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Host location and selection cues in a generalist tachinid parasitoid

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Abstract

Tachinid flies are diverse and ecologically important insect parasitoids. However, the means by which tachinid species locate and select hosts are poorly known. Many tachinids exhibit unusually wide host ranges and they also possess well-developed visual systems. These characteristics suggest that tachinids differ from parasitic wasps in their reliance on various sensory modes and types of cues. A series of behavioral assays using the generalist tachinid *Exorista mella* Walker (Diptera: Tachinidae) were conducted to examine what types of cues this parasitoid uses to locate and accept hosts, and how the cues used may reflect its ecological relationships with hosts. Female *E. mella* responded strongly to host motion in assays using both live hosts and host corpses, and this cue is shown to be an important elicitor of attack behavior. Females also responded to volatile chemicals associated with damaged food plants of their host in an olfactometer. Flies responded only weakly to direct visual contact with stationary hosts and odors directly associated with hosts. The behavior of female *E. mella* changed with experience such that more experienced flies recognized and attacked hosts more readily than did inexperienced flies. The use of general olfactory and visual cues by *E. mella* may be an effective strategy by this polyphagous parasitoid to locate a broad range of potential hosts.

Introduction

The vast majority of analyses of host location and acceptance mechanisms in parasitoids have focused on parasitic wasps (Hymenoptera: Parasitica; e.g., Godfray, 1994). In these parasitoids, olfactory mechanisms of host location have received the most attention and may be the dominant means of finding hosts in many species (van Alphen & Vet, 1986). Hymenopteran parasitoids have been shown to locate hosts using olfactory cues derived from the food of their hosts (usually plants, Weseloh, 1981; Vinson, 1984, 1998; Turlings et al., 1990; Vinson & Williams, 1991; Turlings & Tumlinson, 1992; Morgan & Hare, 1998; Potting et al., 1999; Meiners et al., 2000; Steidle et al., 2001), from host feces or other byproducts (Jones et al., 1971; Hendry et al., 1973; Sullivan et al., 2000), and from host pheromones (McGregor & Henderson, 1998; Colazza et al., 1999). The role of vision has received considerably less attention, though visual cues have been demonstrated to play a role in host location and acceptance in at least some species (Wäckers & Lewis, 1994; Oliai & King, 2000).

Our understanding of host location and selection processes in tachinid flies, another large and ecologically diverse group of parasitoids, is limited to studies of a few species, mostly of economic importance (e.g., Roth et al., 1978, 1982), but we have little idea of the range of mechanisms used in host location and their relative importance. The morphological and physiological disparity between tachinid and hymenopteran parasitoids, as well as broad differences in host-specificity, suggest that they may differ in their reliance on various types of cues to locate hosts. It is doubtful that our growing understanding of host selection processes and their relative importance in the Hymenoptera can be used as a paradigm for all parasitoids (Feener & Brown, 1997).

Most tachinids have relatively large eyes, and are likely to possess well-developed motion detection systems based on studies of related flies (Dethier, 1963; Bushbeck & Strausfeld, 1997). Possible preadaptation for use of visual cues in host location and acceptance is supported by the established preeminence of vision in foraging by several non-parasitoid calyptrate Diptera (Prokopy, 1968; Conlon & Bell, 1991; Henneman & Papaj, 1999). Many tachinids are also known to exhibit relatively wide host ranges given their koinobiont life histories (Belshaw, 1994; Hawkins, 1994). Such polyphagous parasitoids may be expected to use more general, easily detectable, and perhaps less reliable cues than specialized parasitoids, such as generic green leaf volatiles released by damaged plants (Vet et al., 1991; Vet & Dicke, 1992).

Despite these differences, hymenopteran and tachinid parasitoids do exhibit some commonality with respect to host location and selection, possibly representing convergent solutions to the same problems. As with parasitic wasps, tachinid flies have been demonstrated to respond to cues derived from host plants (e.g., Monteith, 1955; Martin et al., 1990; Roland et al., 1995) and host feces (Nettles & Burks, 1975; Thompson et al., 1983). Such similarity may serve as confirmation of the hypothesized constraints and selective pressures on behavior suggested by theory (Vet et al., 1990).

Here, I employed a set of behavioral assays to identify cues important in host location and acceptance in the polyphagous tachinid parasitoid, *Exorista mella* (Walker). These experiments were designed to address three basic questions: (1) Does *E. mella* use visual and/or olfactory cues associated directly with hosts in host location? (2) Does the relative importance of these sensory modes differ? (3) Is host motion important in host location and selection? In addition, the effect of experience on host location and selection was examined. The results of these experiments are discussed with respect to the wide host range of *E. mella* and the predicted importance of vision in tachinids.

Materials and methods

Insects

Exorista mella is a polyphagous endoparasitoid that parasitizes a wide variety of externally feeding Macrolepidoptera (ten families, >50 species; Arnaud, 1978) across the United States and southern Canada (Sabrosky & Arnaud, 1965). Over their 20–40 day lifetimes females are able to deposit an average of 150 ± 80.5 (mean ± SD) of their heavily-chorionated eggs onto the cuticle of their hosts (Adam & Watson, 1971). The eggs undergo a period of embryonic development (48–72 h; Adam, 1968) before the larva hatches and burrows into the host. Females tend to attack late instar caterpillars (Taylor, 1952; Adam & Watson, 1971; pers. obs.), which may support the development of multiple larvae (ca. 1–8; J. O. Stireman, unpubl.). Females readily superparasitize hosts in the laboratory (pers. obs.), though a related species *E. japonica* has been shown to discriminate against hosts bearing ten or more fly eggs (Nakamura, 1997).

Flies used in this study were between second and fifth generation offspring of individuals reared from natural populations of *Grammia geneura* (Lepidoptera: Arctiidae) collected from mesquite grasslands in southeastern Arizona. *Grammia geneura* is a polyphagous caterpillar, rather unpredictably distributed over space and time (Singer, 2000). These hairy, ground-dwelling caterpillars are much more active than most other lepidopteran larvae. A culture of this host was reared in the laboratory to ensure continuous availability of flies, though additional *E. mella* reared from field-collected caterpillars were added regularly to sustain the laboratory culture. Flies were kept in groups of ca. 8–30 in two glass terraria (32 cm × 41 cm × 26 cm high, 43 cm × 62 cm × 33 cm high) with screened openings. These were kept at room temperature (ca. 22–25 °C) but were situated adjacent to a partly shaded south facing window providing a natural light/dark regime. Sunlight provided radiant heat for the flies and also resulted in relatively high temperatures within the terraria (28–30 °C). Each was provided with separate petri dishes containing water, sugar, and a yeast extract/sugar mixture. Males and females were kept together to ensure mating. All females used in experiments were at least four days old to ensure that they had the opportunity to mate and develop fertile eggs (mean preoviposition period of *E. mella*: 3.2 ± 1.1 days; Adam & Watson, 1971).

Grammia geneura caterpillars were second to fourth generation offspring of field-collected individuals. Caterpillars were reared in individual cups (180 ml) on an artificial wheat germ diet (Yamamoto, 1969) at 29 °C and L16:D8. To maintain the fly culture, live caterpillars were parasitized by placing them in the terrarium and removing them once 1–6 eggs had been deposited by the flies. Caterpillars were checked daily for parasitoid emergence, and upon eclosing, flies were released immediately into the terraria.

Response of flies to concealed and exposed hosts

To assess whether visual or non-visual cues are used by *E. mella* to locate and accept hosts, I presented individual flies with four sequential treatments in a clear plastic cylindrical (27.3 cm × 22.5 cm diam.) foraging arena. These consisted of: (1) A control (no odor or visual cues), in which a finely perforated Styrofoam cup (diam.: 6 cm, h: 8 cm) was placed over an empty petri dish (diam: 5.5 cm); (2) A concealed treatment (odor, but no visual cues), in which a caterpillar recently killed by freezing was placed in the petri dish under the perforated cup. (3) An exposed treatment (odor and visual cues, but no motion), in which a dead caterpillar was placed uncovered in the petri dish; and (4) An exposed treatment (odor, visual, and motion cues), in which a live unparasitized caterpillar was placed uncovered in the petri dish. At the initiation of each observation, flies were placed on the floor of the arena facing the single treatment source (ca. 15 cm away). Due to the low number of female flies available, each fly was subjected to all four treatments, each for 10 min separated by a 5 min rest period. Despite the risk of possible order effects, treatments were always presented in the order they are listed to minimize potential effects of experience with live caterpillars on responses to other treatments. Fly (and caterpillar when present) behaviors were recorded continuously using the computer program The Observer 3.0 (Noldus, 1993). This experiment was conducted over a period of several weeks as mated females became available. A total of 33 flies were tested, from 1–4 on each testing date. All flies were categorized as experienced (N = 17) or inexperienced (N = 16) according to whether or not they were present in terraria in which *G. geneura* caterpillars had been previously introduced. Individual flies ranged in age from 7–16 days.

Analysis. Variables used to assess attraction to and acceptance of the treatment were (a) latency to contact of the cup/petri dish, (b) total duration of time spent on the cup/petri dish, and (c) number of oviposition attempts. Statistical analyses were performed using JMP IN 3.2.1 (SAS institute Inc., 1996) and Statview 4.02 (Abacus Concepts Inc., 1993). Latency to contact and total duration were analyzed using a repeated measures ANOVA implemented as a MANOVA to avoid assumptions of sphericity (Zar, 1996). For flies that never made contact with the treatment source, latency was scored as the total length of the trial (600 s). Data were non-normally distributed due to the truncation of trials and the large numbers of flies that did not respond at all to certain treatments. Time data were transformed into proportions by dividing by the total observation time and arcsine transformed to improve the dispersion of the residuals and reduce heteroscedasticity. ANOVA statistical tests are relatively insensitive to violations of normality assumptions (Scheffe, 1959). Pairwise comparisons (specified *a priori*) were made between treatments and control using a series of Wilcoxon paired-sample tests employing a Bonferroni corrected α of 0.01 and 0.0125 for analyses within and between experience classes of flies, respectively (Zar, 1996). The effects of experience, treatment, and their interaction were included in models. The relationships between the time spent on the petri dish and the number of oviposition attempts by the flies and the duration of caterpillar movement were examined using least-squares linear regression. An oviposition attempt was defined as a curling of the abdomen and extension of the ovipositor towards the host. The difference in mean number of oviposition attempts on dead and live caterpillars was examined using separate Wilcoxon paired-sample tests (Zar, 1996) for experienced and inexperienced flies.

Response of flies to odors associated with caterpillars

To further investigate the response of flies to odors associated with their host, the activity levels of 23 females to three no-choice odor treatments in an olfactometer was recorded. The olfactometer chamber consisted of a 1000 ml side arm filtering flask. Lab air was passed at 28 ml s^{-1} over a smaller chamber holding an odor source, and then passed through the olfactometer chamber (Figure 1). Treatments consisted of (a) an empty odor chamber (control), (b) a live caterpillar placed in the odor chamber, and (c) a cut sprig of one of the host's food plants (*Ambrosia confertiflora*) placed in the odor chamber. For each trial, flies were placed into the olfactometer chamber and allowed to explore it for 2 min before airflow and data recording commenced. Resting, grooming, walking, and flying behaviors were recorded continuously using The Observer (Noldus, 1993). After each caterpillar and plant treatment, the olfactometer chamber and odor chamber were washed thoroughly with soap

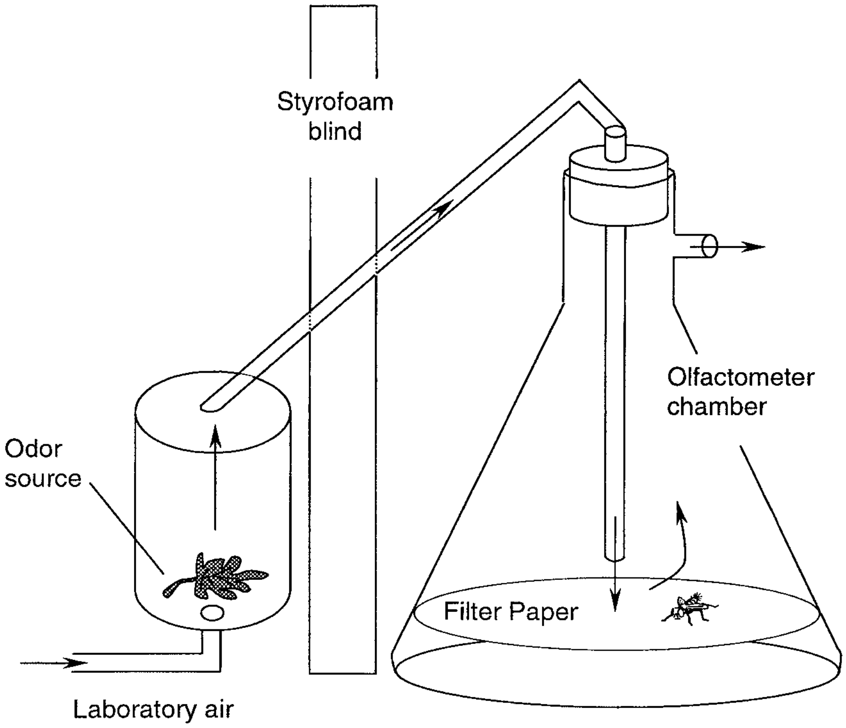

Figure 1. The olfactometer apparatus used to examine the response of flies to odors associated with the host. Arrows indicate the path of air flow.

and water, the filter paper was replaced, and air was flushed through the system for 5 min. Treatments were conducted in random order, and each fly was subjected to only one treatment.

Analysis. To test whether flies responded positively to odor cues associated with hosts, I compared the time they spent walking and the latency to the first walking bout in response to each of the treatments. Walking was selected as a response variable due to the observation that, upon detection of potential hosts, *E. mella* females almost invariably approach them by rapid walking, and this behavior was general indicative of an excited behavioral state. Although the flies do walk in the absence of hosts or host associated cues, these observations suggest that the onset and duration of walking behavior is likely to be elevated in response to host associated cues. Data were analyzed using a Kruskal–Wallis test, and Mann–Whitney U tests (Bonferroni corrected $\alpha = 0.025$) were used to compare individual treatments to the control in JMP IN 3.2.1 (SAS institute Inc., 1996).

Table 1. Results of repeated measure ANOVAs (as MANOVAs) for the latency to contact and duration of time spent in contact with treatment sources in experiment 1. Pairwise comparisons between treatments and controls were assessed with nonparametric Wilcoxon paired-rank P values (Bonferroni corrected $\alpha = 0.01$). Multiple P values are reported where multiple comparisons were significant. (N = 33, $^{*}P < 0.05$, $^{**}P < 0.01$)

Source	d.f.	Exact F	Wilcoxon (P)
Duration			
Treatment	3	8.02**	0.0035, 0.0045 (exposed dead, live vs. control)
Experience	1	13.18**	
Treat. × exp.	3	5.86*	
Latency			
Treatment	3	1.38	n.s.
Experience	1	11.77**	
Treat. × exp.	3	0.871	

Table 2. Results of Wilcoxon sign-rank test and repeated measure ANOVAs (as MANOVA) for the experiments testing fly responses to stationary and moving host corpses (Experiment 1: N = 24; Experiment 2: N = 14 yellow, 15 blue)

Source	d.f.	Statistic	P
Experiment 1		R	
Motion	1	−3.14	0.002
Experiment 2		F	
Motion	1	31.67	0.0002
Color	1	0.33	n.s.
Motion × color	1	0.24	n.s.

Response of flies to host movement and color

To test the importance of host movement in the host selection and acceptance process of *E. mella*, I performed two experiments. In the first experiment, trials were conducted in a clear plastic cylinder (27.3 cm × 22.5 cm diam.). The bottom of the arena consisted of an elevated white laminate board. Caterpillars used in this treatment were frozen, partially dried, and their ventral surface was glued to a small metal paper clip. For all treatments, the fly was released into the arena and allowed to acclimate for 2 min before the caterpillar was introduced. For 'stationary' treatments in which I recorded the response of flies to non-moving caterpillars, a prepared caterpillar was placed in the center of the arena. To examine the response of flies to moving caterpillars, a large magnet held under the laminate board was used to pull the caterpillar around a circular track 15 cm in diameter drawn lightly onto the board at the rate of approximately one revolution per 3 s. Each of the 24 flies was subjected to both treatments with a 10 min rest period between them. Trials lasting 90 s were initiated once the fly was observed to face in the general direction of the caterpillar. Time to first contact of the host was recorded using a stopwatch, at which time the treatment was terminated and the fly removed from the arena. For flies that never made contact with the caterpillar, latency was scored as the total length of the trial. Initial assays, not reported here, did not detect a significant effect of treatment order (repeated measures MANOVA as above: N = 10, F = 0.04, d.f. = 1, P = 0.8); however, for the main experiment 'stationary' treatments were always administered before movement treatments in order to avoid carryover effects of experience with moving caterpillars. The second experiment was identical to the first with the exception that the caterpillar corpses were freeze-dried and spray-painted either yellow or blue. This experiment was performed to corroborate results of the initial motion experiment as well as to examine whether the flies would respond to novel colored host corpses that they had not experienced. The colors yellow and blue were chosen because they are widely separated in wavelength along the visible color spectrum and because another oestroid fly (*Lucilia cuprina*: Calliphoridae) was demonstrated to detect and learn these colors readily (Fukushi, 1989).

Analysis. For the first experiment, the latency to contact moving and stationary host corpses was compared using a Wilcoxon sign-rank test. In the second, a repeated measures ANOVA (implemented as a MANOVA, using ranked data) was used to analyze the effect of treatment and color on latency to first contact.

Results

Responses of flies to concealed and exposed hosts. Flies spent significantly more time in contact with dishes containing exposed dead and live caterpillars than to concealed caterpillars and controls (Table 1, Figure 2a). However, this result depended strongly on whether the flies had previous experience with caterpillars (significant experience and experience × treatment interactions; Table 1). Naïve flies did not respond significantly to any treatment relative to the control (Table 1, Figure 2). In addition, there was no effect of any treatment on the time it took to contact the treatment source (latency), but experienced flies approached treatment sources significantly more rapidly than naïve flies (Table 1; Figure 2b). If live caterpillar treatments in which the caterpillar did not move are excluded from analysis, a significant effect of treatment on latency to contact the caterpillar emerges (MANOVA: Treatment: F = 4.01, d.f. = 3, 19, P = 0.023). In these trials, experienced flies approached live caterpillars more rapidly than control treatments (Figure 2a; Wilcoxon paired-rank: P = 0.039).

The number of oviposition attempts on exposed hosts was significantly greater for experienced than naïve flies on both dead and live caterpillar treatments (Kruskal–Wallis test: live: $\chi^2 = 7.96$, d.f. = 1, P = 0.005; dead: $\chi^2 = 6.61$, d.f. = 1, P = 0.01; Figure 3). Experienced flies oviposited more often on live than dead hosts (Wilcoxon paired-rank: P < 0.01) and inexperienced flies showed a trend in the same direc-

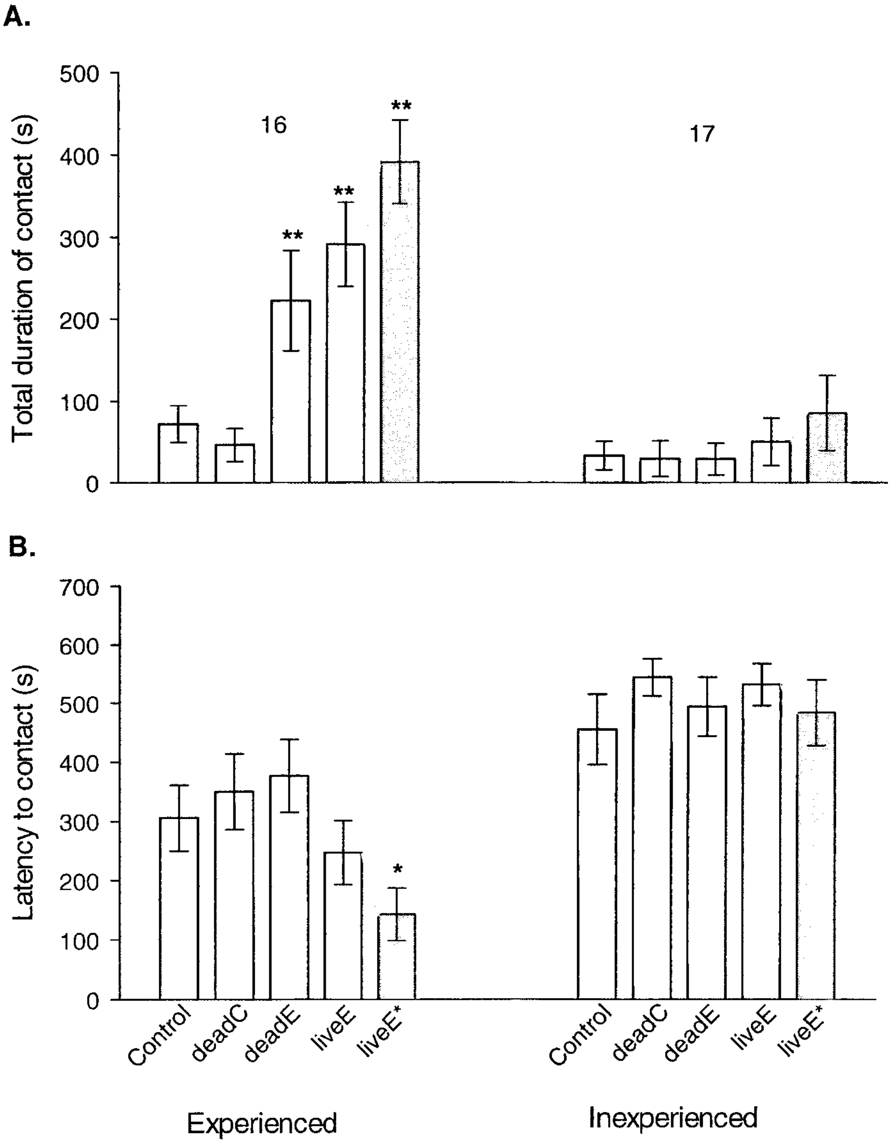

Figure 2. A. The means (±s.e.) of the total time spent in contact with four treatment sources: controls, dead concealed caterpillars (deadC), dead exposed caterpillars (deadE), and live exposed caterpillars (liveE) for experienced and inexperienced flies. B. The latency to contact each treatment for experienced and naïve flies. Numbers of naïve and experienced flies are indicated at the top of A. Gray columns and error bars indicate the mean (±s.e.) duration of contact (A) or latency to contact (B) caterpillars for only those trials in which the caterpillar moved. In each case a significant effect of experience exists. Significant differences of treatments from controls are indicated by asterisks (*P < 0.05, **P < 0.005). See text and Table 1 for statistics.

tion as well (P = 0.1; Figure 3). Both the amount of time spent in contact with the petri dish and the number of ovipositions attempted were significantly correlated with the length of time the caterpillar spent moving (Adj, $R^2 = 0.188$, F = 8.491, P = 0.007; Adj, $R^2 = 0.504$, F = 33.516, P < 0.0001, respectively; Figures 4a and 4b).

Response of flies to odors associated with caterpillars. The latency of walking behavior differed significantly among the three odor treatments ($\chi^2 = 6.11$, d.f.: 2, P = 0.047). Flies responded more quickly to the damaged plant treatment than to the control (Figure 5a; $\chi^2 = 5.40$, d.f. = 1, P = 0.020), however, latency to walking in response to control and live caterpillar treatments did not differ ($\chi^2 = 0.164$, d.f. = 1, P >

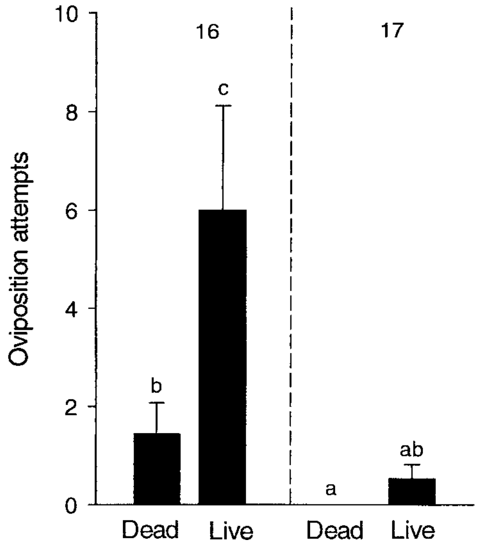

Figure 3. The mean number of oviposition attempts (±s.e.) on dead and live caterpillars for experienced (left), and inexperienced (right) flies. No inexperienced flies attempted to oviposit on dead caterpillars. Numbers above columns indicate the number of flies tested, and letters indicate significantly different means. See text for statistics.

0.5). The total duration of time spent walking also differed significantly among treatments ($\chi^2 = 7.20$, d.f. = 2, P = 0.027). Flies spent more total time walking in response to plant odors than to the control ($\chi^2 = 6.48$, d.f. = 1, P = 0.011; Figure 5b). Although flies appeared to also spend more time walking in response to caterpillar odors than controls, this difference was not significant ($\chi^2 = 3.01$, d.f. = 1, P = 0.083). This increase in walking behavior was associated with an almost 50% decrease in time spent grooming (X±s.e.: Plant: 79.3±23.4, Caterpillar: 99.8±35.5, Control: 180.2±33.5; F = 2.97, d.f. = 2, P = 0.076).

Response of flies to host movement. Flies approached moving host corpses significantly more rapidly than non-moving host corpses in the initial motion experiment (see Table 2 for statistics, Figure 6). The motion experiment using blue and yellow painted caterpillar corpses yielded the same pattern of more rapid responses to moving than to stationary caterpillar corpses (see Table 2 for statistics). No effect of caterpillar color was observed.

Discussion

Taken together, the results of these behavioral assays indicate that *E. mella* responds to at least two general cues associated with hosts: host movement and plant odor. However, *E. mella* females responded only weakly to odors associated directly with hosts and to visual contact with non-moving hosts. In the initial assays involving concealed and exposed hosts, I found no significant evidence that flies were *attracted* to any of the treatments (except moving caterpillars). The presence of an exposed host, dead or alive, served primarily to keep the fly at the treatment source, or to cause it to return once it had made contact. Responses to stationary caterpillars in the motion experiments were also weak. These results suggest that visual detection of a caterpillar is often insufficient to elicit a response from the flies, but that motion is a strong stimulus.

Odor cues. Little evidence was found of a response to odor cues derived directly from the host. The olfactometer experiment was limited by small sample sizes and the indication of increased walking behavior when exposed to caterpillar odors could represent a meaningful response. However, it is still relatively weak (e.g., no effect on latency), and may represent a response to food odors associated with the caterpillars' rearing chambers. In contrast, female flies responded strongly to odors associated with the damaged plant treatment. This plant is one of hundreds of plant species on which this host has been recorded to feed (Singer, 2000), and the cut sprigs had no contact with hosts. Therefore, it is likely that the flies were responding to relatively general 'green leaf volatiles' rather than specific volatile chemicals associated with this plant species or its interaction with hosts. The rapid onset of walking behavior in response to this odor suggests that it may act as an arrestant, inducing the fly to search an area more thoroughly for hosts.

The rapid response of flies to freeze-dried, painted, moving caterpillars, in which odor cues were likely masked or altered, also suggests that olfactory cues derived from the host are at least not necessary to elicit a response from the flies. This result is not surprising, given the wide host range of *E. mella* and the prediction that herbivores should be selected to minimize odors that may attract potential enemies (Vet et al., 1991). However, it is important to note that none of the flies attempted to deposit eggs on these models, suggesting that close range odor or contact cues are also important for host acceptance by *E. mella.*

The results of this study agree well with studies on the related tachinid *Exorista japonica*, which is also known to use a wide range of hosts. *Exorista japon-*

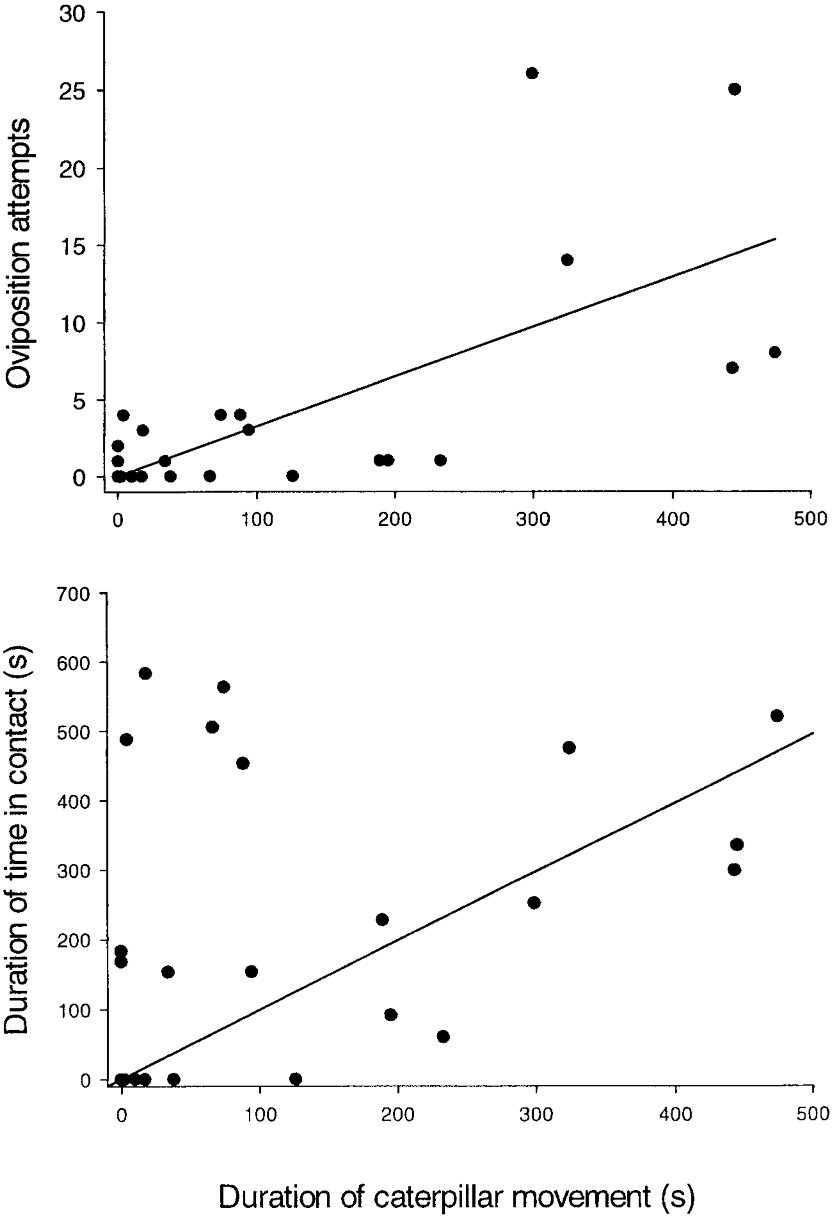

Figure 4. A. Dependence of the number of oviposition attempts on the duration of caterpillar movement measured in seconds (Adj. $R^2 = 0.506$). B. Relationship between duration of time spent in contact with the host and the total duration of caterpillar movement (Adj. $R^2 = 0.188$). See text for statistics.

ica has been shown to be attracted to odors of plants infested with hosts, but not to the hosts alone (Kainoh et al., 1999). It has also been shown to oviposit readily on host models consisting of black rubber tubes (Tanaka et al., 1999b), indicating that at least under laboratory conditions, few specific cues are necessary to elicit oviposition. The effects of egg load on responses to the treatments administered in the current study were not examined. However, most flies used in these experiments probably had high egg loads. High egg loads may lower thresholds for accepting hosts that may not exhibit chemical or visual characteristics representative of an optimal host (Godfray, 1994).

Reliance on visual cues. Exorista mella females responded strongly to moving caterpillars, especially

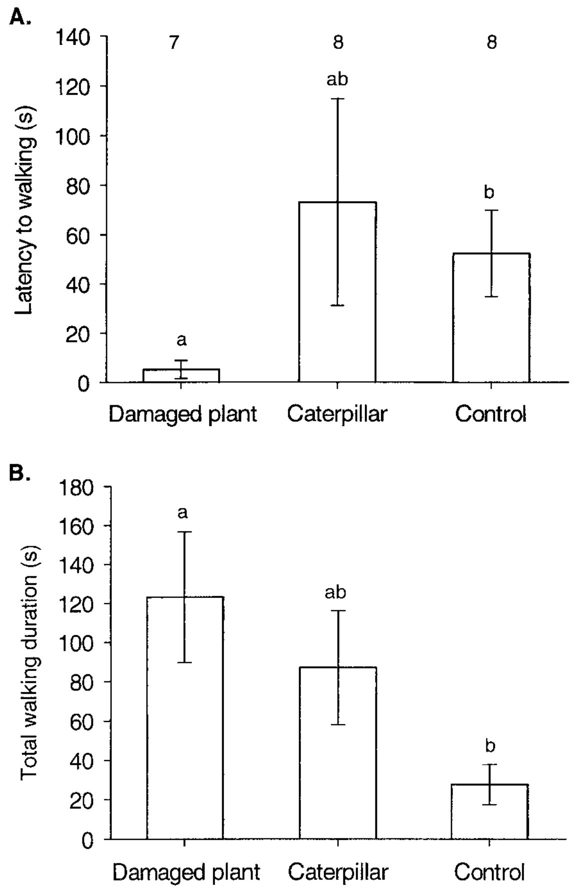

Figure 5. Latency (A) and total duration (B) of the time spent walking in an olfactometer in response to three different odor treatments (±s.e.). Control: lab air, Damaged Plant: cut sprig of *Ambrosia confertiflora*, Caterpillar: live *G. geneura* caterpillar. Letters above the columns indicate significant differences between treatments, numbers indicate the number of flies tested.

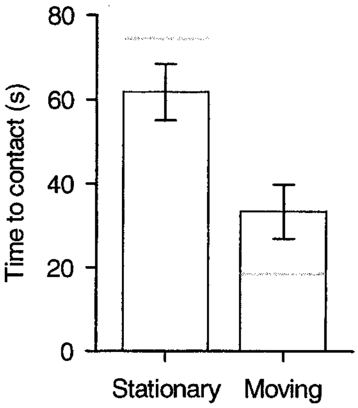

Figure 6. The mean (±s.e.) time to contact stationary and moving caterpillar corpses by female *E. mella* (N = 24). Gray bars indicate the median response times for each treatment within the 90 s trials. See Table 2 for statistics.

with respect to oviposition behavior. In contrast, eight out of 24 flies in the initial motion experiment and 22 of 28 flies in the painted caterpillar experiment did not respond at all to the stationary caterpillars within the trial period. In addition, the strong response to moving painted caterpillar corpses despite their unnatural odor and novel color suggests that the stimulus of host movement is of overriding importance. This is supported by observations that female *E. mella* will oviposit on a wide range of naturally occurring caterpillars in the laboratory that do not support development, providing they move (e.g., *Battus philenor*, *Manduca sexta*, *Danaus gillipus*; J.O. Stireman, unpubl.). The distribution of oviposition attempts on moving caterpillars suggests that there may be a threshold duration of movement before attack is initiated, which may allow partial filtering of non-host stimuli.

Several fly species have been shown to rely heavily on visual cues to locate food sources and oviposition sites. These include the apple maggot fly (*Rhagoletis pomonella*; Aluja & Prokopy, 1993) and blow flies (*Lucilia cuprina*; Fukushi, 1985, 1989). Other dipteran parasitoids have been shown to use visual cues in host location as well. Monteith (1956) demonstrated that a moving feather in an air stream with host-derived odors elicited attack behavior by the tachinid *Drino bohemica*, and Morehead & Feener (2000) showed that ant-parasitizing phorid flies were attracted to host models made of inert material. In addition, movement has been shown to increase the acceptance of encountered hosts for both dipteran and hymenopteran parasitoids (Arthur, 1981; Weseloh, 1980). The use of motion cues in detecting prey, such as described here, is well established in many predatory invertebrates (e.g., Jackson & Pollard, 1996; Gilbert, 1997; Olberg et al., 2000). Given the similarity of *E. mella* to a predator in its relatively catholic host range, it is not surprising that it employs this cue to locate and select hosts.

It is possible that *E. mella* also uses vibratory cues from the host, which may be confounded with the visual detection of motion. However, repeated observations of positive responses of females to moving hosts under conditions in which vibratory stimuli are likely to be minimal (e.g., heavy counter-tops, gravel floor of rearing cage), anecdotal observations of fly attraction to moving forceps and fingers, and the observation that flies tended to respond to moving hosts only when facing them suggests that visual detection of motion is important even in the absence of vibratory cues.

The effect of experience. Although this study was not designed to analyze the effects of experience on the behavior of *E. mella*, the significant effect of this factor on responses to hosts suggests that experience can greatly modify the response of *E. mella* to hosts. Flies classified as inexperienced in the first experiment did not respond to any treatment, whereas experienced flies approached moving caterpillars more quickly and spent more time in contact with exposed caterpillars. Experienced flies may respond more quickly to hosts due to enhanced egg maturation resulting from contact with hosts (Papaj, 2000) or through behavioral changes such as sensitization (or priming) after experience with hosts, as has been demonstrated for many Hymenoptera (Turlings et al., 1993). These two explanations are not mutually exclusive, but in an independent study of this system *E. mella* demonstrated the capacity to learn to associate visual cues with hosts (Stireman, 2001).

A host selection scenario for Exorista mella. The experiments conducted in this study provide only an introduction to the likely complex processes of host location and selection in the tachinid *E. mella.* Still, a general outline of some aspects of the host selection process may be formulated based on these results, field observations, and knowledge of the general biology of this parasitoid. Previous work (Stireman, 2001) has indicated that parasitism rates by *E. mella* vary according to large-scale habitat structure, thus flies may initially use visual or olfactory cues to locate an appropriate macrohabitat. Observations of females in the field suggest they 'cruise' through the habitat and occasionally land on low shrubs and herbs (pers. obs.). It is at this stage that general olfactory cues such as 'green leaf volatiles' derived from herbivore feeding might be used by the flies to restrict their searching area. The host used in this study, *G. geneura*, feeds on a wide diversity of plant species, as do several of the other caterpillars attacked by this parasitoid (e.g., *Lymantria dispar*, *Estigmene acrea*; Arnaud, 1978). Thus using herbivore and/or plant specific volatile chemicals to locate these hosts may not be an effective strategy for *E. mella.* Visual perception of host movement could also be utilized at this 'cruising' stage. At close range, perhaps after landing in the vicinity of an odor source, females likely establish the host's position by detecting host motion and perhaps visual shape cues (as in the related species *E. japonica*, Tanaka, 1999a,b). Experience with the host may then modify the ranking and specificity of host location stimuli, so that more specific visual search images and perhaps olfactory cues are subsequently used (Vet et al., 1990).

Like many hymenopteran parasitoids (West & Rivero, 2000), *E. mella* are probably more host limited than egg limited under most natural conditions. This is suggested by the unpredictable distribution of their usually solitary hosts (Stireman, 2001), their preference for rarer, more mobile late instar hosts (Adam, 1968), and their relatively low fecundities (Adam & Watson, 1971). The co-opting of a well-developed visual motion detection system for use in locating hosts by *E. mella* may allow these parasitoids to combine this relatively general, easily detectable cue, with more refined (innate and learned) visual and olfactory cues, in order to efficiently locate a wide range of potential hosts. If used in conjunction with cues of host shape, motion signals may be very effective close range indicators of the presence of suitable hosts, whereas reliance on color or olfactory signals associated with hosts may be more likely to result in potentially useful host species being overlooked. Although parasitic wasps may also use motion cues in host location, the relatively narrow host ranges of most species (Hawkins, 1994), their frequent use of concealed hosts, and their fine sensitivity to olfactory cues (Quicke, 1997) tend to discourage reliance on such nonspecific visual cues.

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References

Abacus Concepts Inc., 1993. Statview 4.0. Abacus Concepts, Berkeley, California.

Adam, D. S., 1968. Certain biological relationships between the parasite *Exorista mella* and its host *Estigmene acrea.* Master's Thesis. University of Arizona, Tucson, Arizona.

Adam, D. S. & T. F. Watson, 1971. Adult biology of *Exorista mella.* Annals of the Entomological Society of America 64: 146–149.

Alphen, J. J. M. van & L. E. M. Vet, 1986. An evolutionary approach to host finding and selection. In: J. Waage & D. Greathead (eds), Insect Parasitoids. Academic Press, New York, pp. 23–61.

Aluja, M. & R. J. Prokopy, 1993. Host odor and visual stimulus interaction during intratree host finding behavior of *Rhagoletis pomonella* (walsh) (Dipt., Tephritidae). Journal of Chemical Ecology 19: 2671–2696.

Arnaud, P. H. Jr., 1978. A Host Parasite Catalog of North American Tachinidae (Diptera). U.S. Dept. of Agriculture Miscellaneous Publication No. 1319, pp. 1–860.

Arthur, A. P., 1981. Host acceptance by parasitoids. In: D. A., Nordlund, R. L. Jones, & W. J. Lewis (eds), Semiochemicals, their Role Pest Control. J. Wiley, New York, pp. 79–95.

Belshaw, R., 1994. Life history characteristics of Tachinidae (Diptera) and their effect on polyphagy. In: B. A Hawkins & W. Sheehan (eds), Parasitoid Community Ecology. Oxford University Press, New York, pp. 145–162.

Bushbeck, E. K. & N. J. Strausfeld, 1997. The relevance of neural architecture to visual performance: Phylogenetic conservation and variation in dipteran visual systems. Journal of Comparative Neurology 383: 282–304.

Colazza, S., G. Salerno & E. Wajnberg, 1999. Volatile and contact chemicals released by *Nezara viridula* (Heteroptera : Pentatomidae) have a kairomonal effect on the egg parasitoid *Trissolcus basalis* (Hymenoptera : Scelionidae). Biological Control 16: 310–317.

Conlon, D. & W. J. Bell, 1991. The use of visual information by house flies, *Musca domestica* (Diptera: Muscidae), foraging in resource patches. Journal of Comparative Physiology 168: 365–372.

Dethier, V. G., 1963. The Physiology of Insect Senses. J. Wiley, New York.

Feener, D. H. jr. & B. V. Brown, 1997. Diptera as parasitoids. Annual Review of Entomology 42: 73–98.

Fukushi, T., 1985. Visual learning in walking blowflies, *Lucilia cuprina.* Journal of Comparative Physiology A 157: 771–778.

Fukushi, T., 1989. Learning and discrimination of coloured papers in the walking blowfly, *Lucilia cuprina.* Journal of Comparative Physiology A 166: 57–64.

Gilbert, C., 1997. Visual control of cursorial prey pursuit by tiger beetles (Cicindelidae). Journal of Comparative Physiology A181: 217–230.

Godfray, H. C. J., 1994. Parasitoids: Behavioral and Evolutionary Ecology. Princeton University Press, Princeton, New Jersey.

Hawkins, B. A., 1994. Patterns and Process in Host-Parasitoid Interactions. Cambridge University Press, Cambridge Mass.

Hendry, L. B., P. D. Greany & R. J. Gill, 1973. Kairomone mediated host-finding behavior in the parasitic wasp *Orgilis lepidus.* Entomologia Experimentalis et Applicata 16: 471–477.

Henneman, M. L. & D. R. Papaj, 1999. Role of host fruit color in the behavior of the walnut fly *Rhagoletis juglandis.* Entomologia Experimentalis et Applicata 93: 249–258.

Jackson, R. R. & S. D. Pollard, 1996. Predatory behavior of jumping spiders. Annual Review of Entomology 41: 287–308.

Jones, R. L., W. J. Lewis, M. C. Bowman, M. Beroza & B. A. Bierl, 1971. Host seeking stimulant for parasite of corn-earworm: Isolation, identification, and synthesis. Science 173: 842–843.

Kainoh, Y., C. Tanaka & S. Nakamura, 1999. Odor from herbivore-damaged plant attracts the parasitoid fly *Exorista japonica* Townsend (Diptera: Tachinidae). Applied Entomology and Zoology 34: 463–467.

Martin, W. R. Jr., D. A. Nordlund & W. C. Nettles, 1990. Response of the parasitoid *Eucelatoria bryani* to selected plant material in an olfactometer. Journal of Chemical Ecology 16: 499–508.

McGregor, R. & D. Henderson, 1998. The influence of oviposition experience on response to host pheromone in *Trichogramma sibericum* (Hymenoptera: Trichogrammatidae). Journal of Insect Behavior 11: 621–632.

Meiners, T., C. Westerhaus & M. Hilker, 2000. Specificity of chemical cues used by a specialist egg parasitoid during host location. Entomologia Experimentalis et Applicata 95: 151–159.

Monteith, L. G., 1955. Host preferences of *Drino bohemica* Mesn. (Diptera: Tachinidae) with particular reference to olfactory responses. Canadian Entomologist 87: 509–530.

Monteith, L. G., 1956. Influence of host movement on selection of hosts by *Drino bohemica* Mesn. (Diptera: Tachinidae) as determined in an olfactometer. Canadian Entomologist 88: 583–586.

Morehead, S. A., & D. H. Feener, Jr., 2000. Visual and chemical cues used in host location and acceptance by a dipteran parasitoid. Journal of insect behavior 13: 613–625.

Morgan, D. J. W. & J. D. Hare, 1998. Volatile cues used by the parasitoid, *Aphytis melinus*, for host location: California red scale revisited. Entomologia Experimentalis et Applicata 88: 235–245.

Nakamura, S., 1997. Clutch size regulation and host discrimination of the parasitoid fly, *Exorista japonica* (Diptera:Tachinidae). Applied Entomology and Zoology 32: 283–291.

Nettles, W. C. & M. L. Burks, 1975. A substance from *Heliothis virescens* larvae stimulating larviposition by females of the tachinid *Archytas marmoratus.* Journal of Insect Physiology 21: 965–978.

Noldus Information Technology, 1993. The Observer, Base Package for DOS. Version 3.0. Wageningen, The Netherlands.

Olberg, R. M., A. H. Worthington, & K. R. Venator, 2000. Prey pursuit and interception in dragonflies. Journal of Comparative Physiology A186: 155–162.

Oliai, S. E. & B. H. King, 2000. Associative learning in response to color in the parasitoid wasp *Nasonia vitripennis* (Hymenoptera: Pteromalidae). Journal of Insect Behavior 13: 55–69.

Papaj, D. R., 2000. Ovarian dynamics and host use. Annual Review of Entomology 45: 423–448.

Potting, R. P. J., G. M. Poppy, & T. H. Schuler, 1999. The role of volatiles from cruciferous plants and pre-flight experience in the foraging behaviour of the specialist parasitoid *Cotesia plutellae.* Entomologia Experimentalis et Applicata 93: 87–95.

Prokopy, R. J., 1968. Visual responses of apple maggot flies, *Rhagoletis pomonella*: Orchard studies. Entomologia Experimentalis et Applicata 11: 403–422.

Quicke, D. L. J., 1997. Parasitic Wasps. Chapman and Hall, London.

Roland, J., K. E. Denford & L. Jimenez, 1995. Borneol as an attractant for *Cyzenis albicans*, a tachinid parasitoid of the winter moth, *Operophtera brumata* L (Lepidoptera, Geometridae). Canadian Entomologist 127: 413–421.

Roth, J. P., E. G. King & A. C. Thompson, 1978. Host location behavior by the tachinid, *Lixophaga diatraeae.* Environmental Entomology 7: 794–798.

Roth, J. P., E. G. King & S. D. Hensley, 1982. Plant, host, and parasite interactions in the host selection sequence of the tachinid *Lixophaga diatraeae.* Environmental Entomology 11: 273–277.

Sabrosky, C. W. & P. H. Arnaud, Jr., 1965. Family Tachinidae. In: A. Stone, C. W. Sabrosky, W. W. Wirth, R. H. Foote & J. R. Coulson (eds), A Catalog of the Diptera of America North of

Mexico. U.S. Department of Agriculture, Agriculture Research Service, Agriculture Handbook 276, pp. 961–1108.

SAS Institute Inc., 1996. JMP IN. version 3.2.1. SAS Institute Inc., Cary, NC.

Scheffe, H., 1959. Analysis of Variance. Wiley, New York.

Singer, M. S., 2000. Ecological maintenance of food-mixing in the woolly bear caterpillar *Grammia geneura* (Strecker) (Lepidoptera: Arctiidae). PhD Thesis, University of Arizona, U.S.A.

Steidle, J.L.M., J. Lanka, C. Muller & J. Ruther, 2001. The use of general foraging kairomones in a generalist parasitoid. Oikos 95: 78–86.

Stireman, J. O., III, 2001. The Ecology and Evolution of Tachinid-host Associations. PhD Thesis, University of Arizona, U.S.A.

Sullivan, B. T., E. M. Pettersson, K. C. Seltmann & C. W. Berisford, 2000. Attraction of the bark beetle parasitoid *Roptrocerus xylophagorum* (Hymenoptera : Pteromalidae) to host-associated olfactory cues. Environmental Entomology 29: 1138–1151.

Tanaka, C., Y. Kainoh & H. Honda, 1999a. Physical factors in host selection of the parasitoid fly *Exorista japonica* Townsend (Diptera: Tachinidae). Applied Entomology and Zoology 34: 91–97.

Tanaka, C., Y. Kainoh & H. Honda, 1999b. Comparison of oviposition on host larvae and rubber tubes by *Exorista japonica* Townsend (Diptera: Tachinidae). Biological Control 14: 7–10.

Taylor, E. A., 1952. Parasitization of the salt-marsh caterpillar, *Estigmene acrea*, in the Salt River Valley, Arizona. M.S. Thesis. University of Arizona.

Thompson, A. C., J. P. Roth & E. G. King, 1983. Larviposition Kairomone of the tachinid *Lixophaga diatraeae.* Environmental Entomology 12: 1312–1314.

Turlings, T. C. J. & J. H. Tumlinson, 1992. Systemic release of chemical signals by herbivore-injured corn. Proceedings of the National Academy of Sciences USA 89: 8399–8402.

Turlings, T. C. J., J. H. Tumlinson & W. J. Lewis, 1990. Parasite wasps exploit herbivore induced plant distress signals to locate hosts. Science 250: 1251–1253.

Turlings, T. C. J., F. L. Wäckers, L. E. M. Vet, W. J. Lewis & J. H. Tumlinson, 1993. Learning of host-finding cues by hymenopterous parasitoids. In: D. R. Papaj & A. C. Lewis (eds), Insect Learning: Ecological and Evolutionary Perspectives. Chapman and Hall, New York, pp. 51–78.

Vet, L. E. M. & M. Dicke, 1992. Ecology of infochemical use by natural enemies in a tritrophic context. Annual Review of Entomology 37: 141–172.

Vet, L. E. M, W. J. Lewis, D. R. Papaj & J. C. van Lenteren, 1990. A variable response model for foraging behavior. Journal of Insect Behavior 3: 471–490.

Vet, L. E. M., F. L. Wäckers & M. Dicke, 1991. How to hunt for hiding hosts: the reliability-detectability problem for foraging parasitoids. Netherlands Journal of Zoology 41: 202–213.

Vinson, S. B. & H. J. Williams, 1991. Host selection behavior of *Campopletis sonorensis*: A model system. Biological Control 1: 107–117.

Vinson, S. B., 1984. How parasitoids locate their hosts: A case for insect espionage. In: T. Lewis (ed.), Insect Communication. Academic Press, London, pp. 325–348.

Vinson, S. B., 1998. The general host selection behavior of parasitoid Hymenoptera and a comparison of initial strategies utilized by larvaphagous and oophagous species. Biological Control 11: 79–96.

Wäckers, F. L. & W. J. Lewis, 1994. Olfactory and visual learning and their combined influence on host site location by the parasitoid *Microplitis croceipes* (Cresson). Biological Control 4: 105–112.

Weseloh, R. M., 1980. Host Recognition behavior of the Tachinid Parasitoid, *Compsilura concinnata.* Annals of the Entomological Society of America 73: 593–601.

Weseloh, R. M., 1981. Host location by parasitoids. In: D.A. Nordlund, R. L. Jones & W. J. Lewis (eds), Semiochemicals, their Role in Pest Control. J. Wiley, New York, pp. 97–120.

West, S. A. & A. Rivero, 2000. Using sex ratios to estimate what limits reproduction in parasitoids. Ecology Letters 3: 294–299.

Yamamoto, R. T., 1969. Mass rearing of the tobacco hornworm II. Larval rearing and pupation. Journal of Economic Entomology 62: 1427–1431.

Zar, J. H., 1996. Biostatistical Analysis, 3rd ed. Prentice Hall, Inc. New Jersey.