blank control (Fig. 2c). When provided only visual stimuli, wasps that chose the stimulus did not attempt contact with the gall surrogate during the 20 min. trial. Similar time elapsed between those wasps choosing the visual stimuli and those choosing the blank control (Fig. 2d).

Experiment 3. Olfactory + visual stimuli with fresh gall. *Torymus sinensis* responded positively to a combination of host olfactory odor and visual cues; 80% of the wasps assayed chose the olfactory cues associated with a newly excised gall coupled with the visual cues of chestnut foliage placed external to the olfactometer arm (Fig. 2e). The time elapsed for wasps to choose host cues was significantly longer compared to blank controls (Fig. 2f). Those *T. sinensis* choosing the host stimuli made physical contact with the gall surface and initiated oviposition behavior.

Experiment 4. Olfactory + visual stimuli with gall surrogate. Similarly, *T. sinensis* responded positively to the visual cues provided by a surrogate gall and externally placed foliage, coupled with an olfactory stimulus provided by a fresh gall; 75% of assayed wasps chose the stimuli (Fig. 2g) over a blank control. There were no significant differences in time elapsed between choices (Fig. 2h), however the trend appears similar to that observed using freshly excised gall material (Fig. 2f). Those parasitoids that chose the visual stimuli reached the gall surrogate and attempted oviposition on the surface of the glass sphere.

4. Discussion

Here we demonstrate that the simultaneous presence of visual and olfactory stimuli is required to elicit host location behavior in *T. sinensis*, while neither individual stimulus alone triggers this behavior. Parasitoid searching and host location is influenced by a variety of stimuli (Laing, 1937; Lewis et al., 1976; Vinson, 1976; Broad and Quicke, 2000). Olfactory cues are well studied (Weseloh, 1981; Meiners et al., 2003; Schurmann et al., 2009), but the importance of visual cues is less understood. Evidence suggests that visual cues may function as a primary stimulus for host location
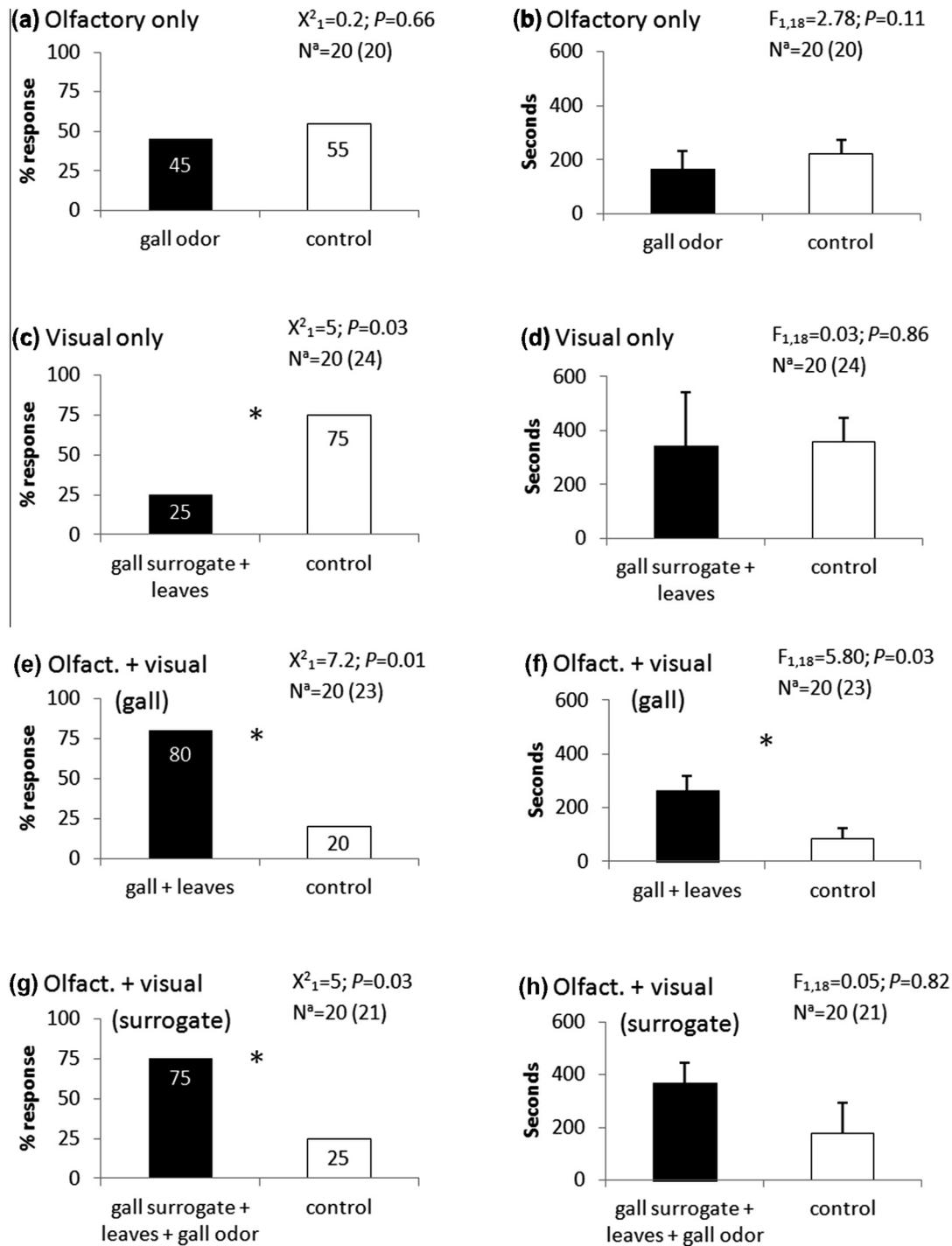
Fig. 2. Proportion of *T. sinensis* female wasps choosing a stimulus (olfactory and/ or visual) versus a blank control in four dual choice experiments (a, c, e, g), and time elapsed (seconds) for *T. sinensis* female wasps to choose a stimulus (b, d, f, h). See text for full description of stimuli. [a]N = number of wasps that chose (total number of wasps evaluated). * Significant ($P < 0.05$) difference.

behavior, or such cues may function in combination with additional environmental cues to elicit behavioral changes (Turlings et al., 1993). Egg surrogate studies using rice grains suggest that *Trichogramma evanescens* Westwood relies primarily on visual cues to locate lepidopteran host eggs; host odors alone appear unimportant in perceiving eggs from a distance (Laing, 1937, 1938). The braconid *Microplitis croceipes* Cresson locates larval hosts using visual cues from the cotton plant on which the host insect feeds, and odor cues emitted by host insect frass (Wäckers and Lewis, 1994). The pupal parasitoid of the greater wax moth, *Pimpla turionellae* (L.), reacts positively to visual or auditory cues emitted

by the host, but when these cues are present simultaneously responsiveness is greatly enhanced, demonstrating that a combination of visual and vibrational cues is used to locate hosts (Fischer et al., 2001). In other cases the synergistic effect of two different odors triggers attraction. For example, the braconid parasitoid *Diachasmimorpha longicaudata* (Ashmead) is not attracted to odors of Asian fruit fly larvae, *Bactrocera dorsalis* (Hendel), unless odors of ripe guava fruits are also present (Jang et al., 2000).

Similarly, a combination of cues appears to stimulate host location behavior in *T. sinensis*. Females demonstrate no response to an odor stimulus alone, and the visual stimulus alone elicits a negative

response, but the two presented simultaneously elicit host finding behavior. This pattern of response clearly has adaptive advantages. Adult *T. sinensis* emerge from galls in an exceedingly complex environment and are exposed to a variety of relevant and irrelevant stimuli. Response to two distinctly different, yet simultaneously occurring, stimuli would allow more correct identification of relevant resources, and represents an efficient strategy to overcome environmental complexity to locate suitable hosts. A positive response of females to only one stimulus, either visual or olfactory, could elicit inefficient or incorrect choices for resource location. For *T. sinensis*, visual cues may act as a behavioral switch that allows female parasitoids to detect relevant odors such as developing *D. kuriphilus* galls, which in turn elicits host seeking behavior. This 'activation hypothesis' corroborates observations that a single cue from a host insect may facilitate detection of other cues (Vinson, 1976). If there is no exposure to the visual stimulus of developing galls and chestnut foliage (i.e., switch turned 'off'), then host odor is not recognized and there is no response to host stimuli. Further, the visual stimulus of galls on chestnut twigs alone does not produce a positive response, since there is no odor present to trigger the host location behavior. Visual cues appear to activate the responsiveness of *T. sinensis* females to relevant odor cues. Our results also indicate that those *T. sinensis* females which respond positively to stimuli require more time to make a choice compared to those not responding to host cues (Fig. 2f), suggesting that female parasitoids require a certain amount of time to interpret meaningful cues in order to successfully locate hosts.

While the use of multiple cues to overcome environmental complexity and an activation response may adequately explain our observations of *T. sinensis* host location behavior, associative learning cannot be discounted. Parasitoid host finding behavior leading to oviposition is driven by environmental cues as well by internal parameters such as hunger, age, physiological condition and experience; this is associative learning (Vinson, 1998). Experience may produce internal changes that increase sensitivity to certain stimuli (Turlings et al., 1993).

Our findings on *T. sinensis* response to environmental stimuli are also interesting when considered in light of the chemical legacy hypothesis (Corbet, 1985) and related studies (Hérard et al., 1988), which hypothesize that traces of chemical cues associated with immature parasitoids are carried through adult emergence, when they affect the responsiveness of adults to specific cues. *Torymus sinensis* adults emerge in spring from previous year *D. kuriphilus* galls still attached to infested trees, where developing shoots and galls are expanding at the time of emergence. Emerging parasitoids are immediately exposed to host insect and host plant odors, as well as visual cues associated with developing leaves and galls. These parasites may be associating relevant odors to visual stimuli. Our test insects were reared under laboratory conditions and lacked the visual and olfactory cues normally present at emergence, thus resulting in inexperienced wasps that respond poorly to individually presented stimuli. However, we did not directly test for either associative learning or innate response in our study.

Auditory cues appear unimportant for initiation of oviposition behavior in *T. sinensis*. Females were positively attracted to an inert gall surrogate in the presence of fresh gall odor, and test wasps initiated oviposition behavior on inert surrogates. Visual and olfactory cues may override any need for vibrational cues in host location behavior of *T. sinensis*, at least in our assay conditions. Given the importance of tactile, vibrational and auditory cues in other parasitoid–host systems (Wäckers et al., 1998; Fischer et al., 2001, 2004; Völkl, 2003), this is somewhat surprising. However, we cannot discount the role of vibrational and/or tactile cues in host acceptance leading to actual oviposition, since no eggs were laid during the oviposition attempts on the gall surrogates.

Outside North America, *T. sinensis* has been intensively manipulated in biological control programs targeting the Asian chestnut gall wasp in Japan (Moriya et al., 2003) and Europe (Quacchia et al., 2008; Aebi et al., 2011; Gibbs et al., 2011). In spite of this intensive manipulation, the host location behavior of *T. sinensis* is poorly understood. Following its initial introduction into gall wasp infested orchards in the USA (Payne, 1978) and with no additional manipulations, *T. sinensis* moved with expanding gall wasp populations, often offering effective population regulation and slowing or dampening gall wasp population outbreaks (Cooper and Rieske, 2006, 2007, 2011). However, its success in reliably suppressing gall wasp populations in North America is somewhat erratic (Cooper and Rieske, 2011). Our results provide groundwork to gain a deeper understanding of its host location behavior to enhance the success of any further manipulations of *T. sinensis* for gall wasp management.

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