

## Larviposition, Host Cues, and Planidial Behavior in the Sound-Locating Parasitoid Fly *Homotrixia alleni* (Diptera: Tachinidae)

Geoff R. Allen,<sup>1,3</sup> Dan Kamien,<sup>2</sup> Oliver Berry,<sup>2</sup> Philip Byrne,<sup>2</sup> and John Hunt<sup>2</sup>

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*Some groups of tachinid flies deposit mobile first-instar larvae (or planidia) on or near their host. Flies within one such group, the tribe Ormiini, parasitize singing species of ensiferan Orthoptera and use sound for long distance host location. However, what induces tachinids to larviposit and whether planidia use any cues actively to locate their host remains poorly known. This paper examines the larviposition and planidial behavior of the ormiine Homotrixia alleni in relation to its bushcricket host, Sciarasaga quadrata. Sound alone was sufficient to elicit larviposition in gravid female H. alleni, where females arriving at an arena placed over a speaker broadcasting host song deposited an equal number of planidia in the presence or absence of a silent S. quadrata. Flies were observed to larviposit by forcibly expelling planidia up to 6 cm in a forward direction from the fly, with less than half of the trials with a host present resulting in physical contact between the host and the fly. In the host's absence, flies walked around the arena significantly more often, remained on the arena for the experimental duration (10 min), and changed orientation frequently. In the host's presence, flies generally maintained a position facing the host, stayed in the quadrant of first approach, and typically flew off the arena within 2 min of arrival. When the oncoming fly approached a forward facing host, more planidia were found in the arena's center (i.e., closer to the host) than in the no-host or rearward-facing host treatment. Planidia experimentally placed on a circular arena averaged 1 cm of movement in 15 min but none of the following cues—host song, host song with song-vibration transmission, a silent host, and a silent host*

<sup>1</sup>School of Agricultural Science, University of Tasmania, GPO Box 252-54, Hobart, TAS 7001, Australia. Fax: (03) 6226 2642. e-mail: Geoff.Allen@utas.edu.au.

<sup>2</sup>Department of Zoology, University of Western Australia, Nedlands, WA 6907, Australia.

<sup>3</sup>To whom correspondence should be addressed.

with host movement-vibration transmission—significantly affected the direction or distance planidia traveled. At  $20 \pm 1^\circ\text{C}$ , over half of the planidia died within 1 h and all died within 2 h of deposition. The significance of these results in relation to reproductive strategies and parasitism is discussed.

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**KEY WORDS:** Tettigoniidae; Ormiini; *Sciarasaga quadrata*; parasitoid; host location; oviposition strategies.

### INTRODUCTION

The Tachinidae form the second largest family of Diptera, with over 8000 species described worldwide (Cantrell and Crosskey, 1989). Though all are parasitoids, their reproductive strategies are diverse and far less understood than those of the parasitic Hymenoptera which usually lay eggs directly on or in the host (Feener and Brown, 1997). A lack of a rigid ovipositor has necessitated the development of other methods by tachinids to gain entry to hosts (Askew, 1971; Wood, 1987). These include laying unincubated or incubated eggs directly on or occasionally in the host, laying eggs on the host-food plant which are then ingested by the host, and producing active first-instar larvae or planidia, which once upon the host bore their way into it through the integument (Belshaw, 1993). The development of an active planidial stage has enabled exploitation and radiation of tachinid host ranges to include previously inaccessible concealed hosts, with some 400 of the 1300 described species of tachinid in North America adopting planidial instars as a reproductive strategy (Price, 1975).

Several tachinids have been demonstrated to use host-associated plant damage, host frass, or host silk as cues in host location (see Belshaw, 1993; Godfray, 1994). Although parasitism success should be enhanced if planidia are laid on or as near to the host as possible, this is not always evident. The tachinid *Dexia rustica* F., a parasitoid of ground dwelling cockchafers, is no more likely to lay its progeny on soil above a host than elsewhere (Walker, 1943). Once laid, the planidia of some species wait passively in an upright stance for a host to pass, while others actively search for a host. Although the planidia of *D. rustica* do often wait on the soil surface, they show a greater inclination to burrow when they are over a host, whereas the planidia of *Eupeleteria magnicornis* Zett. anchor themselves to a substrate and show little discrimination between suitable and unsuitable passing hosts (Askew, 1971). Almost nothing is known about specific cues that may be used by planidia to detect the presence of a suitable host (Feener and Brown, 1997). Furthermore, in many species, planidia display special sclerotized plates that are believed to enhance their ability to remain viable in the environment until a suitable host is encountered (Wood, 1987; Belshaw, 1994). Although it is likely that the life expectancy of planidia has evolved to

meet the average time course to host contact, it may reflect a trade-off with readiness for growth once the host is found (Charnov, 1993).

One unique group of tachinids belongs to the tribe Ormiini, the adults of which use sound to locate their hosts (Cade, 1975). Recorded hosts of ormiines are all within the ensiferan Orthoptera and include field crickets, mole crickets and bushcrickets. One ormiine, *Ormia ochracea* (Bigot), whose hosts include shelter and burrow calling field crickets apparently larviposits using two modes. The first is upon the host while in physical contact with it and the second, which produces a larger number of planidia, is around the cricket (Cade, 1975; Adamo *et al.*, 1995). After landing upon speakers broadcasting host song in the field, the majority of *O. ochracea* remain motionless upon the speaker, whereas *Ormia depleta* (Wiedemann), which attacks burrow calling mole crickets, move rapidly around the speaker and depart within 3 s (Fowler, 1987; Walker, 1993; Fowler and Martini, 1993). For ormiines attacking burrow and shelter calling crickets, larviposition in the vicinity of the host is hypothesized to enable flies to parasitize other crickets, including conspecific females that may visit the burrow. Indeed, female crickets, which do not call, are sometimes parasitized at rates similar to those for males in the field by *O. ochracea* (Walker and Wineriter, 1991).

Males of the Austrosagine bushcricket *Sciarasaga quadrata* Rentz are heavily parasitized by the ormiine *Homotrixa alleni* Barraclough, but unlike the field cricket hosts of *O. ochracea*, females are never parasitized (Allen, 1995a). Male *S. quadrata* call from within dense bushes, frequently moving within nights, even while singing, thereby necessitating a potentially different oviposition strategy by the fly (Allen, 1995b). In the field male *S. quadrata* are typically parasitized by more than one *H. alleni* larva, averaging around two but increasing to four by the end of the 3- to 4-month calling season (Allen, 1995a). This paper documents the larviposition behavior of *H. alleni* and tests several short-distance cues that may be used in larviposition to ensure planidia are deposited close to a suitable host. In addition, it tests whether planidia are involved in actively locating hosts through the use of sound, host, or vibrational-transmission cues. Finally, it examines the viability of planidia in an exposed environment, better to estimate risk of actual and incidental parasitism in the field.

## MATERIALS AND METHODS

All gravid female *H. alleni* were collected at Cape Naturaliste (33°33', 115°01') in southwestern Australia. Flies were trapped in gauze-covered funnel cages that each held a piezoelectric speaker (Arrow PCT 100) broadcasting the synthesized call of *S. quadrata*. Calls were generated by artificial chirper units developed from the prototype of Campbell and Forest (1987). Upon return to the laboratory, each fly was placed in a tubular cage (15.5 × 6.5-cm radius) and then held in a constant-temperature cabinet set at 15 ± 1°C, 14 : 10L : D, uncon-

trolled humidity, and a scotophase onset at 0830 h local time. Flies were kept under laboratory conditions for at least 8 days prior to use in experiments and provided with honey and water ad libitum.

### Larviposition Behavior of Flies

A 1-m wooden dowel rod (1-cm diameter) upon which flies approached the experimental arena was horizontally positioned so that one end adjoined the edge of an upward-facing 5-cm-radius speaker (piezoelectric model; Arrow PCT 100). White paper (90 gsm) was placed on the face of the speaker cone to create a 5-cm-radius circular arena. The arena had four concentric circles, increasing in radius by 1 cm, drawn upon it and was subdivided into four equal quadrants, 3 being closest to the edge of the dowel and quadrant 1 farthest from the dowel. To attract the fly to the arena, the calling song of *S. quadrata* was broadcast through the speaker at an intensity of 82 dB at 50 cm using a Nagra IV-SJ reel-to-reel tape recorder. All earlier attempts at using a live male to provide the call rather than a recorded song were unsuccessful. The model song was taken from a recording of a male *S. quadrata* made at 20°C using a  $\frac{1}{4}$ -in. Brüel & Kjær microphone recorded at 19.5 cm/s.

The larviposition behavior of flies was observed under three experimental treatments: (1) host call with no host present, (2) host call and host present with the host facing the oncoming fly, and (3) host call and host present with the host facing away from the oncoming fly. Orientation of the host was considered important to interpreting the near field approach of the fly. Flies are hypothesized finally to approach calling males by walking rather than flying because *S. quadrata* typically position themselves within the center of dense bushes within which flight would be improbable (Allen, 1995a). A fly walking to a host located on the same branch as itself would therefore approach the host from either its rear or its front. The design did, however, exclude flies from passing underneath the host and from larvipositing on the host from a nearby branch, both of which may occur in the field. Host orientation was achieved by attaching a 3-mm-diameter wooden rod to the thorax of a live male *S. quadrata* and then orienting the rod so that the male was positioned in the desired orientation in the center of the arena with its tarsi touching the arena's surface.

All experiments were recorded with a videocamera for later analyses. Experiments were undertaken during the first 6 h of scotophase in an anechoic room maintained at  $20 \pm 1^\circ\text{C}$  under dim indirect white light ( $9 \mu\text{mol quanta/m}^2/\text{s}$ ). Seven flies were used in the experiments and each was assigned randomly the order of treatments it received. Flies were transferred to the anechoic room shortly before the commencement of scotophase and allowed one hour to adjust before use. At the beginning of each trial, a fly was placed on the dowel rod at a distance of 30 cm from the speaker and the playback of the recording com-

menced. Flies walked along the dowel rod toward the speaker until they made contact with the arena. Timing of the trial commenced when flies first made contact with the arena and ceased after 10 min or earlier in instances where flies left the arena. At the end of each trial, the number of planidia deposited on the arena was counted and the quadrant location and inner circle position (zone) of each planidia were noted. Playback of video recordings enabled quantification of the fly's behavior, including elapsed time on the arena, sequence and number of quadrants crossed by the fly, fly orientation, and time spent in each quadrant.

Repeated-measures ANOVAs were used to compare the following fly behaviors among the three treatments: the time spent on the arena, the number of quadrants crossed, the orientation of the fly, and the total number of planidia deposited. To test if the position of planidia deposited in each treatment was related to the time flies spent in these locations, a chi-square goodness of fit was used, where the expected number of planidia was calculated for each fly from the proportion of time spent in each location and then summed across all seven flies.

#### Host Location Behavior of Planidia

All planidia used in experiments were dissected in physiological saline from the abdomen of 12 gravid female flies collected in the field as before. The planidia of *H. alleni* average 0.8 mm in length (see Cantrell, 1988, Fig. 230). A total of 50 mature planidia (dark, sclerotized, and active) located at the posterior end of the uterus was removed from each fly using a fine paintbrush (the mean  $\pm$  SE of mature planidia per fly was  $183 \pm 26$ ;  $n = 8$ ). Planidia from each fly were allocated, in groups of 10, to five separate treatments. For each treatment, 10 planidia were placed in the center of a 9-cm-radius white paper arena divided into four equal quadrants and marked with concentric circles 1, 2, 4, 6 and 8 cm in radius. The five treatments were set up to determine if planidia increased or directed their movement to the following stimuli.

- (1) *Control*: Arena only, with no stimuli.
- (2) *Host song*: Stimulus provided by the call of a *S. quadrata* recorded on a Sony Professional Walkman (Model WM-D6C) at  $20 \pm 1^\circ\text{C}$ . The call was played back through a 7.6-cm speaker (30 W; 0.7- to 20.0-kHz frequency response) at an intensity of 60 dB at 50 cm. The speaker cone was positioned 1 cm from the edge of the arena. The selected intensity approximated that of a live calling male and the frequency response of the speaker entirely overlaps the call frequency of *S. quadrata*, which has a peak at 5–6 kHz and an upper range of 10 kHz (G. R. Allen, unpublished data).
- (3) *Host strong with song-vibration transmission*: The song of *S. quadrata*

was played back as above except the vibrating speaker cone contacted the arena. Song transmission across the area of the arena was confirmed before each trial using a phonostylus connected to an electrical circuit that monitored vibration.

- (4) *Silent host*: A live *S. quadrata* was tethered by attaching a 4-cm piece of string to its thorax, which was then attached to a platform positioned 1 cm from the edge of the arena. The host was unable to touch the arena, thereby allowing potential kairomones but not host-vibration cues to reach the planidia.
- (5) *Silent host with movement-vibration transmission*: A live *S. quadrata* was set up as before but this time the platform and arena were in contact and up to three legs of the host were able to be in contact with the arena at any one time.

All trials were done under dark (lights-off) conditions for 15 min in an anechoic room held at  $20 \pm 1^\circ\text{C}$  and uncontrolled humidity. The orientation of the stimulus was shifted  $180^\circ$  between trials to randomize any bias in the room. After 15 min the quadrant and zone (or circle boundary) reached by each planidium were recorded. Planidia remaining within the 1-cm circle were defined as not having moved, those found between the 1- and the 2-cm circles as having moved 2 cm, those between the 2- and the 4-cm circles as having moved 4 cm, and so on. A comparison of the behavior of fly-deposited versus extracted planidia was also made in the control treatment, where two trials of fly-deposited planidia, each of 10 planidia per fly, were conducted.

The direction of planidial movement was pooled across flies, subsequent to testing between flies, and analyzed for each treatment using chi-square goodness of fit against the probability of an equal (i.e., random) distribution among the four quadrants. The distance planidia moved was tested between quadrants within treatments and between treatments using repeated-measures ANOVA.

### Survival of Planidia Following Larviposition

Planidia from 11 flies (10 planidia per fly) were used to examine the survival of planidia over time. Planidia were either deposited by live flies ( $n = 4$ ) or extracted from dissected flies ( $n = 7$ ) as before. Each of the groups of 10 planidia were placed in a 7-cm-diameter plastic petri dish and then covered with a lid perforated with holes. All dishes were placed in a controlled-temperature room with lights off held at  $20 \pm 1^\circ\text{C}$  with a relative humidity varying between 56 and 80%. The relative humidity at night in Cape Naturaliste is around 60–70% (Bureau of Meteorology, unpublished data). Planidia were examined under a dissecting microscope every 30 min, until all were dead. Death of planidia was indicated by a lack of movement and a shriveled appearance.

## RESULTS

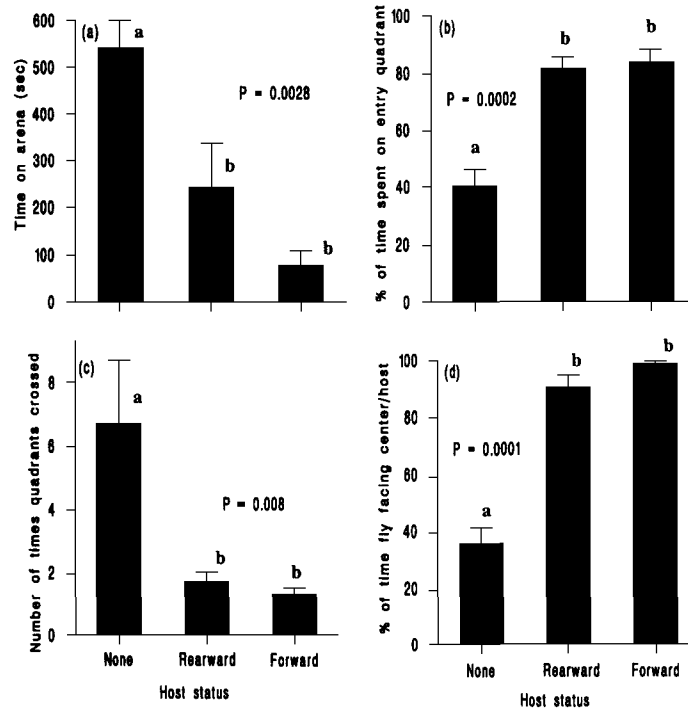
### Larviposition Behavior of Flies

All but one fly, which always flew, approached the arena by walking. However, once on the arena, there were significant differences between treatments in the duration of time that flies stayed (Fig. 1a). When the host was absent, flies generally remained on the arena for the experimental duration (10 min), but when the host was present, they typically flew off within 2 min. Host orientation had no significant effect on the time flies stayed upon the arena.

Flies behaved very differently depending on the presence or absence of a host. In the absence of a host, they spent a significantly shorter percentage of their time within the first-entered quadrant of the arena (Fig. 1b), leaving this quadrant after a mean  $\pm$  SE time of  $158 \pm 46$  s (range, 34–384 s). Moreover, in the absence of a host, flies typically walked around the arena, thereby crossing a significantly greater number of quadrants than in the presence of a host (Fig. 1c). The presence of a host resulted in flies most frequently spending their entire time within the first entered quadrant. A behavior Walker (1993) described as a “headstand” (defined here as when flies raised their abdomens and lowered their head so their body was held at an angle greater than  $45^\circ$ ) occurred significantly more often in the absence of a host, averaging  $1.7 \pm 0.4$  times per fly, and not at all in the forward host treatment (repeated-measures ANOVA:  $F = 8.0$ ,  $df = 2, 12$ ,  $P = 0.006$ ).

Irrespective of host orientation and despite moving backward and sideward on the arena, fly orientation remained facing the host over 90% of the time, whereas in the absence of a host, flies faced the center of the arena only 36% of the time (Fig. 1d). Flies approached the host quite closely, spending  $40 \pm 12$  and  $22 \pm 11\%$  of their time within 1 cm of the host when the host was rearward and forward, respectively (paired  $t$  test,  $t = 1.17$ ,  $df = 6$ , NS). However, contact of the host by the fly was uncommon, occurring only once within four of the seven rearward and two of the seven forward trials. Except in one rearward trial where the fly walked onto the host’s abdomen, all other contacts were brief and with the legs of the host. Movement by the host was infrequent throughout all trials with the exception of the antenna during the forward trials.

Flies deposited an average of  $4.3 \pm 0.7$  planidia (range, 0–10) per trial across the three treatments. Despite significance differences in fly behavior in the absence of a host, the number of planidia deposited by flies was not significantly different across the three treatments (Table I). The majority of planidia were deposited in the quadrant first entered by the fly and, except for the forward treatment, were within the outer zone of the arena (Table I). By mapping fly position relative to planidia location, it was evident that all planidia were deposited within 3 min of the fly reaching the arena and that, in 10 of the 21 trials, some planidia were found up to 6 cm distant from the fly’s closest location. When fly behavior was replayed in slow motion, flies were seen to be ejecting



**Fig. 1.** The comparative larviposition behavior of gravid female *H. alleni* in the absence of a host and in the presence of a tethered live rearward- or a forward-facing silent *S. quadrata* upon an arena positioned over a speaker broadcasting the taped song of *S. quadrata*. Behaviors include (a) the time spent on the arena, (b) the percentage of the total time that the fly spent on the first quadrant it entered, (c) the number of times quadrants were crossed by the fly, and (d) the percentage of the total time that the fly maintained a position facing the host or center of the arena where no host was present. The significances are the outcome of repeated-measures ANOVAs, all  $df = 2, 12$ : (a)  $F = 9.95$ , (b)  $F = 19.00$ , (c)  $F = 7.42$ , and (d)  $F = 57.93$ . Different letters among bars indicate significant differences between treatments.

larvae to distances up to 6 cm forward from themselves: hence their maintenance of a position facing the host when upon the arena. Flies deposited planidia in a pattern that reflected their time in those positions except when the host was forward facing (Table I). In the forward treatment, flies deposited more planidia closer to and on either side of the host.

#### Host Location Behavior of Planidia

Planidia distributed themselves at random around the arena irrespective of any of the stimuli presented (Table II). The majority of planidia adopted an



**Table I.** Mean  $\pm$  SE Number of Planidia Deposited per Fly and Percentage of All Planidia Deposited Located in Each Quadrant and in the Inner Zone (<3-cm Radius) of the Arena

Treatment	Number deposited <sup>a</sup>	<i>n</i>	Quadrant (%)				Significance <sup>b</sup>	Inner zone (%)	Significance <sup>b</sup>
			1	2	3	4			
No host	3.6 $\pm$ 1.1	25	8.0	16.0	76.0	0.0	3.03 (NS)	24.0	1.76 (NS)
Rearward host	5.3 $\pm$ 1.1	37	12.5	6.2	68.8	12.5	5.48 (NS)	32.3	0.01 (NS)
Forward host	4.0 $\pm$ 1.1	28	10.7	10.7	53.6	25.0	319.56 <sup>*</sup>	89.3	68.16 <sup>*</sup>

<sup>a</sup>Repeated-measures ANOVA between treatments ( $F = 0.70$ ,  $df = 2,12$ , NS).

<sup>b</sup>The significance of planidium position in each treatment is tested using a chi-square goodness of fit, where the expected number of planidia was calculated for each fly from the proportion of time spent in each position and then summed across all seven flies.

<sup>\*</sup> $P < 0.0001$ .

upright or “intercept” position, with typically less than 40% of planidia moving, that is, at least crossing the 1-cm radius zone, within the experimental duration. There was no significant difference between any of the treatments in the proportion of planidia to move (see Table II) but there were significant differences among planidia taken from different flies ( $F = 6.62$ ,  $df = 11,48$ ,  $P = 0.0001$ ).

Aside from their overall distribution, the mean movement of planidia within each quadrant did not significantly differ between the quadrants in response to any of the stimuli offered (repeated measures, all  $df = 3,33$ , NS; control,  $F =$

**Table II.** The Percentage of Planidia Found in Each Quadrant to Move (i.e., Cross the 1-cm Radius Zone) and the Mean Distance Traveled Over 15 min in Response to Various Stimuli When Centrally Positioned on a 9-cm-Radius Arena

Treatment	Quadrant (%)				Significance <sup>b</sup>	% planidia to move <sup>c</sup>	Mean cm traveled <sup>d</sup>
	1 <sup>a</sup>	2	3	4			
Control	27.9	28.7	20.5	22.9	2.11 (NS)	36.9	1.03 $\pm$ 0.22
Host song	26.7	32.5	21.6	19.2	5.00 (NS)	30.8	0.85 $\pm$ 0.16
Host song + song vibration	25.6	29.1	23.9	21.4	1.46 (NS)	41.0	1.18 $\pm$ 0.18
Silent host	28.1	28.9	19.0	24.0	3.00 (NS)	32.2	0.87 $\pm$ 0.14
Silent host + host vibration	23.9	23.1	24.8	28.2	0.71 (NS)	42.7	1.32 $\pm$ 0.23

<sup>a</sup>Quadrant where stimuli were positioned.

<sup>b</sup>Significance tested using a chi-square goodness of fit against an expected equal number of planidia per quadrant.

<sup>c</sup>Repeated-measures ANOVA between treatments on the number of planidia that moved ( $F = 1.32$ ,  $df = 4,44$ , NS).

<sup>d</sup>Repeated-measures ANOVA between treatments on the mean distance traveled ( $F = 1.79$ ,  $df = 4,44$ , NS).

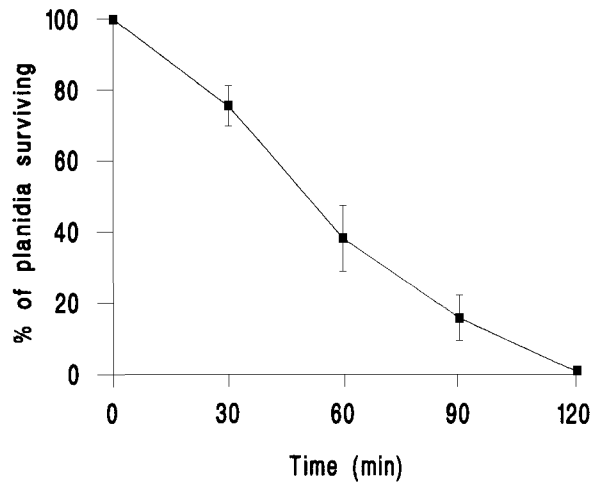


Fig. 2. The percentage survival of 11 different batches of 10 planidia of *H. alleni* at  $20 \pm 1^\circ\text{C}$  monitored every 30 min for 2 h.

0.89; host songs,  $F = 1.48$ ; host song plus vibration,  $F = 0.42$ ; silent host,  $F = 1.74$ ; silent host plus vibration,  $F = 0.22$ ). There was no significant difference between any of the stimuli in the mean overall movement of planidia (see Table II) but there were significant differences between the planidia taken from different flies ( $F = 3.83$ ,  $df = 11,48$ ,  $P = 0.0005$ ). The mean movement of planidia across all treatments was  $1.05 \pm 0.06$  cm (range, 0–8 cm). In a postexperimental trial, no significant differences were found between the amount of movement of extracted planidia ( $n = 12$  batches) and that of fly-deposited planidia ( $n = 2$  batches) ( $t = 1.66$ ,  $df = 12$ , NS).

#### Survival of Planidia Following Larviposition

The survival of exposed planidia significantly declined with time ( $F = 63.74$ ,  $df = 4,40$ ,  $P = 0.0001$ ), with less than 1% of planidia surviving 2 h of exposure (Fig. 2). The origin of the planidia (extracted vs deposited) had no significant effect on survival ( $F = 0.00$ ,  $df = 1,9$ , NS), nor were there any significant differences between the batches in their level of survival ( $F = 0.35$ ,  $df = 10,44$ , NS). On average, less than half the planidia survived for at least 1 h.

### DISCUSSION

*H. alleni* deposits on average the same number of planidia regardless of a host's presence or absence. This average of around four planidia per fly compares

favorably to the two to four found within parasitized males collected in the field (Allen, 1995a) and suggests that deposited planidia are very successful at gaining entry into hosts. Planidia were deposited by flies soon after arrival at the arena, with flies in the absence of a host continuing to walk around the arena, although not depositing planidia. The earlier departure by the fly from the arena when a host is present suggests some interaction between auditory and visual cues. Although auditory cues alone are clearly sufficient to elicit larviposition, visual cues enable larviposition to be directed at the host, significantly affecting fly behavior.

Host movement, which has been shown to be important to ovipositional response in at least one other species of tachinid (Monteith, 1956), was not obvious within our experiment. Only in the forward position, where antennal movement was evident to the oncoming fly, may host movement have had a role in larviposition behavior. Flies in this position deposited more planidia closer to the host. It was unfortunate that no tests could be performed using a live calling host because wing stridulation, which produces the calling song, would be very clear, especially in the rearward position, to the oncoming fly. Unlike the dual mode of larviposition on and then around the host seen in *O. ochracea* (Adamo *et al.*, 1995), *H. alleni* projects planidia for distances of up to 6 cm forward of itself, thereby overcoming any need to contact the host during larviposition. Similarly, some sarcophagid flies of the genus *Blaesoxipha*, which principally parasitize Coleoptera and Orthoptera, have also been reported to attack hosts by the forceful expulsion of larvae from their abdomen (see Allen and Pape, 1996).

If larviposition is stimulated by sound levels above a certain threshold, then the initial location of planidia should be in close vicinity to a suitable host. However, planidia showed no evidence of using sound, host, or vibrational-transmission cues to orient or move toward the nearby host, thereby improving their chance of gaining entry into a host. Similarly, Fowler and Martini (1993) found that the planidia of *O. depleta* failed to use sound or light source cues in orientation. *S. quadrata* does move frequently in the field at night (Allen 1995b) so that passively waiting for the host to pass may be a simple yet effective parasitism strategy. As a counter to this strategy, *S. quadrata* often drops from the bush to the ground when disturbed by a collector (Rentz, 1993), and if it does so if disturbed by a fly, it may reduce the chance of being parasitized. The larviposition strategy used by *O. ochracea* and *O. depleta*, which includes depositing planidia around the shelters and burrows of their calling hosts, is presumed to result in the nontarget parasitism of noncalling females and satellite males (Walker and Wineriter, 1991; Fowler and Martini, 1993). In contrast, the larviposition strategy of *H. alleni* does not result in parasitism of the noncalling female *S. quadrata* even though it is capable of developing in females in the laboratory (Allen, 1995a; Barraclough and Allen, 1996). This may be a result of far lower encounter rates between the sexes of *S. quadrata*. During field collections of over 500 calling male *S. quadrata* across four calling seasons, only 1.7% of males have been found with a female in the same bush at

the time of collection (Allen, 1998). However, the narrow window of survival time of planidia in the environment, demonstrated in our experiments, would also significantly lower any chance of incidental parasitism outside of the immediately intended target host.

The level of precision of larviposition needed by tachinids to parasitize hosts successfully would also be governed by their fecundity and the likelihood of planidia, once deposited, successfully entering and developing within their target host. The fecundity of the field-collected *H. alleni* used in our experiments averaged 183 mature planidia per fly, suggesting that the flies have a fairly high potential fecundity and an ability to cope with a reasonable level of planidial loss to ensure parasitism (Allen and Hunt). Parasitism success once a host is entered is also high, with Hunt and Allen (1998) finding that once two or more planidia of *H. alleni* are inserted into male *S. quadrata* in the laboratory, only 9% of males escape parasitism. Thus, the processes associated with larviposition rather than of parasitism following host entry are most likely to be where the greatest mortality of progeny occurs. In this respect our experiments demonstrate that nearly all the decision making that may improve the chance of successful entry into the host is made by the mother, with planidia playing little, if any role, in actively searching for a host. For ormiines the major cue for larviposition, which alone is sufficient to elicit larviposition, is sound, with visual cues apparently playing a secondary role. Studies, especially of behavioral interactions between live calling hosts and flies, would help elucidate further the role of secondary cues in determining both the level of precision and the level of discrimination involved in larvipositing tachinid flies.

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