Vibration-mediated interactions in a host–parasitoid system

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SUMMARY

The aim of this study was to obtain behavioural evidence of vibration-mediated interactions between the apple tentiform leafminer, *Phyllonorycter malella* (Ger.) (Lepidoptera, Gracillariidae), and its parasitoid *Sympiesis sericeicornis* Nees (Hymenoptera, Eulophidae). The experimental setup allowed the simultaneous recording on video film of both the parasitoid's and the host's behaviour, thus enabling us to contrast their respective responses to the leaf vibrations produced by the other party. We analysed the one-step transition probabilities from one behavioural state to the next. Active larval movements had a marked influence on the parasitoid's behaviour, but *feeding* and *still* had no detectable effect. We found no evidence for vibrotaxis on the part of the parasitoid. Although parasitoid *searching* behaviour on the leaf surface did not seem to alter the leafminer's behaviour, *ovipositor insertions* triggered a characteristic avoidance response. The described interactions are discussed in the context of the 'princess and monster' model developed in search and game theory.

1. INTRODUCTION

Short-range host location is the last, and most tractable, step in the host-finding behaviour of parasitoids and, as such, has been the subject of much current research (Vinson 1984). Although many host location mechanisms have been studied, by far the most attention has been focused on the role of chemosensory orientation. The reason for this is mainly economical, because of the potential use of semiochemicals as biocontrol agents.

Vibrations transmitted through the substrate are known to be used by parasitoids attacking endophytic hosts concealed in plant material and decaying substrates (van den Assem & Kuenen 1958; Quednau 1967; Lawrence 1981; van Alphen & Janssen 1982; Vet & van Alphen 1985; Sokolowski & Turlings 1986; Sugimoto *et al*. 1988; Mills *et al*. 1991; Cheah & Coaker 1992). The significance of vibrations for both the parasitoid and the host has been suggested several times (see, in particular, Schmidt 1991; Gross 1993). Nevertheless, quantitative descriptions of vibratory signals and associated mechanisms of orientation by parasitoids and hosts are still lacking (see Casas 1994 for a review). The aim of this study was to obtain behavioural evidence of vibratory interactions taking place in a leafminer–parasitoid system.

The foraging behaviour of *Sympiesis sericeicornis* Nees (Hymenoptera, Eulophidae), parasitoid of the apple leafminer *Phyllonorycter malella* (Ger.) (Lepidoptera, Gracillariidae), has been studied in detail by Casas (1989). Several of his results indicated that foraging females use vibratory cues for locating and attacking hosts. As leafminers are confined within the boundaries of their mine, once the parasitoid lands on the leaf, their only chance of avoiding parasitism is to escape ovipositor insertions until the parasitoid gives up and leaves the mine (Casas & Mangel 1997). Successful evasive behaviour may account for a proportion of the 15% of healthy hosts that were abandoned by *Sympiesis* in the field (Casas 1989). The leafmining moth, *Cameria hamadryadella* (Lepidoptera, Gracillariidae), survives 80% of the attacks by the parasitoid *Closterocerus tricinctus* (Hymenoptera, Eulophidae), and Connor & Cargain (1994) have suggested that this is due to the evasive behaviour of the leafminer.

In order to study these interactions in detail without interference, we first analysed the vibrations produced by each opponent alone. Vibrations produced by host larvae contain highly reliable and detectable information on both the host instar and the host's activities (Meyhöfer *et al*. 1994*a*, *b*). The parasitoid's insertion of the ovipositor into the mine also produces vibrations that are highly characteristic, and which can be used for evasive manoeuvres by the host (Bacher *et al*. 1994). Manipulative experiments enabled us to capture on video film the behaviour of both host and parasitoid and to analyse the resulting combined ethograms. The aim of this study was to quantify the behavioural changes triggered by substrate vibrations for both the host and the parasitoid. We did not aim at obtaining an estimate of the influence of vibration-mediated information on the overall success of a searching

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sequence, which would require an integration of the responses over the whole foraging sequence.

2. MATERIAL AND METHODS

(*a*) *Biology of the species*

Phyllonorycter malella is a polyvoltine endophytic leaf-mining microlepidopteran. A detailed description of the biology of a closely related host species, *P. blancardella* Fab., is given in Pottinger and LeRoux (1971). Larvae of *P. malella* produce tentiform mines on apple leaves, where they pupate. One aspect of crucial importance for this study is the ability of the larva to move freely inside the voluminous tentiform mine, as it potentially allows the host to escape the stings of the parasitoid's ovipositor. Larvae and pupae are attacked by several parasitoid species (Casas & Baumgärtner 1990). One of them, *Sympiesis sericeicornis*, is a bivoltine larval–pupal ectoparasitoid. The parasitoid immobilizes its host by injecting venom with its ovipositor before laying a single egg.

(*b*) *Handling of host and parasitoid*

Both insects were reared following the procedure described in Casas & Meyhöfer (1994). The behaviour of *Sympiesis sericeicornis* searching on single-mined apple leaves was recorded with a video system (recorder: Panasonic AG-7355; camera: Panasonic WV-BL600 equipped with Computar 18–108/2.5 lens). Only mines with fourth and fifth larval instars (tissue feeders) were used for the observations. Each leaf was cut off the plant and placed in a small glass vial filled with water inside a glass observation box ($17 \times 11 \times 10$ cm^3). The lower epidermis of the mined area was replaced by a clear piece of plastic attached to the leaf with Pritt-Stick® glue. This enabled us to examine the larva's movements inside the mine. Mined leaves to be used for the experiment were prepared 4 h before beginning observation. Preliminary experiments indicated that this experimental setup did not alter the time course or frequency content of the vibrational signals triggered by the larvae (unpublished data). A mirror placed under the mined leaf allowed us to record both sides of the leaf on the same video frame.

Prior to the beginning of the experiment, mated parasitoid females were kept singly in containers with mined host plants. Apple seedlings with mines were replaced by fresh seedlings (without mines) 4 h before observation. This short period of host deprivation increased the probability that females would be motivated to search and oviposit during the experiment. Only experienced *Sympiesis sericeicornis* females were used, to avoid learning effects in the behavioural responses.

Up to six experiments, distributed over several days, were performed with each female. Females were offered three to five mines between experiments for host feeding and oviposition.

(*c*) *Definition of behavioural states*

While foraging on the mine the parasitoid displayed three different behavioural states and the larva four different behavioural states. We defined three behavioural states for the parasitoid, and four for the larva, as follows.

(i) *Behavioural states of the parasitoid*

Searching: included all displacements on the mine from one location to another and antennation of the leaf surface.

Pausing: the parasitoid stood motionless on the mine. The antennae were held straight, often performing alternating up and down movements (small clicks).

Ovipositor insertion: oviposition is often preceded by a complex sequence of behaviours. In order to choose a

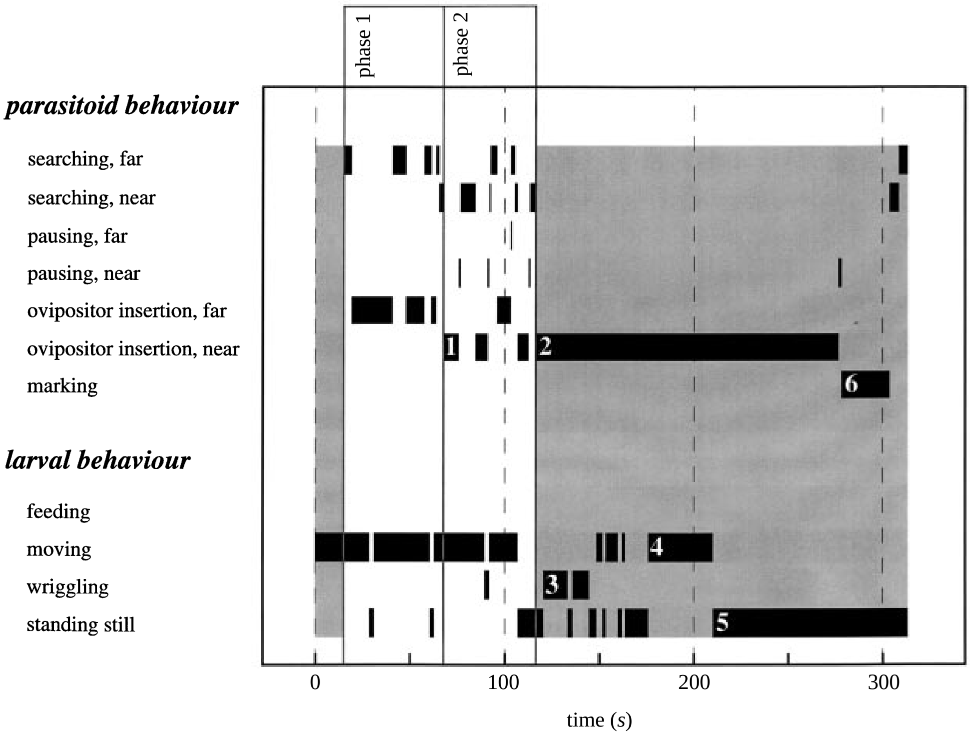

Figure 1. Example of a complete searching sequence of the parasitoid on the mine combined with the corresponding larval behaviour. The numbers refer to typical elements of a successful searching sequence: (1) first ovipositor insertion near the larva; (2) insertion of the ovipositor paralysing the larva; (3) vigorous wriggling of the larva during the beginning of paralysis; followed by (4) a moving sequence; and (5) the final permanent paralysis and egg laying. After egg deposition the parasitoid marks the mine with a pheromone (6). The grey background indicates those parts of the sequence that were not analysed.

Table 1. *Comparing behavioural transition probabilities of the larva while the parasitoid is searching/pausing, far (no vibrations emitted) versus parasitoid ovipositor insertion, far (vibrations emitted) during the first phase*

(*P*-values are calculated using the Fisher exact probability test.)

index	larva transition	parasitoid *searching/ pausing, far* transition probability	counts	parasitoid *ovipositor insertion, far* transition probability	counts	*p*-value
1	*feeding-moving*	0	0/122	0.13	5/38	0.001
2	*feeding-still*	0	0/122	0.03	1/38	0.24
3	*moving-feeding*	0.03	6/181	0.02	1/61	0.68
4	*moving-still*	0.04	7/181	0.30	18/61	0.001
5	*still-feeding*	0.01	1/230	0	0/109	1.00
6	*still-moving*	0.03	7/230	0.12	13/109	0.002

suitable location for insertion the parasitoid will first intensely antennate the leaf surface. Once a suitable spot has been found a move of 4–5 steps forward brings the abdomen directly above the spot before ovipositor insertion actually takes place. Females choose to oviposit through the feeding windows left by the host where only the cell skeleton is left.

The position of the parasitoid relative to the larva was also recorded. A behaviour was said to be carried out *near* the host if the parasitoid was located inside an ellipse with a maximum distance of half its body length from the larva, and *far* if further away. As a result, six possible behavioural states (three types of behaviour × two positions) were obtained. An *ovipositor insertion* near the host could result in a miss, just touching the larva, or lead to an actual piercing of the larva and injection of the venom.

(ii) *Behavioural states of the host larva*

Moving: all movements of the larva, including a change of location and movements of the head from one side to the other, excluding mandible movements.

Feeding: slight head movements accompanied by noticeable mandible movements. This behaviour only takes place on the upper side of the leaf where the leaf parenchyma is located.

Still: lack of movement.

Wriggling: the whole body of the larva shifts abruptly several times from one side to the other. It typically occurs when the larva is hit by the parasitoid's ovipositor, occasionally spontaneously.

(*d*) *Recording and estimating behavioural transitions*

The behavioural recordings were analysed with the software The Observer (Noldus Information Technology 1993). The behavioural observation started when the parasitoid began to walk on the mine and ended with the departure from the mine after oviposition. In those cases in which the parasitoid entered and left the mined area several times, only the behavioural sequence on the mine during which the larva was paralysed was analysed. The analysis was restricted to sequences with successful ovipositions to avoid motivational aspects in the behavioural response.

The combination of four larval and six parasitoid behavioural states resulted in a 24 × 24 transition matrix, in which each state contains larval and parasitoid behaviour. An example of a complete searching sequence of both insects is given in figure 1. The sequence started when the parasitoid entered the mine while searching far from the host, which was moving. Then a sequence of three ovipositor insertions far from the host followed, each separated by searching movements. During the ovipositor insertions of the parasitoid the larva changed its behaviour from moving to still and vice versa. The fourth ovipositor insertion took place near the larva's location (figure 1, number 1, start of phase 2; see data analysis for explanation). After two attempts at hitting the larva by ovipositor insertions near, the parasitoid temporarily lost contact with the larva, but finally succeeded in hitting it (figure 1, number 2, end of phase 2). In the last part of this example sequence the larva wriggled vigorously (figure 1, number 3), moved (figure 1, number 4) and was finally paralysed by the parasitoid's venom (figure 1, number 5). The sequence ended with an oviposition and marking of the mine (figure 1, number 6). We analysed the data both in terms of transition probabilities from one state to another and in terms of the time spent in each state. Transition probabilities were calculated as the number of transitions from one behavioural state to the next divided by the total number of transitions of both the parasitoid and the host larva. For example, the combined state of larva *moving* parasitoid *oviposition, far*, was observed 61 times (denominator; index 1 and 2, table 2). Index 1 in table 2 (larva *moving*) refers to 26 observations of the parasitoid behaviour *searching, far*, which followed the behavioural state *oviposition, far*. In 16 cases the following behaviour was *pausing, far* (index 2, table 2). The remaining 19 cases were behavioural transitions by the host (index 3 and 4, table 1) while the parasitoid was still in *oviposition, far*.

(*e*) *Data analysis*

We split the sequences into two different phases. The first phase started when the parasitoid stepped on the mine and ended when the parasitoid inserted its ovipositor near the host for the first time. The host was either stung or touched by this ovipositor insertion. The second phase started with the first insertion of the ovipositor near the host and ended

Table 2. *Comparing behavioural transition probabilities of the parasitoid while the larva is still (no vibrations emitted) versus moving (vibrations emitted) in the first phase.*

(*P*-values are calculated using the Fisher exact probability test. Transitions from ovipositor insertion, near to any other behavioural states are missing by definition.)

index	parasitoid transition	larva *moving* transition probability	counts	larva *still* transition probability	counts	*p*-value
1	o,f-s,f	0.43	26/61	0.64	70/109	0.01
2	o,f-p,f	0.26	16/61	0.23	25/109	0.71
3	p,f-s,f	0.88	38/43	0.89	40/45	1.00
4	p,f-o,f	0.05	2/43	0.02	1/45	0.61
5	p,n-s,n	0.89	8/9	0.67	2/3	0.46
6	p,n-o,n	0.00	0/9	0.33	1/3	0.25
7	s,f-s,n	0.25	24/95	0.24	35/144	0.88
8	s,f-p,f	0.25	24/95	0.13	18/144	0.02
9	s,f-o,f	0.42	40/95	0.61	88/144	0.005
10	s,n-s,f	0.27	9/34	0.37	14/38	0.45
11	s,n-p,n	0.27	9/34	0.08	3/38	0.06
12	s,n-o,n	0.38	13/34	0.53	20/38	0.25

o,f = *ovipositor insertion, far*; s,f = *searching, far*; p,f = *pausing, far*; o,n = *ovipositor insertion, near*; s,n = *searching, near*; p,n = *pausing, near*.

with the paralysis of the host. Typically the larva was stung by the ovipositor, wriggled and became motionless within several seconds. The distinction between these two phases allowed us to separate with confidence responses triggered by substrate vibrations alone (phase 1) from those triggered by a combination of substrate vibrations and physical contact between both insects (phase 2). Because we were mainly interested in behavioural interactions triggered by substrate vibrations the behavioural analysis is restricted to the first phase.

Because we analysed the chain of events, a change of state could only occur when one animal changed its behaviour. The analysis was conditional on homogeneity between behaviours of females and on time invariance. Forty-two behavioural sequences from 19 females were recorded. We tested the effect of using the same female on several occasions by analysing the time elapsed until the first insertion of the ovipositor near the host. Two observations, each by a different female, were detected as outliers using quantile plots and were discarded from the analysis. Denoting the number of females (x) used in a number of experiments (y) as $x:y$, the data set is composed of the following sequences; 12:1, 5:2, 3:3, 1:4 and 1:6. A variance component analysis on the logarithm of the time elapsed until the first insertion near the host did not detect a female effect ($p = 0.6$). This was confirmed by a visual examination of the scatter plot of the same data.

We paid particular attention to those states in which characteristic vibrations were emitted. Within the parasitoid's foraging sequence, *ovipositor insertion* is the only behavioural event that produces high frequency and high intensity vibrational signals, while *pausing* and *searching* vibrations are rather scarce and of low frequency and intensity (Bacher *et al.* 1996). We therefore compared the host's responses to *ovipositor insertion* with its reaction when the parasitoid was *searching* or *pausing*. There was no difference in the behavioural response of the host during periods when the parasitoid was *searching* or *pausing* (phase 1: $p = 0.45$; Fisher exact probability test, unpublished data). Therefore the host's response to *pausing* and *searching* was pooled for analysis.

Only larval *moving* and *wriggling* produced characteristic strong vibrations, while *feeding* and *still* produced very weak signals or no signal at all (Meyhöfer *et al.* 1994*b*). We therefore compared the parasitoid's responses to the host *moving* to those while the host is *still*.

3. RESULTS

A sequence of behavioural events is characterized by the probability of changing from one behaviour to another and the time spent in the different behavioural states. We do not show the results for the time spent in the different behavioural categories. Neither parasitoid nor larval movements influenced the amount of time spent by the other party in any of their respective behavioural states (tested using the Mann–Whitney *U*-test at the 0.05 significance level). The only exception was the insertion of the ovipositor, which lasted significantly longer when the host was *still* compared with moving (larva *moving*: median 7.4 s; larva *still*: median 13 s, $p = 0.017$ Mann–Whitney *U*-test).

(*a*) *Larval behaviour as influenced by the parasitoid's behaviour*

When the larva was *feeding* at the beginning of the interaction, a searching parasitoid did not induce any behavioural changes (table 1, indexes 1 and 2). In contrast, the host was significantly more likely to stop *feeding* and to start *moving* as soon as the parasitoid inserted its ovipositor into the mine, even if this was far from the host (table 1, index 1). Insertion of the ovipositor induced more behavioural changes than *searching* for the ensuing interactions. There was a four-fold increase in the probability of changing from *still* to *moving* (table 1, index 6) and a seven-fold increase in changing from *moving* to *still* (table 1, index 4) when the parasitoid inserted its ovipositor into the mine. Once a larva stopped *feeding* it hardly ever resumed doing so.

(*b*) *Parasitoid behaviour as influenced by larval behaviour*

A parasitoid started its foraging bout on a mine with *searching* the leaf, generally far from the *feeding* host. The influence of larval movement on the behavioural transitions was a function of the distance between the two parties. If the parasitoid was *searching* far from the host, larval *movement* as compared with *still*, doubled the probability that the wasp would *pause* (table 2, index 8) and decreased the probability of *ovipositor insertion* by 20% (table 2, index 9). This pattern weakened and even partly vanished if the parasitoid was *searching near* the host (table 2, indexes 10–12). Larval movement did not help the parasitoid to approach the host (table 2, index 7), nor to stay in the neighbourhood of the host if it was already there (table 2, index 10). Thus, larval movement did not act as an attractant nor as an arrestant. In addition, larval movement decreased the probability that the parasitoid resumed *searching* after an insertion of the ovipositor (table 2, index 1).

4. DISCUSSION

Several of the parasitoid's behavioural transitions were markedly influenced by larval movement. This strongly suggests that the parasitoid uses vibratory information coming from the host's activities. Furthermore, our results confirm previous speculations that being *still* is indeed associated with host location using vibratory information. Being *still* is interpreted as a posture for selective responsiveness to vibrations, and may enable the parasitoid to detect host vibrations without the interference of its own movements (Vet & van Alphen 1985). We did not, however, find any indications for the presence of vibrotaxis. The reasons for this may be three-fold. First, the duration of a signal of a certain quality (frequency, amplitude) may be too short for the parasitoid to rely on it for orientation over several behavioural steps. Second, vibrations reaching the parasitoid may not contain information about the origin of the signal, due to wave interference, for example. Finally, it is possible that an analysis of movement finer than the simple binary classification of *far* and *near* presented here is required for the parasitoid to reveal taxis. Vibrotaxis in host location has been postulated in several host–parasitoid systems (see Casas 1994 for a review), but formal proof is still lacking. A rigorous demonstration of such a host location mechanism has to include (i) what information is available to the forager, (ii) the type of information processing, (iii) the search patterns elicited by the stimulus, in this case vibrations, and (iv) the nature of the guidance system (Bell & Tobin 1982). Although kinesis could not be detected using our approach, statistical analysis of the distribution of turning angles on the mine showed that this orientation behaviour is indeed displayed on the mine (Casas 1988). Unfortunately, concomitant information about the timing of larval activity and the resulting kinesis reaction is still missing in that study too. At this stage, the available information suggests that a parasitoid may use vibrations both as a means of classifying the host's state (instar and activity) and as a trigger to continue hunting.

The marked changes in larval behaviour induced by an insertion of the ovipositor when the parasitoid is *far* show that the host is quite sensitive to vibrations. It is likely to stop *feeding* at the first insertion of the ovipositor and never to resume *feeding* for the rest of the searching sequence. Furthermore, the probability of changing behaviour from *moving* to *still* strongly increases when the parasitoid inserts its ovipositor. More difficult to explain is the change in behaviour from *still* to *moving* that takes place during *ovipositor insertions*, as this type of behaviour would only serve to give the parasitoid information as to its host's whereabouts.

The 'princess and monster' game developed in game theory (Stone 1989 and references therein) bears a lot of resemblance to this interaction, and may help us to unravel this puzzle. The optimal strategies to be followed by the monster and the princess in order to minimize (monster) or maximize (princess) the time until capture depend on the value of many parameters, such as the geometry of the arena, the cost of search and escape, the detection laws, etc. Several elements from search theory help us in understanding the observed interactions. The model describes a two-person game with a monster and a princess moving with a maximal speed of 1 and $v < 1$, respectively, in a bounded and connected two-dimensional region. Models of the princess's strategy are easily described. Let $Q1$, $Q2$, … be an identically independent distributed random variable (IID) of points uniformly distributed in the arena. The princess starts at $Q1$, stays there for T time units, moves to the next point $Q2$ at full speed, stays there for T time units, etc. If the princess is allowed some partial information in the form of knowledge about the monster's position at some time interval, then she could elude it indefinitely. The monster's strategy is more complicated and Lalley & Robbins (1988) have defined a set of trajectories for the monster's displacements that would lead to a uniform distribution of visited points over the arena. The key element in the monster's strategy is the randomness in the successive locations, as any partial information available to the princess quickly loses its value. For the leafminer–parasitoid interaction, the analogy implies that by remaining still the host faces a trade-off between giving out information to the parasitoid as to its whereabouts and increasing the chances of escaping parasitization as the percentage of area covered by the parasitoid increases progressively. Indeed, the parasitoid does remain and probe within a small area of the mine for some time before moving to another area (unpublished data), suggesting that some sort of pseudosystematic coverage of the surface of the mine does indeed take place. The numerous insertions of the ovipositor distant from the host cannot be dismissed as mere errors. In a system where tracking a host is difficult, if not impossible, models of princess and monster tell us that elements of randomness in the choice of the location for inserting the ovipositor may be part of the best available strategy for the parasitoid.

Similarly, the quick and short escape movements followed by long motionless periods which we observed may be one of the few escape strategies available to the host larva. As a result of incomplete information about the whereabouts of the other party, the optimal strategies for both the host and the parasitoid may necessarily involve a high degree of randomness about what to do next and where.

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