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Parasitoid vibrations as potential releasing stimulus of evasive behaviour in a leafminer

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Abstract. The aim of this study was to characterize the vibratory signals produced by the parasitoid *Sympiesis sericeicornis* Nees (Hymenoptera: Eulophidae) while foraging on apple leaves infested by one of its hosts, the spotted tentiform leafminer *Phyllonorycter malella* (Ger.) (Lepidoptera: Gracillariidae). This leafminer changes its behaviour as a function of the parasitoid's behaviour to escape parasitization. We propose that the leafminer uses vibrations triggered by the parasitoid to detect the presence of its enemy.

We measured vibrations produced by a foraging parasitoid on a mine with a laser vibrometer. By recording concurrently the behaviour of the parasitoid on video, vibrations could be assigned to particular behaviours. Subsequently, vibrations were characterized by their dominant frequencies and intensities. The behaviours *Landing* and *Take-off* both produced strong impact-like vibrations characterized by an initial irregular phase during which frequencies up to 25 kHz occurred followed by a slow decaying regular phase. Vibrations elicited by *Moving, Standing* and *Probing* showed no clear temporal pattern. During *Probing*, dominant frequencies of up to 5.6 kHz were observed frequently at intensities well above the background noise (>10 dB). During *Moving* and *Standing*, vibrations were more scarce and of lower frequencies and intensities. Due to their impact-like nature, vibrations produced by *Landing* and *Take-off* are probably not specific to the parasitoid. Vibrations produced by *Moving* and *Standing* are difficult to detect and not reliable because of their non-specificity. Therefore, only *Probing* provides a reliable and detectable source of information for the host. The vibrations elicited during *Probing* could account for the evasive behaviour that is observed in this and other leafminers.

Key words. Vibratory communication, sensory ecology, laser vibrometry, evasive behaviour, mechanoreception, leafminer, parasitoid, *Phyllonorycter, Sympiesis*.

Introduction

Sensory stimuli which reach endophytic insects are widely different from those that free-living insects experience. Visual and olfactory signals from the environment are strongly filtered, if not completely blocked by the plant material surrounding the endophyte. Mechanostimuli (sound and vibration), on the other hand, are transmitted through plant material very well (Michelsen *et al.*, 1982). Vibratory communication has been studied in detail in a number of free-living arthropod groups that use plants as transmission channels: e.g. in alderflies (Megaloptera) (Rupprecht, 1975); in leafhoppers, planthoppers and cydnid bugs (Homoptera) (Michelsen *et al.*, 1982; Butlin, 1993); in grasshoppers (Orthoptera) (Kalmring, 1985); in ants (Hymenoptera) and butterflies (Lepidoptera) (DeVries, 1990); in parasitic wasps (Hymenoptera) (Field & Keller, 1993); in lacewings (Neuroptera) (Devetak & Pabst, 1994); in spiders (Araneae) (Schmitt *et al.*, 1994); etc. In contrast, vibratory communication involving endophytic insects has rarely been studied, probably because of the inherent difficulty of measuring these systems.

The two last larval instars (L4 and L5) and the pupae of the apple leafminer *Phyllonorycter malella* (Ger.) (Lepidoptera: Gracillariidae) live in a tentiform mine. This special type of mine allows the inhabitant considerable freedom of movement. We occasionally observed that leafminers react with evasive

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behaviour when attacked by the polyphagous ectoparasitoid *Sympiesis sericeicornis* Nees (Hymenoptera: Eulophidae). Field observations in our system showed that the parasitoid abandons the host without parasitizing it in 10% of the cases, sometimes after a long game of 'hide-and-seek' (Casas, 1989). The most prominent reaction of an attacked leafminer was denoted as 'wriggling' (Meyhöfer *et al.*, 1994): the host violently moves with its whole body in order to escape stings from the ovipositor. This evasive behaviour is also known from other leafminers (Connor & Cargain, 1994, and E. F. Connor, personal communication) and from a whole range of free-living lepidopterous larvae and pupae (Gross, 1993). We observed 'wriggling' in three different situations: after mechanical disturbance; when an insect, not necessarily harmful to the leafminer, was landing on the leaf; and during host location and attack behaviour by the parasitoid. This led us to hypothesize that the host uses vibrations to perceive a foraging parasitoid. Such a hypothesis could explain the presence of hair sensillae on the body of the late-instar host larvae and pupae (Pottinger & LeRoux, 1971). A visual comparison of their external morphology with known types of hairs (McIver, 1985) suggests that they probably serve as mechanoreceptors.

In this paper we characterize and quantify the vibrations that are produced during the foraging of female *S.sericeicornis* on apple leaves infested by the leafminer *P.malella*.

Material and Methods

Insects and plants. We used insects and plants from our continuous laboratory rearing as described in Casas & Meyhöfer (1994). The laboratory strain of *P.malella* was established in 1989 with moths collected in the region of Emilia Romana (Italy) and reared on apple seedlings (*Malus sylvestris* cf. Golden Delicious). The parasitoid strain originated from material collected in autumn 1993 in South Tirol (Italy). Experiments were conducted in spring 1994. Eight apple leaves with a single mine were used for vibration measurements (fresh weight 93 ± 42 mg, dry weight 40 ± 12 mg, length of leaf lamina 56 ± 7 mm, width of leaf lamina 29 ± 3 mm, values are means ±SD). Only leaves with either paralysed hosts or empty mines were used to ensure that vibrations were exclusively triggered by the parasitoid. The weight of a female *S.sericeicornis* was approximately 0.7 mg, the weight of a leafminer was about 1 mg.

Experimental set-up. Vibrations of foraging female *S.sericeicornis* were measured with a laser Doppler vibrometer (Dantec 41 × 62 Compact Laser Vibrometer, 2 mW He-Ne-Laser). The output of the vibrometer is a voltage directly proportional to the instantaneous velocity (i.e. speed in the direction of the laser beam) of the surface of an object at the measurement point.

Vibrations were measured on the upper side of the leaf surface on the centre of the mine. For better reflection of the laser beam and a better signal-to-noise ratio, a small piece of retroreflexive tape was glued on the mine centre (Scotchlite, 3M; ~1 mm^2). The extra weight added was very small (<0.1 mg) compared with the weight of the leaves. Therefore its influence on the mechanical behaviour of the leaf was considered to be negligible (see Michelsen *et al.*, 1982).

Experiments were conducted using the cantilever set-up described by Meyhöfer *et al.* (1994) for measurements of leafminer vibrations: leaves were cut off from their plants and their petioles were placed in a water-filled vial through a hole in its lid. The petiole was fixed to the lid with plasticine at a distance of 0.5 cm to the leaf base.

Leaves were adjusted so that the leaf surface was perpendicular to the laser beam. To avoid leaf vibrations due to air turbulence, prepared leaves were placed in a closed glass box (17 × 11 × 10 cm). The laser beam passed through the lid of the glass box. To reduce background vibrations, the laser unit of the vibrometer as well as the glass box containing the apple leaf to be studied were mounted on an air-buffered vibration-damped table (Photon Control, Cambridge). Female *S.sericeicornis* which had prior oviposition experience were released singly into the glass box. Females were investigated more than once on the same leaf, and on different leaves.

The analog output of the vibrometer was passed through a programmable low-pass filter (Stanford Research SR650, attenuation 105 dB per octave) to avoid aliasing effects during digitizing. The filtered vibration signals were sampled with a Mac Adios II/16 A/D converter and stored on a Macintosh Quadra 800 computer using the software SoundScope (GW Instruments, 1993). The monitor output of the vibrometer was followed on an oscilloscope (Hameg HM 205-3) to enable an optional adjustment of the vibrometer during the experiments.

Alongside the vibration recordings, the behaviour of the parasitoid on the leaf was recorded with a video camera (Panasonic WV-BL600) equipped with a macro zoom lens (Computar 18-108/2.5). A mirror was placed behind the leaf to enable observations on both the upper and the lower side of the leaf. Video data were stored on a recorder (Panasonic AG-7355) at a rate of fifty half-frames per second, i.e. one video image every 20 ms. A time code generator (iec Pro Gamma, Noldus) provided time information for each video image.

To synchronize video and vibration recordings, a light-emitting diode (LED) was placed in the field of vision of the video. The computer program that controlled the vibration recording flashed the diode once directly prior to data acquisition. With this method, the beginning of vibration recording could be assigned to a video image with an accuracy of 20 ms (Fig. 1a). During a recording session, the beginning of a parasitoid behaviour could be determined from the video images with an accuracy of 20 ms (i.e. one half-frame). Therefore, during recording the vibratory events could be assigned to a behaviour of the parasitoid with a constant maximal error of 40 ms (Fig. 1b).

Behavioural categories. Based on the definitions in Casas (1989), the behaviour of foraging female parasitoids on the leaf was divided into the following categories: *Landing*: landing on the leaf, after approach by flight. *Take-off*: departure from the leaf by flight. *Moving on the leaf lamina*: change of location on the leaf lamina outside the mined area. Movements were in general much quicker compared with movements on the mine. *Moving on the mine*: change of location on the mine. The movements on the mine were considered as searching activity. In general, the female moved slowly, often intensely examining the mine surface with the tips of her antennae seemingly to find a suitable spot for ovipositor insertion. *Standing*: all actions either

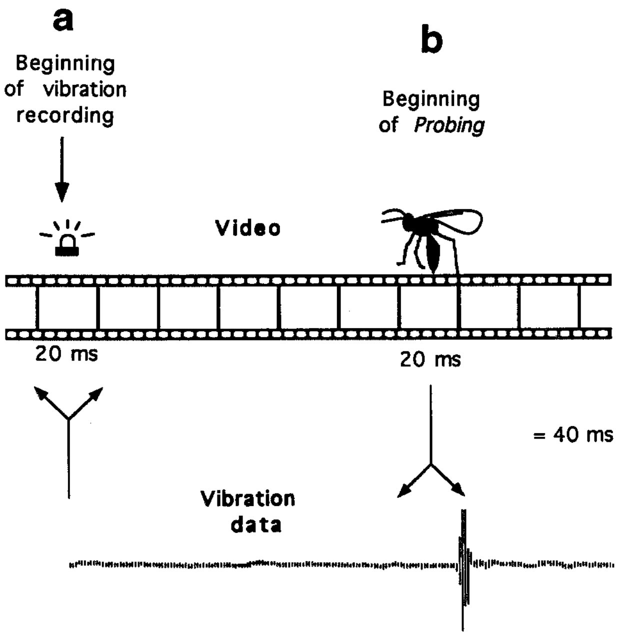

Fig. 1. Synchronization of video and vibration recording. Details are given in the text.

on the leaf lamina or on the mine without a change of location, i.e. resting, stiffness, cleaning behaviour. *Probing*: started when the tip of the abdomen was put on the mine surface to position the ovipositor. It ended when the body axis of the parasitoid was parallel to the leaf surface again after the ovipositor was removed from the mine. We did not distinguish if the ovipositor had been inserted into the mine or not.

Data acquisition. Vibration data acquisition had a sampling frequency of 50 kHz. This enabled detection of frequencies up to 25 kHz. The anti-aliasing low-pass filter was set to 25 kHz to attenuate higher frequencies. The frequency tracker of the vibrometer was set in the range 10–100 kHz so velocities in the range 6.3×10^{-6} to 13×10^{-3} m/s and a maximal acceleration of 1.8 m/s^2 could be detected (Dantec, 1991). A linear frequency response of the vibrometer up to 7.4 kHz at this tracker range is reported by the manufacturer. We carried out our own experiments with sinusoidal vibrations of different frequencies produced by a vibration exciter (Brüel & Kjaer 4810 + 2706) controlled by a function generator (Stanford Research DS345). No deviations from linearity were observed up to 10 kHz with this setting. In the range 10–20 kHz the frequency of a sinusoidal vibration was still detected correctly. However, the accuracy of the corresponding intensities decreased approximately linearly with increasing frequency. At 20 kHz the velocity amplitude was underestimated by 30%. Thus, vibrations above 10 kHz were identified correctly in the frequency domain, but underestimated in their intensity depending on their frequency.

In each experiment, vibrations were recorded for 50 s. Using the information on the video tapes, the records were cut into segments according to the behaviour of the parasitoid (Fig. 2a, b). Segments of vibratory signals triggered by the same behaviour were denoted as replicates. One record may therefore contain several replicates.

The total recording time was *c.* 30 min of various foraging activities, and the acquired vibration data amounted to 112 MB. All records in which parasitoids contacted the leaf were included.

Frequency analysis. Frequency spectra were calculated by Fast Fourier Transformation (FFT, on 2048 points) of the velocity. Intensities were calculated as uncalibrated sound intensity levels (*SIL*). Like in acoustics, intensities were given on a logarithmic scale as decibel values (dB). We used the same algorithm as in Meyhöfer *et al.* (1994):

$$SIL = 10 \cdot \log_{10}\left(\frac{2}{FFTpoints}\sqrt{\frac{real^2 + imag^2}{0.001}}\right),$$

where *real* is the real part of the complex notation of the FFT, *imag* the imaginary part of the complex notation of the FFT and *FFTpoints* the number of points used for the FFT. The algorithm returns a spectrum of 1024 dB values for frequencies between 0 and 25 kHz. To gain accuracy in the location of frequency peaks, spectra were smoothed by calculating a five-point moving average, and afterwards by compressing the number of dB values to 512 by calculating the average of two successive points. The resulting spectrum has a frequency resolution of about 49 Hz.

Each replicate was divided into successive intervals of 40 ms (Fig. 2c) which corresponds to the time resolution that could be assigned to an action of a foraging parasitoid. The frequency spectrum was calculated for each interval. A 40 ms time interval contained 2000 sample points (sampling frequency of 50 kHz). To obtain the 2048 points necessary for the FFT (the number of source points to perform a FFT has to be a power of 2), the first forty-eight points of the following 40 ms interval were appended to the current interval. The background noise level was estimated for each replicate by calculating the average +2 SD of ten spectra of the closest time series in which the parasitoid was not on the leaf. It was calculated at least once for each experiment, as the background noise was found to vary from leaf to leaf and over time for the same leaf. The spectra were obtained from 40 ms intervals as described above. The range of the background noise during all experiments is given in Fig. 3. Every frequency spectrum obtained from a foraging female was compared to a spectrum of the background noise by calculating signal-to-noise ratios (Fig. 2d). These ratios were obtained by subtracting the background noise spectra (in dB) from the dB values of frequency spectra obtained from foraging parasitoids. The obtained signal-to-noise ratio vibration spectra were characterized by their dominant frequency, i.e. the location of the frequency peak with the maximum intensity (Fig. 2e).

The dominant frequencies of each replicate were then sorted by their intensities. Only segments in which the signal-to-noise ratio of the dominant frequency was higher than 3, 5, 7 or 10 dB were further analysed. These thresholds correspond to intensities at least twice, 3 times, 5 times, or 10 times the intensity of the background noise. The frequency scale was divided into eight frequency classes corresponding to octave bands from <178 Hz to 22.4 kHz (Table 1) and dominant frequencies were accordingly assigned to the different frequency classes.

The analysis is based on thirty-five recording sessions of eight *S.sericeicornis* foraging on eight apple leaves.

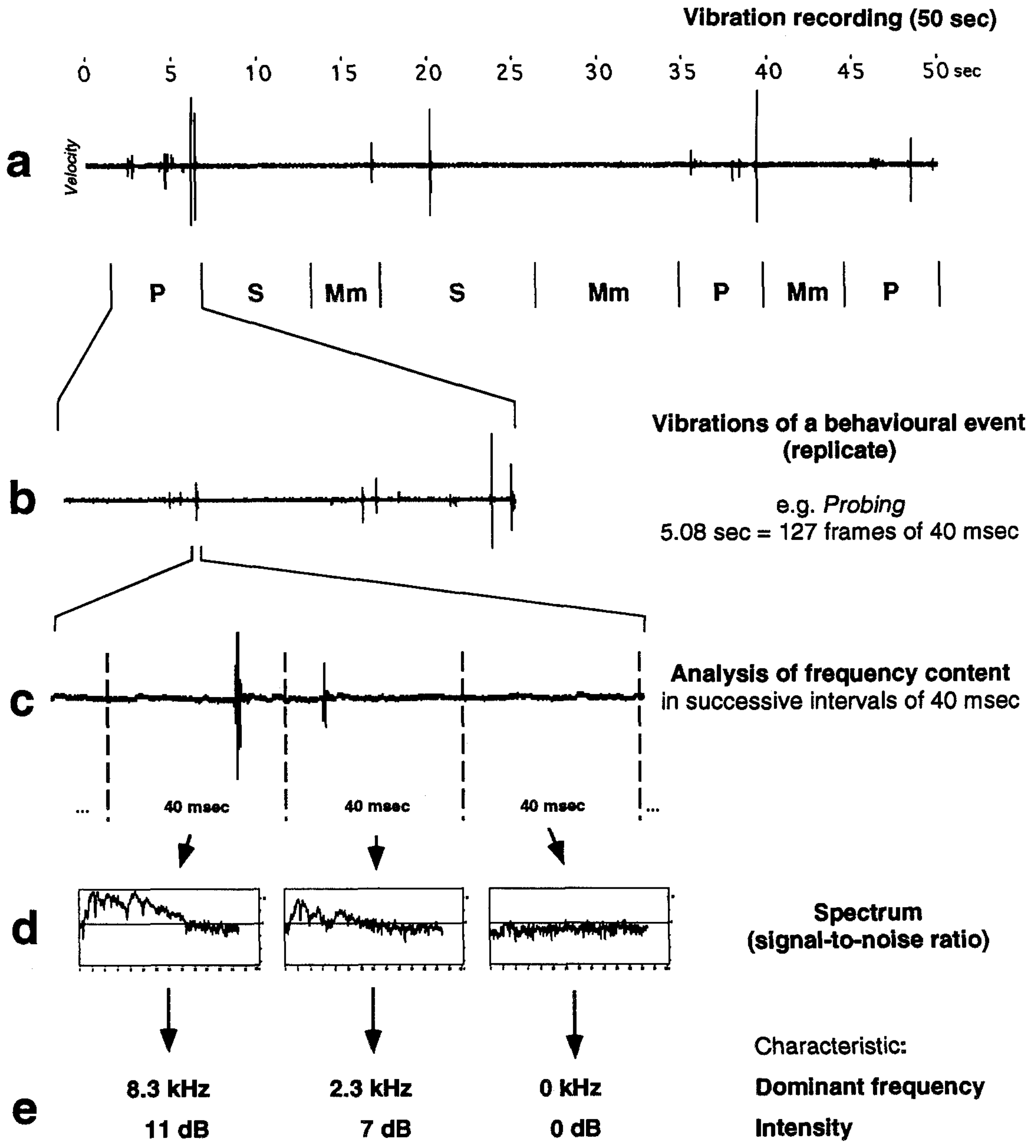

Fig. 2. Frequency analysis of vibration recordings. S: *Standing*; Mm: *Moving on the mine*; P: *Probing*. Details are given in the text.

Table 1. Range of frequency classes.

Frequency class	Frequency range (Hz)
1	<178
2	178–355
3	355–708
4	708–1410
5	1410–2820
6	2820–5620
7	5620–11,200
8	11,200–22,400

Results

Short-lasting behaviours: Landing and Take-off

Landing. The impact by an alighting parasitoid resulted in a vibrational signal in which a short initial irregular phase followed by a longer regular phase could be discriminated (Fig. 4a). The irregular phase was characterized by irregular changing velocity amplitudes, which caused broad frequency bands up to our measurement range of 25 kHz, and presumably above. The maximal velocity of the leaf surface during the irregular phase was 5.3 ± 2.4 mm/s (mean ±SD; $n = 11$). A parasitoid caused higher velocity amplitudes when approaching the leaf from a

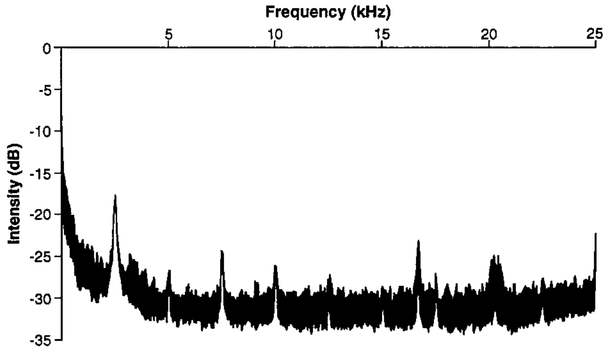

Fig. 3. Range of background noise during all experiments.

greater distance (e.g. from the glass box; $n = 8$) than from a point close by (e.g. the mirror or the edge of the vial; $n = 3$). The irregular vibrations merged into regular oscillations with a basic frequency between 11 and 16 Hz. There was no sharp transition between the first irregular and the second regular phase and we set the border between both phases by eye. The duration of the irregular phase was between 20 and 100 ms. The amplitude of the basic oscillation decreased in the course of the regular phase (Fig. 4a). Since the absolute duration of the basic oscillation could not be determined accurately, we calculated the half life of the amplitude for each recording. The period of the basic oscillation and the attenuation from one maximum to the next were constant for five successive maxima. Therefore we approximated the basic oscillation by a damped harmonic oscillation of the form $y = \sin(2pft) \cdot e^{-kt}$, with y being the vibration amplitude, f the frequency of the basic oscillation, t the time, and k the damping constant. The amplitude of the basic oscillation decreased exponentially with a half life of 137 ± 28 ms (mean ±SD; $n = 9$). When the impact on the leaf was weak (e.g. approach from a short distance), the regular phase was not clear enough to discern the basic frequency ($n = 2$). The basic oscillation was super-imposed with dominant high frequencies directly proportional to the absolute value of the velocity of the basic oscillation during the whole regular phase (Fig. 4a).

Take-off. Vibrations produced when a female took off can be separated into two phases with the same broad characteristics as described for *Landing*. The initial, irregular phase during *Take-off* was much shorter (<20 ms, $n = 12$) than in *Landing* (Fig. 4b). The maximal velocity during this phase was 2.7 ± 1.3 mm/s

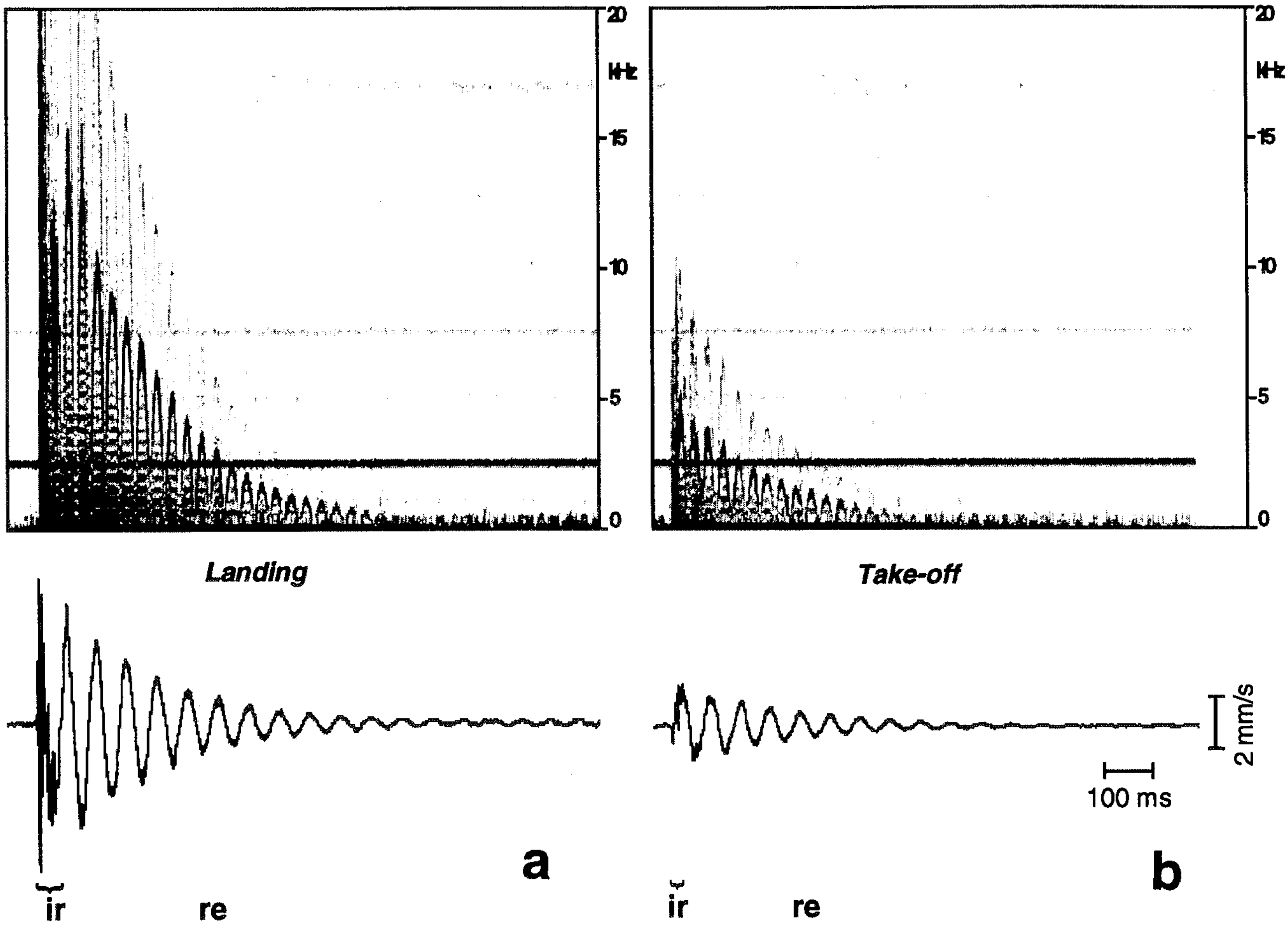

Fig. 4. Velocity time course and spectrogram of typical vibrations triggered by a female *S.sericeicornis* during *Landing* and *Take-off* (ir: irregular phase; re: regular phase). Spectrograms were calculated from the velocity series using the software SoundScope (settings: 512 FFT-points, Hamming window 184 Hz (8 ms), intensity range: black 30 dB to white 0 dB, frame advance 0.1 ms, no 6 dB pre-emphasis). The frequency bar at 2.5 kHz belongs to the background noise (see Fig. 3).

Table 2. Duration of behavioural events and maximal velocity triggered during such an event. *n* = total number of replicates in a behavioural class; $\%n_{\mathrm{eff}}$ = percentage of replicates in which the maximal velocity exceeded the maximal velocity of the background vibrations (mean +2 SD = 0.2 mm/s).

	Duration (s)		Maximum velocity (mm/s)			
	Mean ±SD	Range	Mean ±SD	Range	*n*	$\%n_{\mathrm{eff}}$
Background			0.10 ± 0.05	0.26–0.05	19	
Standing	5.9 ± 6.6	26.8–0.7	0.19 ± 0.38	1.68–0.05	18	22
Moving on the leaf lamina	8.7 ± 9.4	42.3–0.4	0.28 ± 0.27	1.30–0.08	28	53
Moving on the mine	9.2 ± 8.2	35.7–1.1	0.23 ± 0.27	1.17–0.06	48	25
Probing	7.5 ± 5.2	26.8–3.4	1.49 ± 1.08	4.46–0.13	31	97

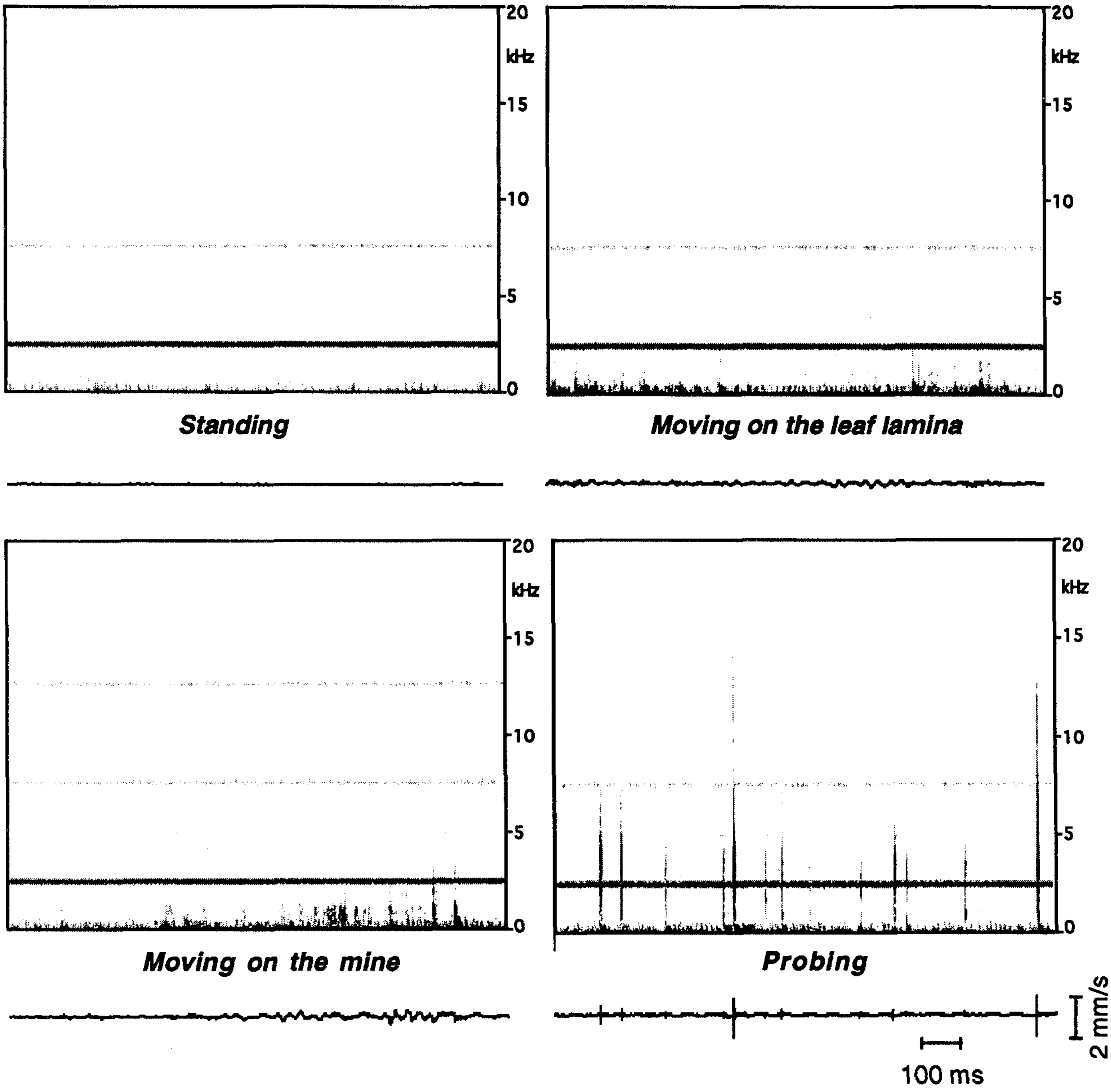

Fig. 5. Velocity time course and spectrogram of typical vibratory signals triggered by a female *S.sericeicornis* during *Standing, Moving on the leaf lamina, Moving on the mine* and *Probing.* To allow a direct comparison with *Landing* and *Take-off,* the spectrogram settings were chosen the same as for Fig. 4. The frequency bar at 2.5 kHz belongs to the background noise (see Fig. 3).

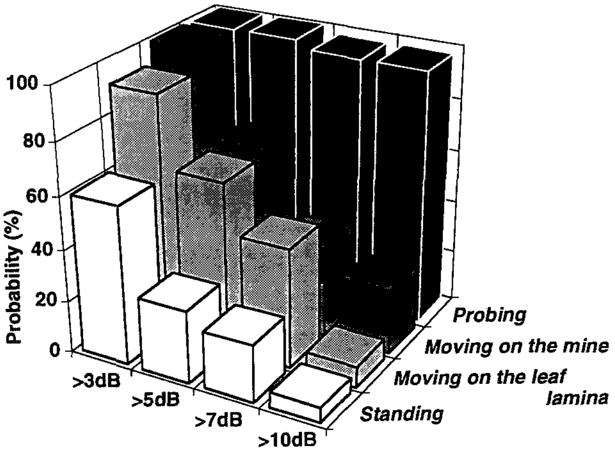

Fig. 6. Probabilities that a vibrational signal whose dominant frequency exceeds a certain threshold above the background noise occurs at least once in the course of a complete behavioural event.

(mean ±SD), which is about half the velocity elicited by a landing parasitoid. There was no difference between the regular phases triggered by *Landing* or *Take-off* (basic oscillation: frequency between 11 and 16 Hz; half life of 147 ± 28 ms (mean ±SD)).

Long-lasting behaviours: Moving, Standing and Probing

The duration of these behaviours was highly variable, ranging from <1 to >30 s (Table 2). The maximal velocity elicited by *Probing* was much higher than for the other long-lasting behavioural states (Table 2). Velocities elicited during *Probing* were about half as high as velocities triggered by *Take-off* and a quarter as high as triggered by *Landing*. For *Probing*, 97% of replicates contained velocities clearly higher than in the background noise (mean ±2 SD = 0.2 mm/s), while for *Moving* and *Standing* a high proportion of replicates contained no velocities higher than the background noise (Table 2).

In contrast to vibrations triggered by short-lasting behaviours, the velocity amplitude of vibrational signals elicited by long-lasting behaviours was irregular, without a clear temporal pattern. During a single behaviour, phases with obvious vibration signals alternated with phases indistinguishable from the background noise (Fig. 5). We characterized the signals quantitatively by calculating the probability of their occurrence during two different kinds of intervals. Intervals of the first kind lasted 40 ms and corresponded to the smallest time interval for which we could assign a behavioural event with good confidence. The second kind of interval was variable in time and represented the integration of intervals of the first kind over the period of time needed for completion of a behavioural event. Thus, using intervals of the first kind we investigated the probability of occurrence of a vibration signal in time ('time scale'), and using intervals of the second kind we investigated the probability of occurrence of a vibration signal at least once during a behavioural event ('behavioural scale').

Behavioural scale. During complete behavioural events of *Probing*, vibrations with dominant frequencies of intensities at least 10 times higher (>10 dB) than the background noise were triggered with almost certainty (97% of replicates, Fig. 6). For

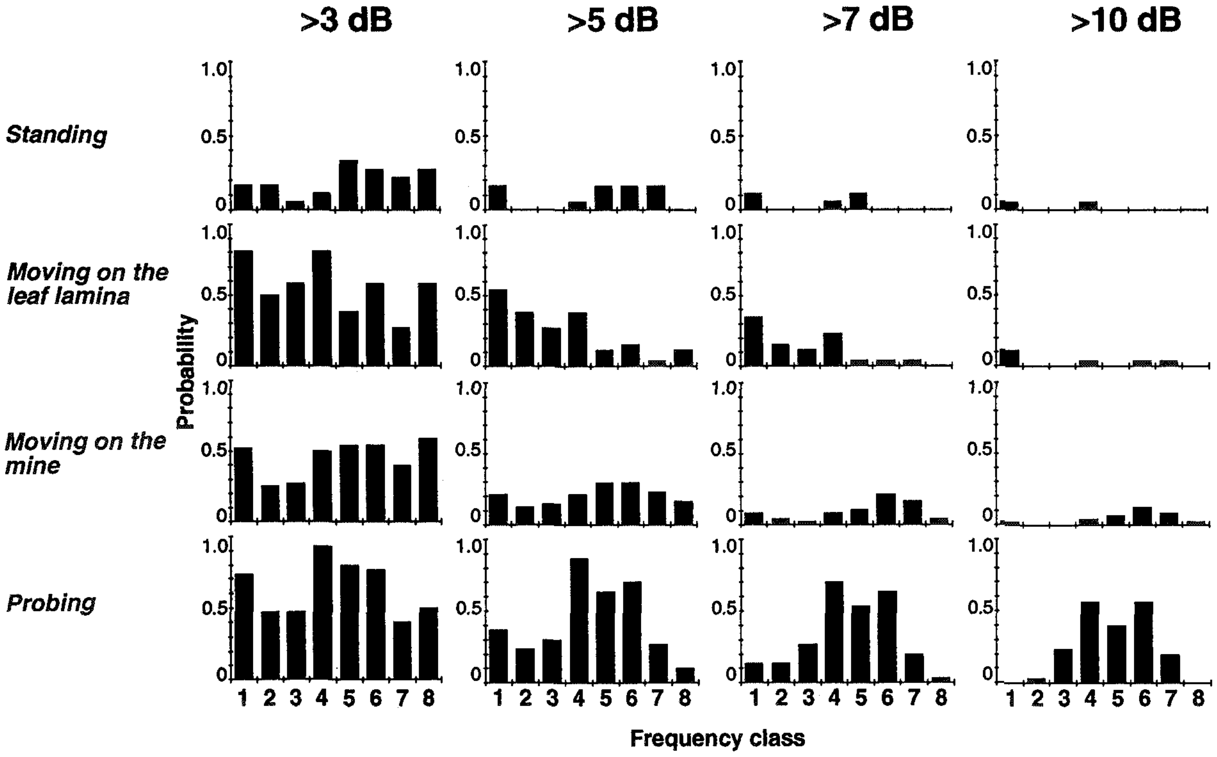

Fig. 7. Probabilities that dominant frequencies of a certain frequency class and intensity occur at least once in the course of a complete behavioural event.

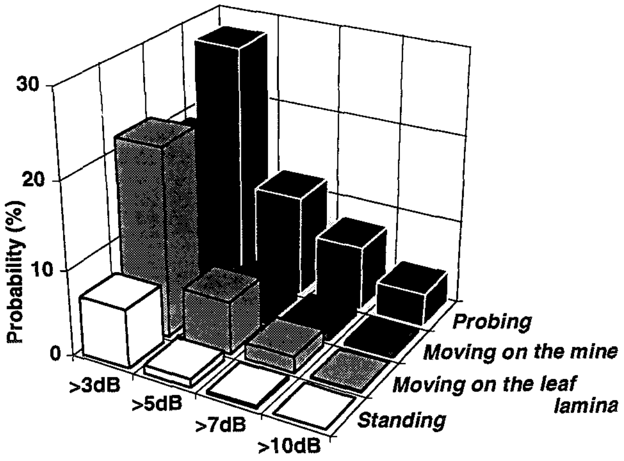

Fig. 8. Probabilities that the dominant frequency of a 40 ms interval exceeds a certain threshold above the background noise, calculated for different behavioural classes.

the other behaviours, dominant frequencies of such high intensities were rarely found, whereas vibrations with dominant frequencies of low intensities (at least 3 dB above background noise) occurred quite often. The probability that vibrations of a given intensity above the background noise were elicited was consistently highest during *Probing* and lowest during *Standing*, with *Moving* (either on the leaf lamina or on the mine) being intermediate (Fig. 6). In all behavioural states the lowest threshold (>3 dB) above background noise) was exceeded by dominant frequencies of all frequency classes (Fig. 7). However, dominant frequencies of high intensities (>10 dB), that were triggered during *Probing*, originated primarily from frequency classes 4–6 (708–5620 Hz). It should be noted that dominant frequencies triggered during *Moving on the leaf lamina* belonged to low frequency classes, whereas dominant frequencies triggered during *Moving on the mine* belonged to high frequency classes.

Time scale. The analysis of the same signals at the 40 ms time scale showed that vibrations of high intensity occurred as rare events (Fig. 8). *Probing* was the only behaviour with abundant vibrations of high intensities (>10 dB; Figs 8 and 9). The dominant frequency of such vibrations was located in frequency classes 3–6 (355–5620 Hz; Fig. 9). In *Moving on the leaf lamina*, the dominant frequency was most likely in the lowest frequency class.

Discussion

Implications and origin of the high variability between replicates

In our experiments some replicates show no vibrations over the total duration of the behaviour, whereas in other replicates vibrations were found in a large number of 40 ms intervals. This variability between replicates provides one reason to analyse the vibrations on both the behavioural and the time scale. There is *a priori* a simple theoretical relation between the two different scales: let p be the probability that a vibratory event would occur in a 40 ms interval. Then $q = 1-p$ would be the probability that this event would not occur during a 40 ms interval. The number of 40 ms intervals i comprised in a behavioural event can be

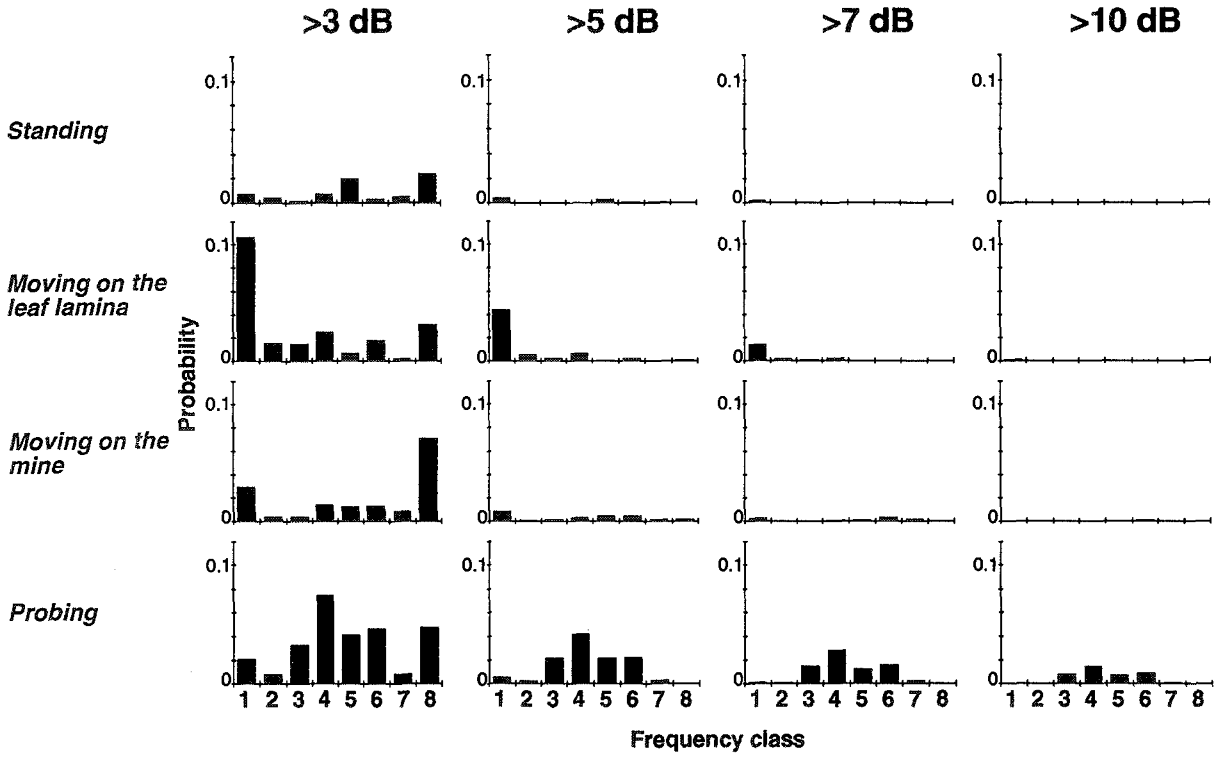

Fig. 9. Probabilities that the dominant frequency of a 40 ms interval is located in a certain frequency class, calculated for different behavioural classes.

obtained from the average duration of a behavioural event. The probability P that at least one vibratory signal would occur during a complete behavioural event is then $P = 1-q^i$. This relationship does not fit our data, as the assumption of independence between 40 ms segments is underlying the calculation of P. The strong heterogeneity between replicates implies that the relationship between the two scales is therefore more complex.

Another reason for the usefulness of the two different scales is that the restriction to a single occurrence at the behavioural level for scoring replicates discards any information about multiple occurrences. On the behavioural scale a replicate with a single occurrence will be scored the same as a replicate with a large number of occurrences. In contrast, when analysed at the 40 ms time scale, replicates with multiple occurrences will result in a marked increase of the probability p. It appears that the most important contributors to the high variability between replicates are the varying distance between the parasitoid and the point of measurement, the different leaf characteristics, and the heterogeneity of the plant material through which vibrations were travelling (see also Michelsen *et al.*, 1982; Barth *et al.*, 1988).

The characterization of parasitoid vibrations on both the behavioural and the time scale also provides a useful tool for future work, in which we will play different kinds of vibratory signals to the leafminer to elicit evasive behaviour. Combination with an analysis of the behavioural coupling between leafminer and parasitoid (Meyhöfer *et al.*, in preparation), will yield profitable information, whether the leafminer uses single vibratory events or whether it integrates vibratory events over a period of time to detect the presence of a parasitoid.

Vibrational signals produced by different behaviours

Landing and *Take-off* imparted relatively strong forces to the leaf. Studies on the velocity of vibration propagation in stems of different plant species (Michelsen *et al.*, 1982) suggest that, in our experiments, induced vibrations travelled several times across the leaf during the fade away period. Because the duration of the irregular phase approximately corresponds to the duration of the actual landing or take-off of the parasitoid, we assume that vibrations during the irregular phase are directly elicited by the impact of the parasitoid on the leaf. Since the insect does not impart force onto the leaf during the regular phase, vibrations of the regular phase must be reverberations which travel several times across the leaf. The fact that there are no differences between the regular phases of *Landing* and *Take-off* indicates that vibrations during the fade away depend to a high degree on the set-up and the leaf properties, rather than on what actually caused such vibrations. Therefore we suppose that vibrations during the regular phase are of low informational value for the leafminer.

When a parasitoid is standing on a leaf it is not necessarily immobile. Vibrations elicited during *Standing* most probably originate from actions such as cleaning, lifting and lowering the wings and dropping faeces.

Moving on the leaf lamina show vibrations of higher intensities more often than *Moving on the mine*, despite the fact that in the latter case the impact point and the measurement point are closer to one another. In both cases vibrations are triggered mainly by leg movements. The quicker movements outside the mined area may induce stronger vibrations in the leaf than the slow movements on the mined area.

During *Probing*, the strongest vibration peaks occur when the ovipositor is inserted into the mine, when it is withdrawn, or when the parasitoid is swinging around the inserted ovipositor, most probably to locate the host by touching it. However, during both ovipositor insertion and withdrawal several distinct vibration peaks occur rather than a continuous complex of vibration peaks (= 'pulse complex' as defined by Meyhöfer *et al.*, 1994). Therefore we assume that neither ovipositor insertion into the mine nor its withdrawal is a smooth process.

Reliability and detectability of vibrational signals

The type of system in which vibrational communication is studied will, to a great extent, determine the characteristics of the signals involved. In mating systems, the subject of most studies on vibrational communication, both mating partners, sender and receiver, benefit from successful communication. For easy identification of the partner, signals will generally have evolved to be easily detectable and reliable. In predator–prey and parasitoid–host systems, however, producing signals usually is disadvantageous to the sender, since it may lead to detection and identification by its opponent. In most studies on such systems, however, only vibrations elicited by the prey/host and used by the predatory/parasitoid for attack have been investigated (e.g. Brownell, 1977; Lang, 1980; Klärner & Barth, 1982; Bleckmann, 1985; Barth *et al.*, 1988; Sugimoto *et al.*, 1988). With a few exceptions (e.g. Camhi *et al.*, 1978; Tautz & Markl, 1978; Gnatzy & Kämper, 1990), the possibility of the prey/host to detect and escape from its enemies has not been discussed. In our parasitoid–leafminer system there is a strong behavioural coupling between the opponents, both being sender and receiver of vibrations (Casas, 1994; R. Meyhöfer *et al.*, in preparation). The parasitoid as a sender of vibrational signals has a strong disadvantage in alerting the leafminer to its presence, whereas the leafminer as a receiver benefits from this information which enables it to initiate evasive actions. The reverse situation is also true: the moving leafminer may give useful information to the parasitoid about its location and suitability. Thus, selection should act on both opponents for vibratory inconspicuousness.

Minimizing vibrations during foraging is one way for the parasitoid to accomplish this. The detectability of vibrations is highly dependent on the intensity and frequency composition of the background noise. This is well known in humans and vertebrates, but also applies to insects (Ehret *et al.*, 1982; Römer *et al.*, 1989). Vibrational signals of a foraging parasitoid may be masked by environmental vibrations. Wind and rain are major sources of vibrations that determine the background noise level for plants in the field. Both raise the noise level over the whole frequency scale, but low frequencies increase more in intensity than high frequencies (Barth *et al.*, 1988; S. Bacher *et al.*, unpublished data). Therefore high frequencies should be easier to detect than low frequencies in a noisy environment. Because *Landing*, *Take-off* and *Probing* produce the highest frequencies, these are the parasitoid behaviours that are most likely to be detected by a leafminer in the field.

Producing vibrations which might originate from other sources would be another strategy for vibratory inconspicuousness (e.g. vibratory camouflage: Barth *et al.*, 1988). Such unspecific signals have a low reliability and therefore should not elicit evasive behaviours in the leafminer. *Landing, Take-off, Moving* and *Standing* are behaviours not specific to a parasitoid. Many insects show these behaviours. We assume that vibrations elicited during these behaviours by other insects are very similar to vibrations elicited by *S.sericeicornis* during the same behaviour. This is supported by studies on ants moving on apple leaves (S. Bacher *et al.*, unpublished data). Furthermore, waterdrops falling on apple leaves (simulated rainfall) produce vibrations with similar temporal and frequency pattern as *Landing* and *Take-off* (S. Bacher *et al.*, unpublished data). Therefore we expect no behavioural response of leafminers tuned to vibrations triggered by *Landing, Take-off, Moving* and *Standing*. *Probing* is the only behaviour that is characteristic of parasitoids. Vibrations triggered by a probing parasitoid were clearly distinct from vibrations triggered by other behaviours with respect to density and frequency content. Vibrations of high intensity were measured almost every time a parasitoid probed and occurred often on a shorter time scale during *Probing*. Therefore, in addition to their high detectability, vibrations triggered during *Probing* offer reliable signals through which a leafminer could detect the presence of a parasitoid. In a recent study R. Meyhöfer *et al.* (in preparation) showed that the insertion of the ovipositor without touching the host had indeed a marked influence on the behaviour of leafminer larvae, whereas other behaviours of the parasitoid did not elicit a behavioural response.

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