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Matching host reactions to parasitoid wasp vibrations

Imen Djemai[*], **Jérôme Casas and Christelle Magal**

Institut de Recherche sur la Biologie de l'Insecte (CNRS UMR 6035), Faculté des Sciences et des Techniques, University of Tours, Avenue Monge, 37200 Tours, France

The sensory ecology of predator detection by prey has been little studied for any arthropod prey–predator system, in contrast to the sensory ecology of prey finding by predators. The aim of this study was to quantify the foraging signals produced by the parasitoid *Sympiesis sericeicornis* (Hymenoptera: Eulophidae) and the sensory ecology of enemy detection and the avoidance behaviour of the leaf-mining host, *Phyllonorycter* spp. (Lepidoptera: Gracillariidae). We used synthetic vibrations approximating the signals generated by ovipositor insertions to stimulate the host in its mine. To the authors' knowledge, this is the first manipulative study to describe a match in the frequency range between a parasitoid foraging stimulus and a host behavioural response. We discuss our findings in relation to other predator–prey systems for which a coevolution between prey sensitivity and predator signal has been described.

Keywords: vibrations; host–parasitoid system; sensory ecology; coevolution

1. INTRODUCTION

Many insects show defensive behaviours. Responses of prey to the stimuli produced by predators range from simple reactions, such as freezing and immediate escape, to complex behavioural sequences (for reviews see Edmunds (1974) and Sih (1987)). There are only a few examples where vibrations produced by a predator have been reported to elicit such behavioural responses (Tautz 1977; Camhi *et al.* 1978; Tautz & Markl 1978; Gnatzy & Kamper 1990). Moreover, the vibrations reported in these systems are exclusively airborne. The great significance of vibrations for both parasitoid and host has been suggested several times. There is a lack of quantitative studies of the substrate vibrations produced by predators. In particular, substrate vibrations are known to be used by parasitoids attacking endophytic hosts concealed in plant material and decaying substrates (reviewed in Meyhöfer & Casas 1999). Nevertheless, quantitative descriptions of vibratory signals and associated mechanisms of orientation by both antagonists are still lacking. The general aim of this study was to obtain experimental proof of vibratory interactions in a host–parasitoid system.

Late instar larvae and pupae of the spotted tentiform leaf-miner *Phyllonorycter* spp. group *blancardella* (Lepidoptera: Gracillariidae) show characteristic defensive reactions when they are attacked by the parasitoid *Sympiesis sericeicornis* Nees (Hymenoptera: Eulophidae). Whereas pupae can only wriggle, which is an evasive defence (Gross 1993), larvae may also escape ovipositor stings by changing location inside their mines. This behaviour may also increase the handling time of the parasitoid. In about 10% of cases the parasitoid abandons the mine without parasitizing the host (Casas 1989), so it seems likely that defensive behaviour has an adaptive value. The leaf-miner–parasitoid interaction described above is similar to the princess–monster game developed in search theory (Fitzgerald 1979). The game is played in a confined arena, and the monster and the princess are to minimize and maximize the time to capture, respectively. Many parameters influence this time, one of which is the information available to the monster about the location of the princess in the arena. The optimal strategies of the princess and the monster limit the information available, in order to avoid their localization, like in a hide-and-seek game. For effective defensive behaviour, leaf-miners must be able to detect the presence of the attacking parasitoid at an early stage. We hypothesized that *Phyllonorycter* spp. perceive the presence of the parasitoid through the vibrations produced during host location on the mine. Indeed, such vibrations provide both detectable and reliable cues for leaf-miners to identify the enemy (Bacher *et al.* 1996). However, the question of which components of the vibratory signal are actually involved in eliciting defensive behaviour remains to be answered.

The specific aim of this study was to analyse host behavioural responses to synthetic substrate vibrations similar to those produced by foraging parasitoids. The behavioural responses of fourth and fifth larval instar and pupae to synthetic stimuli were investigated using vibratory signals approximating the signal produced by the insertion of the ovipositor by the parasitoid. We found that the frequency range at which the host reacts best matches the frequency range of the parasitoid's signal. For the first time, to our knowledge, our results demonstrate a good sensory match between predator stimuli and prey behavioural responses in the large class of host–parasitoid systems.

2. MATERIAL AND METHODS

(a) *Biology of the species*

The biology of *Phyllonorycter blancardella* Fab. is described by Pottinger & LeRoux (1971), and also applies to the species studied here. Larval development can be divided into five instars. The first three larval instars are sap feeders, whereas the following two are tissue feeders. Sap feeders, with a dorsoventral compressed body, produce a flat surface mine on the lower side of the leaf. The structure of the mine changes with the larval development into a tissue feeder, which spins silky threads. Its mine is tent shaped. Selective feeding on the leaf parenchyma causes a spotted surface appearance of the upper epidermis. Larvae and pupae are attacked by several parasitoid

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[*] Author for correspondence (canova@u-bourgogne.fr).

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species (Casas & Baumgärtner 1990). One of the largest is *S. sericeicornis* (Hymenoptera: Eulophidae), a bivoltine larval–pupal ectoparasitoid that attacks the fourth and fifth larval instars and pupae.

(b) *Vibrations produced by foraging parasitoids*

Apple-seedling leaves containing mines were cut off for the experiments. The petiole was placed through a hole in the lid of a glass tube containing water. Plasticine was used to prevent any further movement of the petiole. An unwrapped section of the petiole was left between the Plasticine and the leaf lamina. All experiments were carried out on a vibration-free table to reduce background noise.

The vibrations produced by a foraging female *S. sericeicornis* were recorded using an Ometron laser vibrometer VS 100 (London, UK; sensitivity range of 1 $\mu\text{m s}^{-1}$ to 1000 mm s^{-1} and with a maximum frequency of 50 kHz). Mined leaves were adjusted so that the surface was perpendicular to the laser beam. To avoid leaf vibrations due to air turbulence, prepared leaves were placed in a glass box (25 cm × 14 cm × 12 cm), which the laser beam passed through. *S. sericeicornis* females that had prior oviposition experience were released singly into the glass box.

The vibration signals were sampled using a Siglab data recorder (Spectral Dynamics Corporation, San Jose, CA, USA). Alongside the vibration recording, the behaviour of the parasitoid on the leaf was recorded using a video camera (Sony CCD-RGB) equipped with a macro-zoom lens (18–108/2.5). Based on Casas' (1989) definitions, the behaviour of the foraging female was divided into five categories, with probing producing the only reliable signals (Bacher *et al.* 1996). Probing started when the tip of the abdomen was put on the mine surface to position the ovipositor, and ended when the ovipositor was withdrawn from the mine. In each experiment, the signals emitted during probing were recorded for 150 ms due to limited sampling at 50 kHz.

The data-acquisition equipment had a sampling frequency of 50 kHz. Frequency spectra were calculated using the toolbox SPTOOL of Matlab (Mathworks Inc.) using fast Fourier transformation (Welch method, window length 1024, Hanning window). The background noise level was estimated for each run. For every frequency spectrum calculated, we subtracted the one obtained from the background noise. An analysis of the background noise showed no differences between leaves. The study was based on more than 100 probings by six females foraging on 10 apple leaves.

(c) *Bioassays*

The same experimental design as that described in § 2b was used. In each experiment, fourth and fifth instar larvae or pupae (28 pupae and 10 larvae) concealed in their mines were stimulated. Leaves bearing single mines were used. Mines were illuminated from above with a glass fibre. The lower epidermis of the mine was removed and replaced by a piece of transparent paper. This paper was adjusted to the mine, and glued in such a way as to keep the shape of the mine as far as possible. A mirror was placed behind the leaf to enable observations inside the mine. The behaviour of leaf-miners inside the mines was monitored through the lower epidermis of the leaf using a video camera (Sony CDD-RGB) equipped with a macro-zoom lens (18–108/2.5). For better reflection of the laser beam, a small piece of retroflexive tape was glued to the centre of the mine. The extra weight added was very small compared with the weight of the leaves; therefore, its influence on the mechanical behaviour of the leaf was considered to be negligible. Vibrations were produced using an electromagnetic vibration exciter (Ling Dynamics V101, Royston, UK). The vibration exciter was equipped with a fine needle, which allowed the vibrations to be transmitted through a single point on the upper surface of the mine. The signals produced by parasitoid females were first numerically approximated, then fed to a function generator (Siglab, Spectral Dynamics Corporation, San Jose, CA, USA) and finally sent to the mine. The integrity of the output signal was checked using the laser vibrometer. The frequency and the velocity of the signal were modulated. Frequencies of 200 Hz, 500 Hz, 1000 Hz, 2000 Hz, 5000 Hz and 10 000 Hz and intensities of 2 mm s^{-1}, 5 mm s^{-1}, 10 mm s^{-1}, 15 mm s^{-1} and 20 mm s^{-1} were used. For each frequency, the amplitude was increased from 2 mm s^{-1} to 20 mm s^{-1}. Thus, each individual received 30 different stimuli of varying intensities and frequencies. One signal per second was sent for 1 min. The large range of frequencies and intensities included the range of frequencies and intensities of signals produced by foraging parasitoids (Bacher *et al.* 1996).

Different categories of behaviour for each instar were defined, and the change of behaviour, if any, when a stimulus was sent was recorded. For pupae, behavioural changes were from immobility to motionless starred position, and to movement without net body displacement. Undisturbed larvae were either feeding or moving. The changes were to motionless, if this state was held during the entire stimulation plus for at least one further minute, to movement without net body displacement, and to movement with net body displacement. This last behaviour was called 'evasive behaviour'. The behavioural observations started just before the onset of the stimulation and ended 2 min after the end of each signal.

3. RESULTS

(a) *Behavioural responses to vibrations*

Overall, 68% of the pupae and 100% of the larvae reacted at least once to the synthetic signals, whereas 100% of larvae and pupae showed no reactions without vibrations: pupae were immobile and larvae continued their activity inside the mine (for pupae: contingency table $\chi^2 = 30.27$, $p = 0.0001$; for larvae: contingency table $\chi^2 = 20$, $p = 0.0001$).

Among those pupae that did react, the percentage of responses obtained was much higher between 1 kHz and 5 kHz than at lower and higher frequencies ($n = 570$ stimuli, Kruskal–Wallis $\chi^2 = 11.993$, d.f. $= 4$, $p = 0.017$). Furthermore, the percentage of responses increased with an increase in the velocity of the signal (Kruskal–Wallis $\chi^2 = 7.756$, d.f. $= 4$, $p = 0.101$). Movement without net body displacement accounted for 78% of those pupae showing a reaction. The proportion of the reactions in each of the two behavioural categories, motionless starred position and movement without net body displacement, were independent of the velocity and frequency of the signal (figure 1*a*).

The percentage of larval responses was higher between 2 kHz and 5 kHz than at lower and higher frequencies, but the trend was not statistically significant ($n = 300$ stimuli, Kruskal–Wallis $\chi^2 = 7.076$, d.f. $= 4$, $p = 0.132$). The percentage of responses was independent of signal velocity (Kruskal–Wallis $\chi^2 = 4.508$, d.f. $= 4$, $p = 0.342$). The

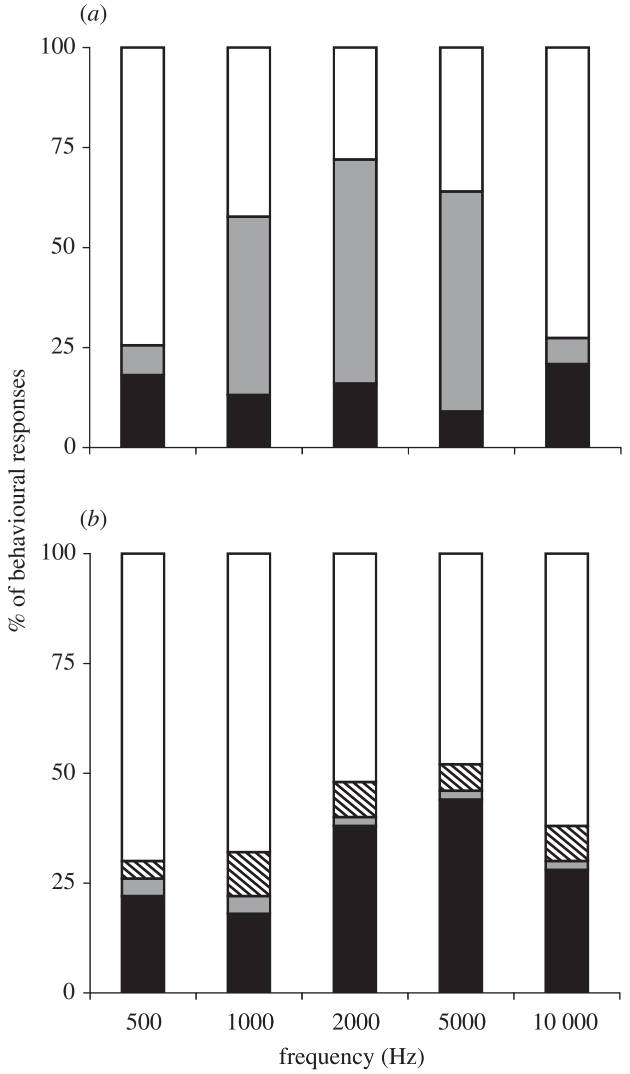

Figure 1. Behavioural reactions of (*a*) pupae and (*b*) larvae to vibrations modulated in frequency. White: no reaction; grey: movement without net body displacement; hatched: movement with net displacement; black: motionless.

proportion of reactions in each of the behavioural categories was independent of the velocity and frequency of the signal (figure 1*b*). The motionless position was the most frequent behavioural response, while evasive behaviour accounted for 23% of the reactions (table 1).

(b) *Matching host sensitivity to parasitoid signal characteristics*

Probing produced signals containing phases with obvious vibrations interspersed with phases that were indistinguishable from background noise (figure 2). The duration of probing was highly variable, ranging from 1 to 30 s. Therefore, we focused on the reliable signals, named 'impact' signals hereafter, which had a short mean duration of 4.16 ms (s.d. = 1.8 ms, $n = 32$) and a mean velocity of 3.55 mm s^{-1} (s.d. = 2.52 mm s^{-1}, $n = 32$). The dominant frequencies of these impacts were between 1.5 kHz and 4 kHz (with intensities between 30 dB and 50 dB, $n = 32$) (figure 2).

The minimal threshold for evasive behaviour was obtained in the frequency range 1–5 kHz. The occurrence of behavioural changes was also maximal in the frequency range 2–5 kHz (figure 3). Thus, the frequency range within which the host reacted defensively with the greatest sensitivity matched well with the frequency range of the vibration signals produced by the parasitoid.

Table 1. Larvae behavioural modifications (expressed as percentages) in the presence of vibratory signals.

behavioural modifications	to motionless	to movement without net body displacement	to displacement (evasive behaviour)
from feeding	46	7	10
from displacement	35	2	13
total	81	9	23

4. DISCUSSION

Most works on the role of vibrations in host–parasitoid interactions deal with the host-location behaviour of the parasitoid (Meyhöfer & Casas 1999). Moving and immobile hosts have been used in choice tests to analyse the behavioural reactions of parasitoids as a function of the presence or absence of vibrational stimuli. However, according to Meyhöfer & Casas' review (1999), these behavioural tests are insufficient to provide conclusive evidence about the orientation mechanisms of the parasitoid. A large amount of information is already available about the vibratory interaction between this leaf-mining host and its eulophid parasitoid, including behavioural interactions during the foraging sequence (Meyhöfer *et al.* 1997), the characterization of the vibratory signals of the host and the parasitoid (Meyhöfer *et al.* 1994; Bacher *et al.* 1996), and the role of the leaf as a channel for signal transmission (Magal *et al.* 2000). Furthermore, the host's behavioural responses to vibrations produced by foraging parasitoids have never been studied for any host–parasitoid system. The closest study (Bacher *et al.* 1997) does not use parasitoid signals, and uses a restricted set-up. To our knowledge, this study is, therefore, the first to use a manipulative experimental approach based on a rigorous biotest to extract relevant information contained in a parasitoid's vibratory signal, and to characterize the behavioural response of its host.

(a) *Vibratory cues and evasive strategies*

The results of Bacher *et al.* (1996) show that probing is the only behaviour that produces reliable vibrations and differentiates parasitoids from other insects. Meyhöfer *et al.* (1997) showed that ovipositor insertions in the mine without touching the host had a marked influence on the behaviour of larvae, whereas other behaviours of the parasitoid did not induce a strong response. The vibratory signals produced by probing behaviour were, therefore, chosen to stimulate hosts. However, we could not reproduce the changing location of ovipositor insertion observed in the real situation.

The experiment by Bacher *et al.* (1997) used a sinus or band-limited noise signal to stimulate mainly free pupae

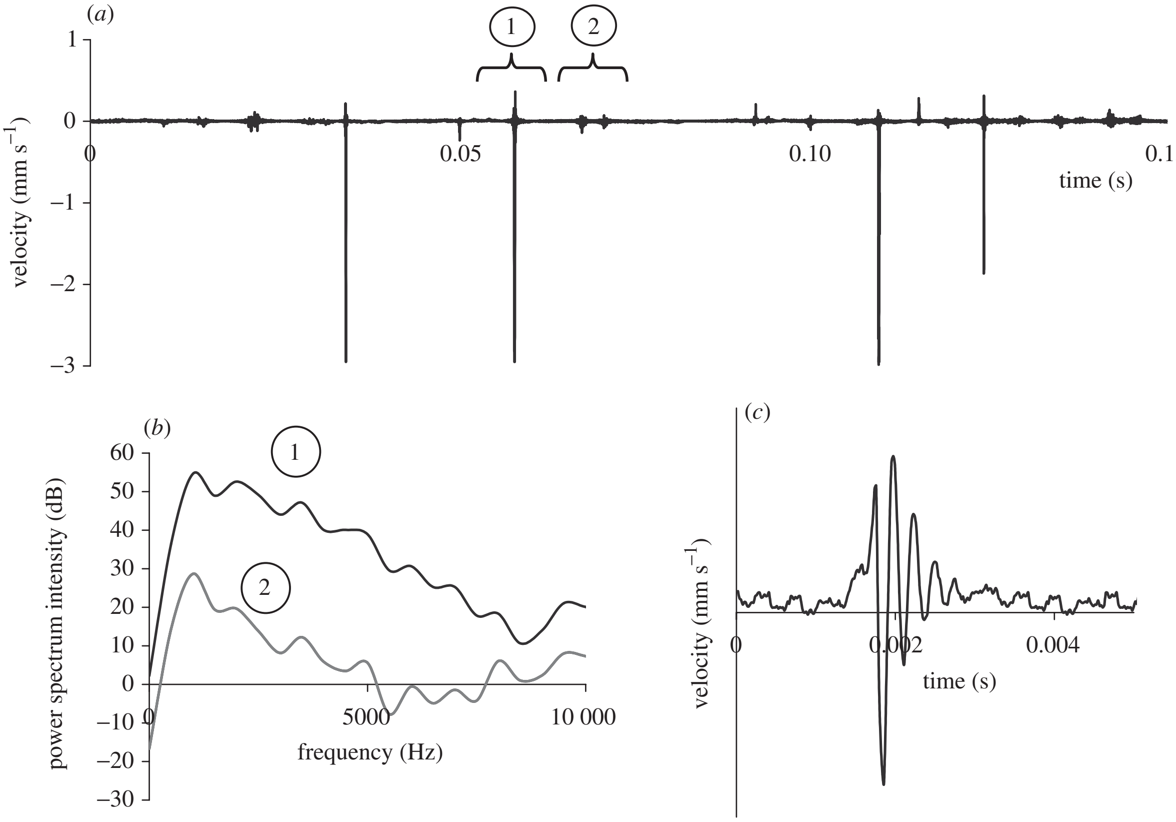

Figure 2. (*a*) Structure of parasitoid signal due to ovipositor insertion. (*b*) Power spectrum of different phases of the vibratory signal. (*c*) Wave skeleton produced in the phase shown by the upper line in (*b*). This wave skeleton is modulated in velocity and frequency, and sent to the host.

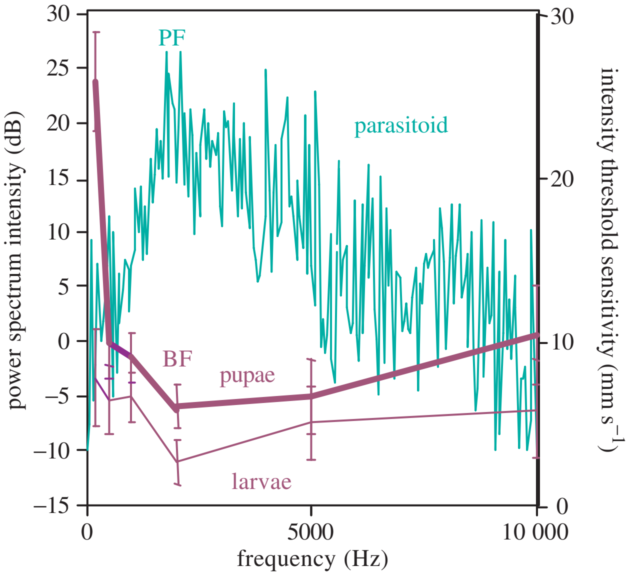

Figure 3. Spectrum of the parasitoid's signal ($n = 32$), and threshold sensitivities of a larva and a pupa. The sensitivity of the host has it best frequency (BF) at the peak frequency (PF) of the parasitoid's signal.

and a few concealed ones in their mines. The poor reactivity of the host may have been due to the use of such signals, which were not approximations of the natural signals. The poor reactivity could also have been due to the lack of a proper propagation channel, which has a crucial influence on signal transmission (Magal *et al.* 2000). Consequently, we tried to preserve the three-dimensional structure of the mine, and stimulated hosts only in their microhabitat. An analysis of propagation waves in the three-dimensional mines will ultimately be necessary to understand the signal transmission towards the receiver and the subsequent behavioural response. For example, it would be interesting to see whether the three-dimensional mine enhances the warning system of the host by amplifying the external vibrations, and whether it also enhances the inconspicuousness of the inhabitant by attenuating its vibrations.

All larvae and 68% of pupae reacted to the synthetic signal by changing their behaviour, as in natural conditions. The pupae that did not react to vibrations might have been those that were remodelling their nervous systems (Huber 1964). Nevertheless, for the receptive pupae, the dominant response to the synthetic signal is to move. This dominant response of the pupae enables them to escape the insertion of the ovipositor when the parasitoid touches them (Cole 1959).

The dominant behavioural response of larvae to synthetic signals is to become motionless. In the context of the princess–monster game, the host faces a trade-off between giving out information to the parasitoid about its location and increasing the chances of escaping parasitization (Djemai *et al.* 2000). In this way, a larva that reacts to the vibratory signal by stopping its activities increases its chances of being inconspicuous to the parasitoid. A moving larva may give useful information about its location and suitability to the parasitoid, which could detect the vibrations emitted. However, for the host, waiting and freezing is not always a good strategy because the parasitoid uses a pseudosystematic search, and covers most of the surface during a searching bout (Casas 1989). The larva has to move. The wrong decision may have fatal consequences. Hence, our results are consistent with princess–monster game theory, which predicts some level of randomness in the decision of the princess.

(b) *Matching host reactions to parasitoid signals*

The host's greatest sensitivity is in a frequency range of 2–5 kHz. This frequency range corresponds to the properties of the parasitoid's signal. The threshold sensitivity of pupae is lower than that of larvae. This reduction in sensitivity is due to the fact that pupae can adopt only one type of defensive behaviour, wriggling, and could escape ovipositor insertion in the vicinity of the parasitoid (Cole 1959). The threshold sensitivity of larvae is lower than the parasitoid's velocity signal for all frequencies. Larvae have a larger repertoire of behaviours and may have developed a considerably wider sensorial system, which may allow them to maximize their response to the range of signals emitted during the attack of the parasitoid. Furthermore, the large community of parasitoids attacking leaf-miners could explain the greater sensitivity of the host. This community contains about 20 species (Casas & Baumgärtner 1990), so we may expect the host to be able to detect other parasitoids having significantly different frequency ranges.

The sensory ecology of predator detection by prey has been little studied for any insect prey–predator system, in contrast to the much-studied sensory ecology of prey finding by predators. There are only two other comprehensive studies of insect prey–predator systems in which the mechanosensory ecology of predator detection by prey has been investigated (i.e. the signal structure of the predator and the prey behaviour have been identified). These studies deal with geometrid caterpillars reacting to the wing-beat frequency of foraging wasps (Tautz & Markl 1978), and with gryllids reacting to the airflow produced by sand-wasps (Gnatzy & Kamper 1990). In both cases a good match was reported between the peak frequency in the predator vibration signals and the best response frequency in the warning system of the prey. This is also true for vertebrates preying on invertebrates, in particular for bats catching moths, where a very good match between the bat's signal and the hearing capacities of the moths has been reported (for reviews see Fullard 1998).

Our finding of a good match between the frequency range of highest sensitivity in the host, either larva or pupa, and the vibrations produced by the insertion of the ovipositor has three implications. First, it demonstrates for the first time, to our knowledge, a good sensory match between predator stimuli and prey behavioural response in an exceptionally large class of interactions (host–parasitoid systems, which encompass more than 100 000 parasitoid species (Eggleton & Belshaw 1992)). Even though we are unable, at present, to put a precise figure on the proportion of systems in which hosts react defensively to stimuli from their parasitoids, it is likely to be substantial (Gross 1993). Second, it extends the match to a new channel of communication, adding substrate-borne sound to airborne sound. While mechanoreception is involved in both cases, different sensory cells and organs are likely to be at work: filiform hairs and tympanic organs in the former case and touch hairs in the latter (Hoy *et al.* 1998). This may have profound implications for the kind of information available to the host, and, hence, the range of escape possibilities. Finally, a good match is evidence, at the sensory ecology level, that behavioural host defence is as crucial as physiological host defence in determining the success of parasitism (Carton & Nappi 1997; Kraaijeveld & Godfray 1997; Kraaijeveld *et al.* 1998). The paucity of studies on behavioural host defence compared with physiological host defence gives a distorted view of the relative importance of the different defence mechanisms (Malcolm 1992; Gross 1993; Quicke 1997). Our findings show that the coevolutionary race in relationships as intimate as those of host–parasitoid systems spans all instants and mechanisms of an interaction.

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