



# Eavesdropping on sexual vibratory signals of stink bugs (Hemiptera: Pentatomidae) by the egg parasitoid *Telenomus podisi*

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Males and females of the Neotropical brown stink bug, *Euschistus heros*, communicate with vibratory songs transmitted through plants. In this study, we examined the responses of the egg parasitoid *Telenomus podisi* to vibratory signals of these bugs. *Telenomus podisi* females responded with orientated movements to the vibratory signals of female songs on plants and on an artificial substrate, whereas male songs, duets or continuous pure tone vibratory signals failed to elicit any response. In addition, *T. podisi* females had a higher turning rate when stimulated with female songs, indicating some effect on their kinetic behaviour. This is the first demonstration of a parasitoid eavesdropping on the sexual vibratory signals of insects. The potential mechanism of this directionality and its adaptive significance are discussed.

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Animal communication is the exchange of information between individuals. In this exchange, one individual (signaller) transmits information to others (receivers), with both signaller and receivers being expected to benefit (Greenfield 2002). Sexual communication in particular is characterized by the use of conspicuous, long-range, nondirectional signals (Mougeot & Bretagnolle 2000) that can be intercepted by eavesdroppers to extract information. Unintended or 'illegitimate' receivers can be competitors, predators or parasites (Burk 1982; Zuk & Kolluru 1998; Mougeot & Bretagnolle 2000; Deecke et al. 2005).

Signals that are used for sexual communication can also be used by predators and parasitoids to locate prey/hosts, thereby increasing the risk of mortality for the signaller, especially for males, which are the main signallers (Burk 1982). This exploitation has been well documented for

insects and birds that use visual signals, for arthropods, reptiles, birds and mammals (bats and opossums) that use acoustic signals and for insects (parasitoids and predators) that use chemical signals (Zuk & Kolluru 1998 and references therein; Mougeot & Bretagnolle 2000; Müller & Robert 2002).

Predation pressure can have important implications for the evolution of prey communication. Antipredatory behaviour, especially in acoustic communication, includes the production of signals when predators are not active, a reduction in the duration of calling, the cessation of calling when predators are present or singing in choruses (Ryan et al. 1981; Zuk & Kolluru 1998; Mougeot & Bretagnolle 2000). Other forms of antipredatory behaviour can include changes in signal characteristics (Verrel 1991; Rotenberry et al. 1996), switching from an advertisement call to a lower-intensity courtship call (Greenfield 2002) and supplementing acoustic communication or shifting towards substrate-borne vibratory communication (Belwood & Morris 1987).

In parasitoids, which are known to eavesdrop on the chemical and acoustic signals of their hosts, host location includes several steps that are mediated by different types of cues. Chemical cues are used mainly

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on a long-range scale (Vinson 1985; Godfray 1994), whereas over short distances, visual and mechanical cues may also be included (Vinson 1985; Godfray 1994). This information can be used separately, hierarchically or in a combined, integrated multimodal signal (Fischer et al. 2001).

To date, there are no records of parasitoids eavesdropping on the substrate-borne vibratory communication of insect hosts. However, several reports have shown that some species of parasitoid wasps (Braconidae, Eulophidae and Pteromalidae) locate their hosts, such as miners, stem and fruit borers, seed predators and litter dwellers that live in concealed habitats, by using the vibrations produced during host movement, foraging or other activities (Meyhöfer et al. 1997; Meyhöfer & Casas 1999; Broad & Quicke 2000; Vilhelmsen et al. 2001). Additionally, some orussid (Vilhelmsen et al. 2001) and ichneumonid (Wäckers et al. 1998; Broad & Quicke 2000) parasitoid wasps use echolocation to find their hosts.

Egg parasitoids, especially *Telenomus* spp. and *Trissolcus* spp. (Hymenoptera: Scelionidae), are the most common natural enemies of pentatomid bugs. These parasitoids use chemical signals from plants (Colazza et al. 2004; Moraes et al. 2005b) and cues from host chemical communication (Mattiacci et al. 1993; Medeiros et al. 1997; Borges et al. 1998; Colazza et al. 1999; Conti et al. 2003) for long-range orientation, whereas chemical and visual cues are used for short-range orientation and host selection (Sales et al. 1980; Bin et al. 1993; Borges et al. 1999, 2003; Colazza et al. 1999; Conti et al. 2003). The use of vibratory signals for host location has not yet been demonstrated for any scelionid parasitoid.

Stink bugs (Hemiptera: Pentatomidae) communicate with substrate-borne vibratory signals during mating. Species- and sex-specific songs have been described in several species (Čokl & Virant-Doberlet 2003; Gogala 2006), and different vibratory songs have recently been described and correlated with reproductive behaviour in the Neotropical species *Acrosternum impicticorne* (Stål), *Euschistus heros* (F.), *Piezodorus guildinii* (Westwood) and *Thyanta perditor* (F.) (Moraes et al. 2005a).

Vibratory communication may have evolved in response to predation pressures (Henry 1994), and may be a strategy that prevents the hosts from being perceived by predators (Belwood & Morris 1987). However, specialized natural enemies (such as scelionid egg parasitoids in stink bugs) can evolve mechanisms to breach this gap and use these signals to search for hosts.

In this work, the hypothesis that the scelionid wasp *Telenomus podisi* (Ashmead) uses the vibratory signals of pentatomid bugs when searching for hosts was tested using the vibratory songs of the Neotropical brown stink bug, *Euschistus heros* (F.). In addition, we also examined the influence of a gradient in signal intensity on the movement of the wasps to the source of vibration. We chose *E. heros* because it is the main host of *T. podisi* (Corrêa-Ferreira & Moscardi 1995; Medeiros et al. 1997; Corrêa-Ferreira 2002) and it is the main soybean pest in Brazil (Panizzi & Rossi 1991).

## METHODS

### Insects

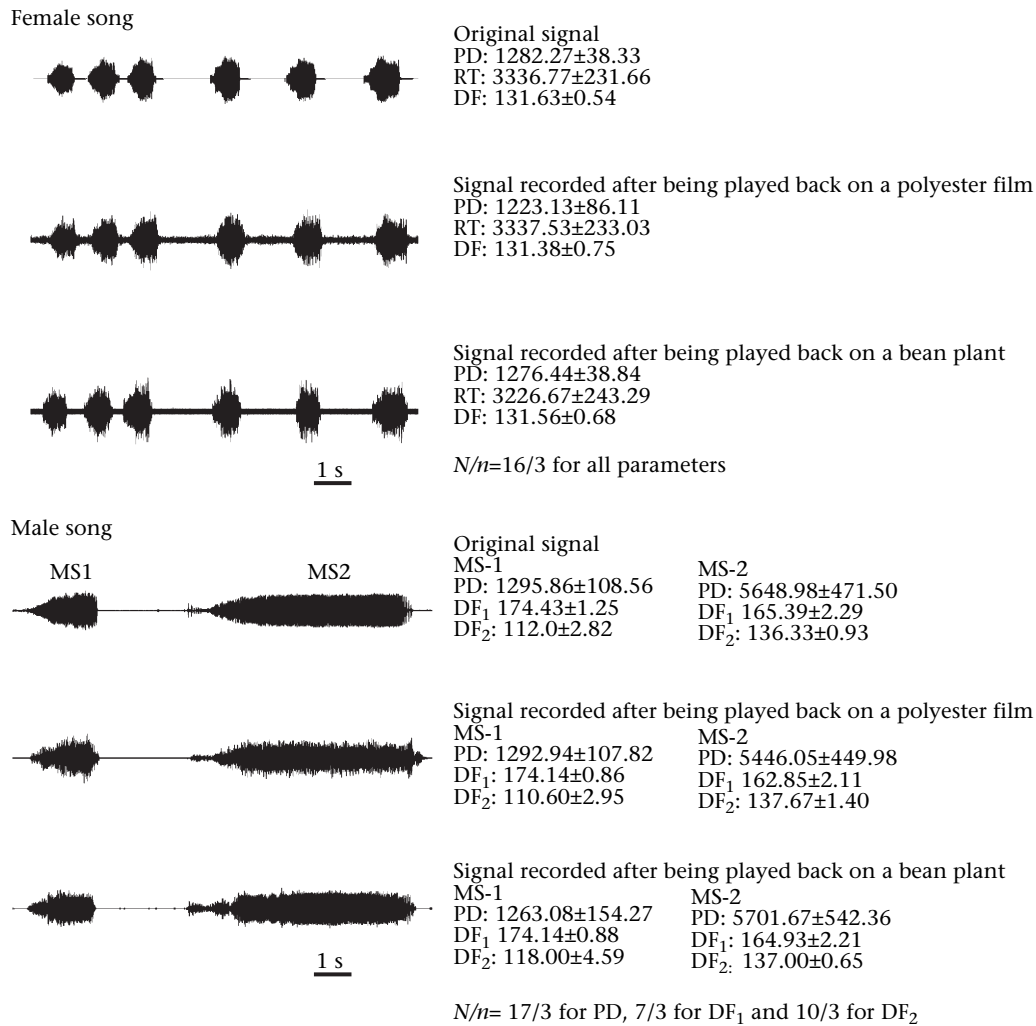
Individuals of *T. podisi* were obtained from a laboratory colony started from adults collected near the Embrapa Genetic Resources and Biotechnology Laboratory in Brasilia, DF, Brazil (15°47'S, 47°55'W). The insects were maintained in an environmental chamber in plastic cages (25-cm<sup>2</sup> angle-necked tissue culture flasks; ICN Biomedicals, Irvine, California, U.S.A.). Host (*E. heros*) eggs were glued onto cardboard strips and exposed to parasitoids for 24 h and then removed and placed in glass tubes (7.5 × 1.3 cm) for incubation. Before their use in the bioassays, adult parasitoids were housed for 24–48 h in plastic cages to allow mating.

Nymphs and adults of *E. heros* were reared on sunflower seeds (*Helianthus annuus* L.), soybeans (*Glycine max* (L.) Merrill), raw peanut seeds (*Arachis hypogaea* L.) and green beans (*Phaseolus vulgaris* L.) in separate containers. The eggs were collected daily and kept separately in petri dishes until eclosion. Both insect species were reared on a 14-h photophase at 26.0 ± 1°C and 65 ± 10% relative humidity.

### Vibratory Signals

Parasitoids were stimulated artificially by continuous, pure-tone signals of 130 Hz (artificial signal) produced with Sound Forge 4.5 software (Sonic Foundry Inc., Madison, Wisconsin, U.S.A.) and by pre-recorded, naturally produced songs obtained from virgin and sexually mature *E. heros* adults, 15–25 days after the final moult (Costa et al. 1998). Female songs, male songs and duet songs were used. Five recordings of each song type obtained from different individuals were used in the experiments and each song was used in at least 5–10 bioassays. Control tests using no stimulus (no vibration) were also done.

Naturally produced *E. heros* songs were recorded from bugs singing on a nonresonant loudspeaker membrane and the signals captured by the loudspeaker were digitalized (Aardvark-Direct Pro 24/9; Aardvark Computer Systems, Ann Arbor, Michigan, U.S.A.) and stored on a computer using CoolEdit Pro software (Syntrillium Software 2001, Fort Wayne, Indiana, U.S.A.). The female stimulatory song consisted of short pulses (median pulse duration of 948 ms; Moraes et al. 2005a) in which a female started vibratory communication (females song 1, FS1, as defined by Moraes et al. 2005a). In contrast, male stimulatory song consisted of two types of male songs: male song 1 (MS1), which was characterized by short pulses with a mean pulse duration of 1756 ms, and male song 2 (MS2), which was characterized by long pulses with a mean pulse duration of 4407 ms (Moraes et al. 2005a). Male songs were normally produced in response to female pulses, and male song pulses were characterized by two spectral peaks within the dominant frequency domain (Fig. 1). A duet stimulatory song consisted of female song pulses that alternated with or were often superimposed between short (MS1) and long (MS2) male pulses that were produced in an irregular pattern.



**Figure 1.** Representative oscillograms, temporal characteristics and dominant frequency (mean  $\pm$  SE) of the original signals used in the bioassays and of the signals recorded from polyester film and bean plants after being played back. The oscillograms represent six pulses of a female song and one pulse of male song 1 (MS1, as defined by Moraes et al. 2005a) and one pulse of male song 2 (MS2, as defined by Moraes et al. 2005a). PD: pulse duration; RT: repetition time; DF: dominant frequency. Original song: signal recorded from females or males, as described in Methods. Polyester film: signals recorded on polyester film at 1 cm from the point of emission. Bean plants: signal recorded on the leaf of a bean plant at 1 cm from the point of emission. For recording, the original signals were played back using the set-up condition of the bioassays described in Methods and an iron-carbon wire was used to transmit the vibratory signal from the recording point to a loudspeaker acting as a microphone.  $N$  = number of pulses,  $n$  = number of signals (individuals).

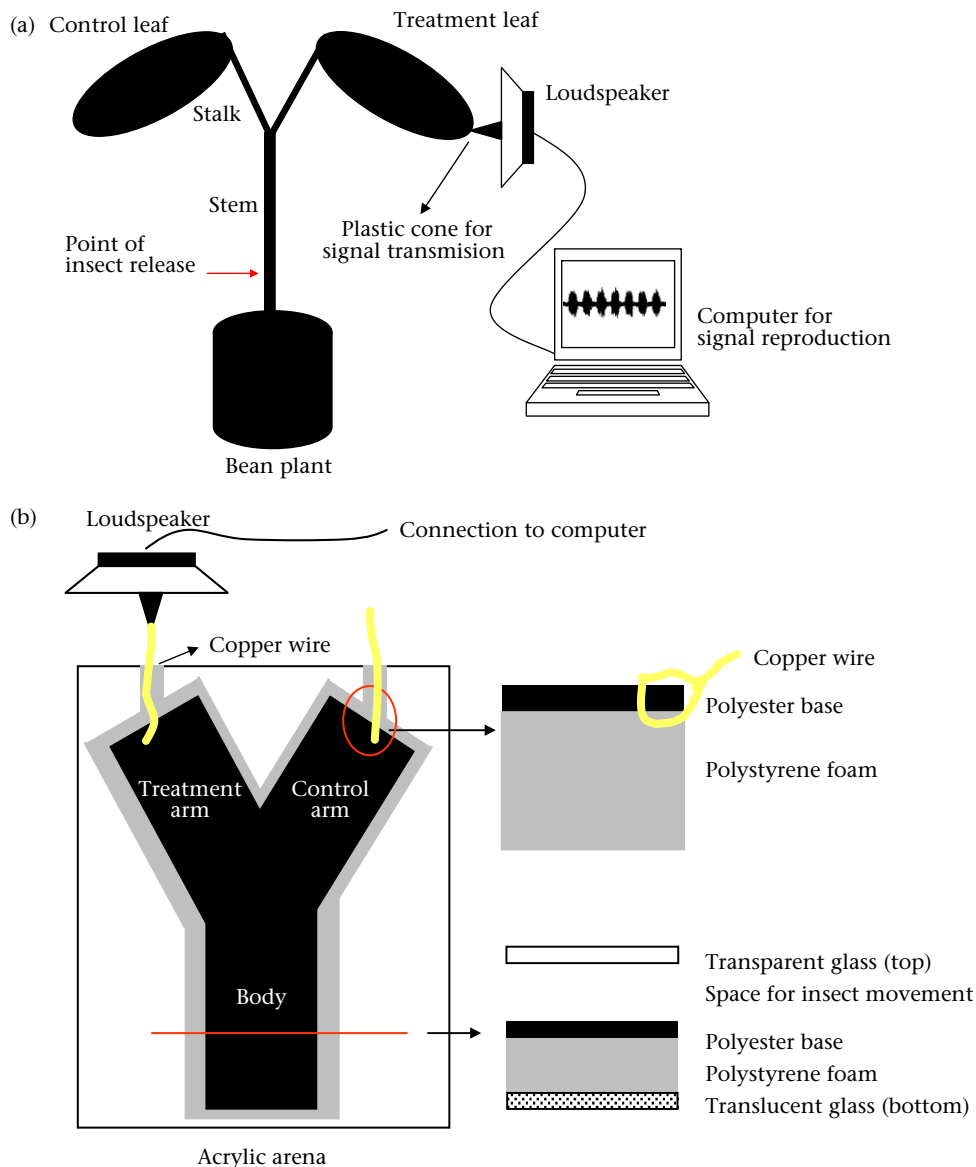
## Transmission of Vibratory Signals

The movement of the parasitoids in the absence (control) and presence (treatment) of substrate vibration was tested on green beans (*P. vulgaris*) and on polyester film (printer film). Green bean plants were chosen because they represent a natural medium for transmission. On the other hand, the use of polyester film coupled to an arena allowed the parasitoid movement to be monitored with a video-tracking system (S. Colazza, D. Peri, E. Peri, M. Lo Pinto & G. Liotta, unpublished data), with subsequent detailed analysis of the parasitoid behaviour. Compared to plants, the greater homogeneity of artificial substrates helps to reduce the variability in bioassays.

For tests on natural substrates, we used green bean plants that were 20–30 cm tall with two completely expanded opposite leaves. The plants were divided into

three regions: treatment area (vibrated leaf + stalk), control area (nonvibrated leaf + stalk) and stem (area below the point at which the stalks crossed). The treated area of each plant was vibrated with a plastic cone (plastic pipette tip, 50 mm long and 5.5 mm wide at the base) glued with instant adhesive to the middle of a low–midrange loudspeaker (4 inches (10.2 cm) in diameter, frequency response of 40–6000 Hz, impedance 8  $\Omega$ ; Radioshack FE103, Taiwan) and placed in contact with the leaf to be treated (Fig. 2a).

Additional tests were done on an artificial substrate in an arena constructed with a modified Y-shaped olfactometer. The arena consisted of an acrylic block (27.5  $\times$  21.0 cm) containing a Y-shaped cavity that had a 9-cm-long body with a release area at the end and two 8-cm-long arms with an internal diameter of 1.5 cm placed at an angle of 130° (Fig. 2b). The arena was placed



**Figure 2.** Schematic diagram of the experimental set-up for the plant (a) and arena (b) bioassays. See text for dimensions and particular characteristics of the materials.

on top of a translucent glass plate and covered with transparent glass. The insects moved on the polyester film, which was placed over moulded polystyrene foam (4 mm thick) in the Y-cavities of the olfactometer. The polyester film was vibrated by a 3-cm-long copper wire attached to the treatment arm on one side and connected to the plastic cone glued to the loudspeaker membrane, as described above. The other arm was conditioned with a copper wire that was not fixed to a plastic cone (control arm) (Fig. 2b).

The signals used in the bioassays were played back and recorded from bean leaves or polyester membrane to determine whether the vibratory signals reproduced in the two experimental set-ups were similar to natural songs. To do this, one of the ends of a fine steel-carbon wire (5 × 0.5 mm) was attached to the vibratory polyester

membrane with adhesive paper strips or placed in contact with the vibratory leaf of the bean plant (in each case, 1 cm away from the point of emission) and the other end was attached with an adhesive paper strip to a nonresonant loudspeaker membrane that served as a microphone. Vibratory signals played back through each experimental set-up were captured by this loudspeaker, digitalized and stored as described above, then compared with those of natural songs.

To test the hypothesis that a gradient in signal intensity contributes to the directional movement of the parasitoids, we measured the signal intensity (expressed as peak velocity values) at different distances from the source of female and male songs and a 130-Hz pure tone signal (artificial signal) transmitted through natural (green bean) or artificial (polyester film) substrates. Duet

songs were not tested because male and female pulses overlapped.

The vibrations were recorded with two laser vibrometers (OFV-353 sensor head and OFV-2200 controller and PDV 100; Polytec, Waldbronn, Germany) simultaneously at the point of vibration (reference point) and at different distances from this point. The difference between simultaneously recorded signals at peak velocity was expressed in decibels and correlated with the distance from the source.

## Bioassays

### General procedures

All of the bioassays were done between 0800 and 1700 hours in a sound-insulated chamber with artificial illumination (four 40-W fluorescent lamps) at  $26 \pm 1^\circ\text{C}$  and a relative humidity of  $65 \pm 10\%$ .

The vibration of the left or right leaf/arm was alternated every three replicates to avoid any positional bias, and the stimulus signals (female song, male song, duet song, artificial signal and no stimulus) were changed periodically. The intensity of stimulation was adjusted to the level of *E. heros* emissions recorded on the same loudspeaker using a home-made operational amplifier TL081CN ([www.mouser.com](http://www.mouser.com)). The signals were played back continuously for 10 min throughout the bioassay.

Insects used in bioassays were naïve *T. podisi* females that were 24–48 h old. Each female was used in one bioassay and then discarded.

### Plant bioassays

We released one insect on the stem just above the hypocotyls and observed it for 10 min using a manual chronometer. We measured the time that the females spent on the plant (searching time) and the percentage of time that they spent moving (activity). We also recorded the number of plant areas visited by each female, the first area that the insect entered and remained in for more than 10 s (first-choice area) and the percentage of the total time that the insect spent in each area of the plant (residence time). Tests were done with vertically or horizontally positioned plants to avoid any possibility that geotropism influenced the interpretation of behaviour. We conducted 20–40 replicates for each song in each plant position. Insects that did not move beyond the release point or that did not choose an area after 5 min were scored as nonresponders.

### Arena bioassays

We released one insect in the release area of the arena and recorded its movements from above using a video system with a monitor (Sony SSM-14N5E) connected to a monochromatic CCD camera (Sony SPT M324CE) fitted with a 12.5–75.0 mm/F1.8 zoom lens. A video frame grabber (PC-Studio PCTV Pinnacle System) digitalized the analogue video signals from the camera, and the data were processed with Xbug software (Colazza et al., unpublished data). This software records and processes the position of the insect at preset time intervals and allows the analysis

of different behavioural parameters (e.g. residence time, linear velocity, turning rate and tortuosity). The use of Xbug software in conjunction with our experimental set-up for artificial substrates allowed the detailed analysis of behavioural parameters that could not be studied in natural substrate (plant) bioassays because our system was unable to capture and process parasitoid images in three dimensions.

Insect movement and behaviour were monitored and analysed by computing the first-choice area and residence time, as defined above. We analysed the data for linear velocity (mm/s), turning rate (number of directional changes/s) and tortuosity of insects that moved in the two choice arms of the olfactometer (treatment and control) using the Xbug software. Tortuosity was measured using the tortuosity index, which quantifies insect kinetic movement by the formula:  $T = 1 - mp/tl$ , where *mp* is the projection of the track in the general straight line of the plant, and *tl* is the total length of the track (Borges et al. 2003). The index varies from 0 (zero) for minimal tortuosity to 1 (one) for maximal tortuosity.

We performed 20–25 replicates for each vibratory stimulus. Insects that did not move beyond the release point or that did not choose an area after 5 min were scored as nonresponders. Insects (6 of 128) that moved onto the walls or upper glass of the arena were also excluded. The apparatus was cleaned with fragrance-free liquid soap, rinsed thoroughly with water, and dried after every six replicates.

## Statistical Analyses

We compared the mean values of the temporal and spectral parameters of original songs and of songs captured during playback in each experimental set-up using Student's *t* tests or Mann–Whitney *U* tests (for variables without a normal distribution). We compared the mean search time, activity and number of areas visited in response to each signal in each experiment using Kruskal–Wallis tests because the data were not normally distributed, and we used Dunn's test ( $P < 0.05$ ) to compare the means. We analysed the data for the first-choice area (considering only insects that reached the treatment or control areas) in each set of bioassays (e.g. female songs in horizontal plants or male songs in the arena) using the chi-square test, and we used the Mann–Whitney *U* test to compare the residence time in the treatment and control areas. Student's paired *t* test was used to compare the mean linear velocities, turning rate and tortuosity index in the treatment and control arms of the arena for each signal (only insects that entered the two areas of the arena during the bioassays were used for these calculations). All statistical analyses were done using SigmaStat 2.0 (SYSTAT Inc., Richmond, California, U.S.A.).

## RESULTS

### Transmission of Vibratory Signals

Signal parameters recorded from artificial or natural substrates did not differ significantly from those of



original signals, verifying that the signals that were played back were faithfully reproduced in both experimental set-ups (Fig. 1). In addition, the transmission efficiency of the general set-up for the plant experiments was consistent with that of previous studies (e.g. Ćokl et al. 1999). Temporal and spectral characteristics of the signals used in the bioassays also did not differ significantly from those described by Moraes et al. (2005a); see Table 1.

For vibration signals on bean substrates, the intensity of the signals (expressed in terms of velocity) did not decrease linearly with increasing distance, but showed repeated peaks of minimal and maximal values at regular distances from the point of vibration (Fig. 3a). The peak values for minimal velocity for all three stimuli (FS, MS, 130-Hz pure tone signal) could be measured on the stem about 6–12 cm from the point of vibration, with mean values of approximately 15–20 dB below the input velocity (reference value at the source) (Fig. 3a). In contrast, the peak values for maximal velocity reached the reference value on the stem at about 9 cm from the source (Fig. 3a). The signal velocity recorded on the vibrated stalk remained around 5 dB below the reference value at both measuring points, while on the opposite side (nonvibrated stalk), it was 10–20 dB below the reference value at the most distal recording point (~7 cm) (Fig. 3b).

The velocity of the vibratory stimuli decreased linearly with increasing distance from the measuring point on the vibrated arm of the polyester film (3–4 cm from the vibration source) to the most proximal measuring point on the body of the polyester film (~6 cm from the point of vibration; Fig. 3c) or on the opposite (nonvibrated) arm of the polyester film (~6 cm from the point of vibration; Fig. 3d). On the vibrated arm, the mean values of the vibratory signals exceeded the input signals by about 10 dB (Fig. 3c, d). At distances greater than 7 cm from the source, the velocity of the stimulus was approximately similar to the level of background noise (Fig. 3c, d). The velocity

gradient was about 7.5 dB/cm between the vibrated arm and the body of the Y (Fig. 3c) and about 10 dB/cm between the vibrated and nonvibrated (opposite) arms (Fig. 3d). This gradient could not be measured in bean substrate. The intensity gradients showed the same pattern for the three types of vibratory signals evaluated (Fig. 3).

## Plant Bioassays

*Telenomus podisi* females showed significant differences in their choices between vibrated (treatment) and nonvibrated (control) areas of plants only in bioassays with female songs. Regardless of plant orientation, the parasitoids chose leaves vibrated with female songs more often than they did control leaves (chi-square test: vertical plants:  $\chi^2_1 = 33.78$ ,  $P < 0.001$ ; Fig. 4a; horizontal plants:  $\chi^2_1 = 18.65$ ,  $P < 0.001$ ; Fig. 4c). There were no significant differences in the choices of females in any of the other treatments, regardless of plant orientation.

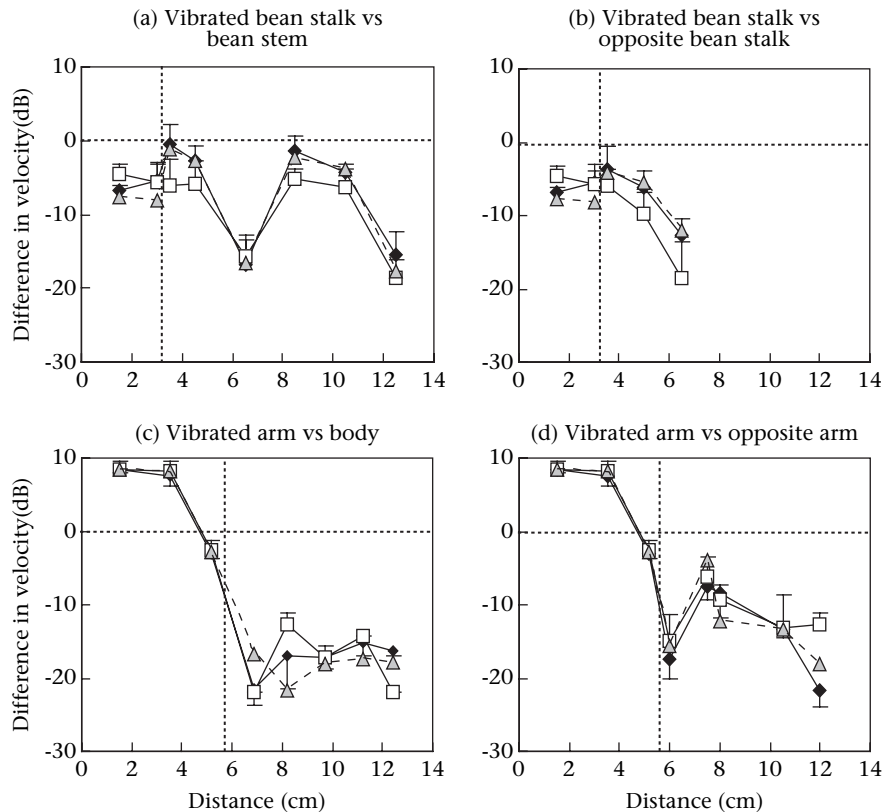
The residence time on leaves vibrated with female songs was also significantly greater than that for nonvibrated (control) leaves on vertical plants (Mann–Whitney  $U$  test:  $U = 1855.5$ ,  $N_1 = N_2 = 37$ ,  $P < 0.001$ ) and on horizontal plants ( $U = 1319.5$ ,  $N_1 = N_2 = 31$ ,  $P < 0.001$ ). Compared to the controls, there were no differences in the residence times when other signals were used to vibrate the leaves of plants in either position (Fig. 4b, c).

The responsiveness of female parasitoids was influenced by different treatments. Although the experimental design did not allow detailed analyses of the responsiveness of parasitoids among treatments, more females were unresponsive in control (no stimulus) conditions involving vertical and horizontal plants (36.1% and 35.3% of the insects tested, respectively) and in the artificial signal treatment involving horizontal plants (40.7% of the insects tested) than in the other treatments (<15% of the insects tested) (Fig. 4a, c).

**Table 1.** Comparison of temporal and spectral characteristics (mean  $\pm$  SD) of the *E. heros* signals used in the bioassays and those previously described by Moraes et al. (2005a)

| Signals | Pulse duration (ms) (N/n) | Repetition time (ms) (N/n) | Dominant frequency (Hz) (N/n) |
|---------|---------------------------|----------------------------|-------------------------------|
| FS      |                           |                            |                               |
| A       | 948 $\pm$ 183 (79/5)      | 3566 $\pm$ 1043 (74/5)     | 145 $\pm$ 7 (77/5)            |
| B       | 989 $\pm$ 221 (30/5)      | 3548 $\pm$ 2245 (34/5)     | 143 $\pm$ 7 (35/5)            |
| MS1     |                           |                            |                               |
| A       | 1756 $\pm$ 598 (40/5)     | 4378 $\pm$ 1046 (36/5)     | 137 $\pm$ 12 (173/9)          |
| B       | 1705 $\pm$ 2631 (12/3)    | ND                         | 173 $\pm$ 9 (37/5)            |
|         |                           |                            | 136 $\pm$ 3 (12/3)            |
|         |                           |                            | 173 $\pm$ 3 (12/3)            |
| MS2     |                           |                            |                               |
| A       | 4407 $\pm$ 582 (20/3)     | ND                         | 136 $\pm$ 13 (20/3)           |
| B       | 5123 $\pm$ 1661 (37/5)    | ND                         | 172 $\pm$ 9 (20/3)            |
|         |                           |                            | 137 $\pm$ 9 (37/5)            |
|         |                           |                            | 169 $\pm$ 5 (37/5)            |

$N$  = number of pulses;  $n$  = number of individuals; FS: female signal; MS1: pulses of male signal, as defined by Moraes et al. (2005a); MS2: pulses of male signal, as defined by Moraes et al. (2005a); A: data from Moraes et al. (2005a); B: data from signals used in the bioassays of this work; ND: not determined. There were no significant differences between the values (A and B) of a given parameter for any signal (paired  $t$  tests:  $P > 0.05$ ).



**Figure 3.** Differences in velocity (dB) between the vibratory signals recorded simultaneously on bean plants (a, b) and polyester film (c, d). Velocity gradients are shown for two points, one at the site of vibration (bean stalk or arm of polyester membrane) and the other at an opposite point: (a) bean stem, (b) opposite bean stalk, (c) body of the polyester film, (d) opposite arm of the polyester film. Points are means  $\pm$  SE. ◆: female song; □: male song; △: continuous pure tone vibration. Horizontal dotted lines indicate the reference values for velocity. Vertical dotted lines indicate the crossing points between the vibrated stalk and nonvibrated stem or stalk of bean plants and between the vibrated arm and nonvibrated body or arm of the polyester film.

The general searching behaviour of the parasitoid females was similar when the insects were stimulated with different vibratory signals (Table 2). Significant differences were seen only in the level of activity between artificial signals and no-stimulus situations and in the number of areas visited between male songs and duet songs in vertical plant bioassays. When in movement, the parasitoid females showed the searching behaviour typical of scelionid wasps, which involves antennating the substrate (Colazza et al. 1999; Borges et al. 2003); when they reached the chosen area (i.e. the point of dichotomy on the stalks), the wasps stopped for a few seconds before choosing one side.

### Arena Bioassays

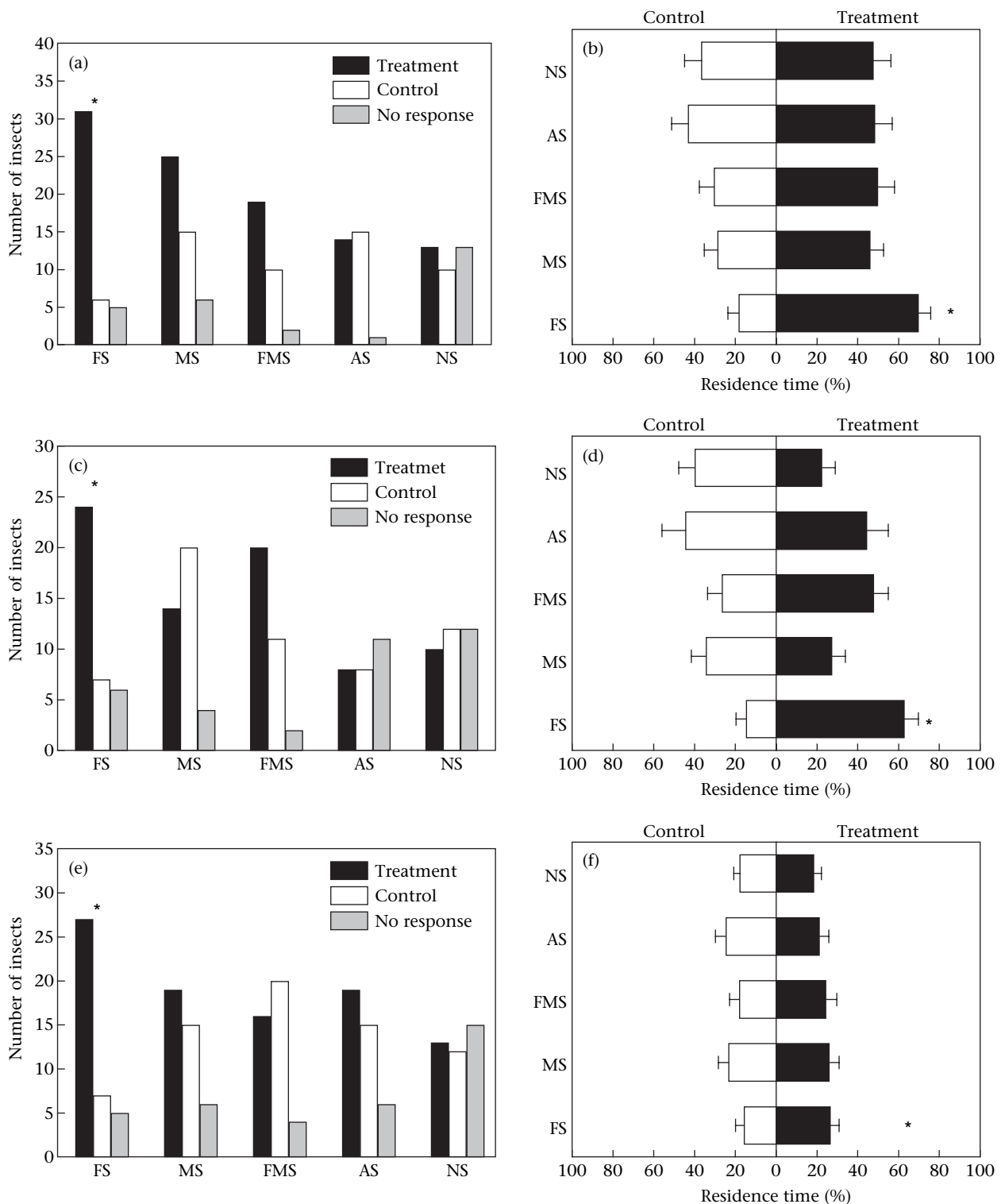
The vibration of polyester film triggered the same behavioural pattern in the parasitoids as described above for plants. When the substrate was vibrated with female songs, *T. podisi* females were significantly more attracted to the stimulated side (chi-square test:  $\chi^2_1 = 23.53$ ,  $P < 0.001$ ; Fig. 4e) and spent significantly more time there than on the opposite arm (Mann–Whitney *U* test:  $U = 897.0$ ,  $N_1 = N_2 = 34$ ,  $P < 0.001$ ; Fig. 4f). The residence times in the chosen areas were generally lower in the arena bioassays than in the plant bioassays (Fig. 4b, d, f).

Automatic tracking analyses of the behavioural parameters showed that linear velocity and tortuosity of movements of *T. podisi* females did not differ between the control and treatment areas, and turning rate was significantly higher in the treatment area only when the parasitoid was stimulated with *E. heros* female songs (paired *t* test:  $t_{24} = 2.34$ ,  $P = 0.03$ ; Fig. 5).

*Telenomus podisi* females were generally more active in the arena bioassays than in the plant bioassays. The mean number of areas visited in the arena bioassays ( $4.17 \pm 2.57$ ,  $N = 128$ ) was significantly greater than that in the plant bioassays (vertical plants:  $2.44 \pm 1.28$ ,  $N = 181$ ; horizontal plants:  $2.65 \pm 1.38$ ,  $N = 166$ ; Kruskal–Wallis test:  $H_2 = 64.52$ ,  $P < 0.001$ ; Dunn's test:  $P < 0.05$ ). However, only parasitoids' responses to male songs and artificial signals differed significantly in the arena experiments (Table 2). In experiments in which there was no stimulus (no signal), 37.5% of the insects tested did not respond, whereas in the treated groups, this percentage was less than 15%.

### DISCUSSION

During mating behaviour, stink bugs communicate using species- and sex-specific chemical (McBrien & Millar 1999)



**Figure 4.** Searching behaviour of *T. podisi* females on natural (plants) and artificial (polyester film) substrates. Bars indicate the number of insects that entered and remained in each area (leaf or arm) for more than 10 s (first choice) and the mean  $\pm$  SE percentage of total time spent in each area (residence time). (a) First choice in bioassays with vertical bean plants, (b) residence time in bioassays with vertical bean plants, (c) first choice in bioassays with horizontal bean plants, (d) residence time in bioassays with horizontal bean plants, (e) first choice in arena bioassays and (f) residence time in arena bioassays. \*Indicates a significant difference between the control and treated groups (chi-square test for first choice, Mann–Whitney *U* test for residence time,  $P < 0.05$ ). Treatment: leaf or arm of arena with stimulus (vibratory signal); control: leaf or arm of arena without stimulus; FS: female song; MS: male song; FMS: duet song; AS: artificial signal (130 Hz); NS: no signal.



**Table 2.** General behavioural parameters (mean  $\pm$  SE) for searching by *T. podisi* in the plant and arena bioassays

|                         | Searching time (s) | Activity (% time)               | Number of areas visited       | N  |
|-------------------------|--------------------|---------------------------------|-------------------------------|----|
| <b>Vertical plant</b>   |                    |                                 |                               |    |
| FS                      | 433.22 $\pm$ 31.92 | 44.56 $\pm$ 6.15 <sup>ab</sup>  | 2.49 $\pm$ 0.19 <sup>ab</sup> | 37 |
| MS                      | 438.70 $\pm$ 31.80 | 49.58 $\pm$ 5.71 <sup>ab</sup>  | 2.10 $\pm$ 0.10 <sup>a</sup>  | 40 |
| FMS                     | 524.10 $\pm$ 24.43 | 75.14 $\pm$ 14.78 <sup>ab</sup> | 3.17 $\pm$ 0.31 <sup>b</sup>  | 29 |
| AS                      | 485.03 $\pm$ 31.93 | 39.32 $\pm$ 29.61 <sup>a</sup>  | 2.83 $\pm$ 0.45 <sup>ab</sup> | 29 |
| NS                      | 392.09 $\pm$ 35.06 | 67.43 $\pm$ 6.35 <sup>b</sup>   | 2.21 $\pm$ 0.10 <sup>ab</sup> | 23 |
| <b>Horizontal plant</b> |                    |                                 |                               |    |
| FS                      | 422.45 $\pm$ 38.63 | 40.82 $\pm$ 6.59                | 2.32 $\pm$ 0.20               | 31 |
| MS                      | 433.12 $\pm$ 41.47 | 39.66 $\pm$ 4.92                | 2.71 $\pm$ 0.24               | 34 |
| FMS                     | 405.45 $\pm$ 40.42 | 54.63 $\pm$ 6.65                | 2.77 $\pm$ 0.22               | 31 |
| AS                      | 421.52 $\pm$ 43.09 | 37.00 $\pm$ 8.67                | 2.50 $\pm$ 0.40               | 16 |
| NS                      | 421.21 $\pm$ 60.43 | 56.25 $\pm$ 6.73                | 3.28 $\pm$ 0.35               | 22 |
| <b>Arena</b>            |                    |                                 |                               |    |
| NA                      | NA                 | ND                              | 4.11 $\pm$ 0.38 <sup>ab</sup> | 27 |
| MS                      | NA                 | ND                              | 3.14 $\pm$ 0.31 <sup>a</sup>  | 21 |
| FMS                     | NA                 | ND                              | 3.83 $\pm$ 0.31 <sup>ab</sup> | 30 |
| AS                      | NA                 | ND                              | 5.40 $\pm$ 0.51 <sup>b</sup>  | 32 |
| NS                      | NA                 | ND                              | 4.53 $\pm$ 0.69 <sup>ab</sup> | 18 |

FS: female song; MS: male song; FMS: duet song; AS: artificial signal (130 Hz); NS: no signal. Values for a given parameter with different superscript letters differed significantly within a particular experiment (Kruskal–Wallis test followed by Dunn's test:  $P < 0.05$ ). Searching time: time (in seconds) that parasitoid females spent searching the plant before flying away from it. Activity: percentage of time that parasitoid females spent moving when searching on plants. NA = not applicable; ND: not determined.

and substrate-borne vibratory signals. Vibratory signals provide information about species, sex, position on a plant and receptivity to mating (Čokl & Virant-Doberlet 2003; Gogala 2006). In addition, the vibratory signals produced by pentatomids are efficiently transmitted through the plant (Čokl et al. 2005) and can be used by natural enemies to obtain information about host presence and position.

Our results indicate that when *T. podisi* females were stimulated with songs of *E. heros* females, they showed an oriented response (taxis) towards the source of the vibratory emission, and differed significantly in their first-choice of areas and in their residence time in the chosen areas (leaves of plants or arms of the arena) that were vibrated. In addition, *T. podisi* females had a higher turning rate when stimulated with this song, indicating some effect on their kinetic locomotory behaviour.

To our knowledge, this is the first demonstration of a parasitic wasp eavesdropping on the sexual vibratory communication of its host. To date, information on the use of vibrations by parasitoids to locate hosts has been related to parasitoids using vibratory signals from general host activity such as feeding or locomotion (Meyhöfer et al. 1997; Meyhöfer & Casas 1999; Broad & Quicke 2000; Vilhelmsen et al. 2001) or vibratory signals produced by the parasitoid itself and used in echolocation (Wäckers et al. 1998; Broad & Quicke 2000; Vilhelmsen et al. 2001).

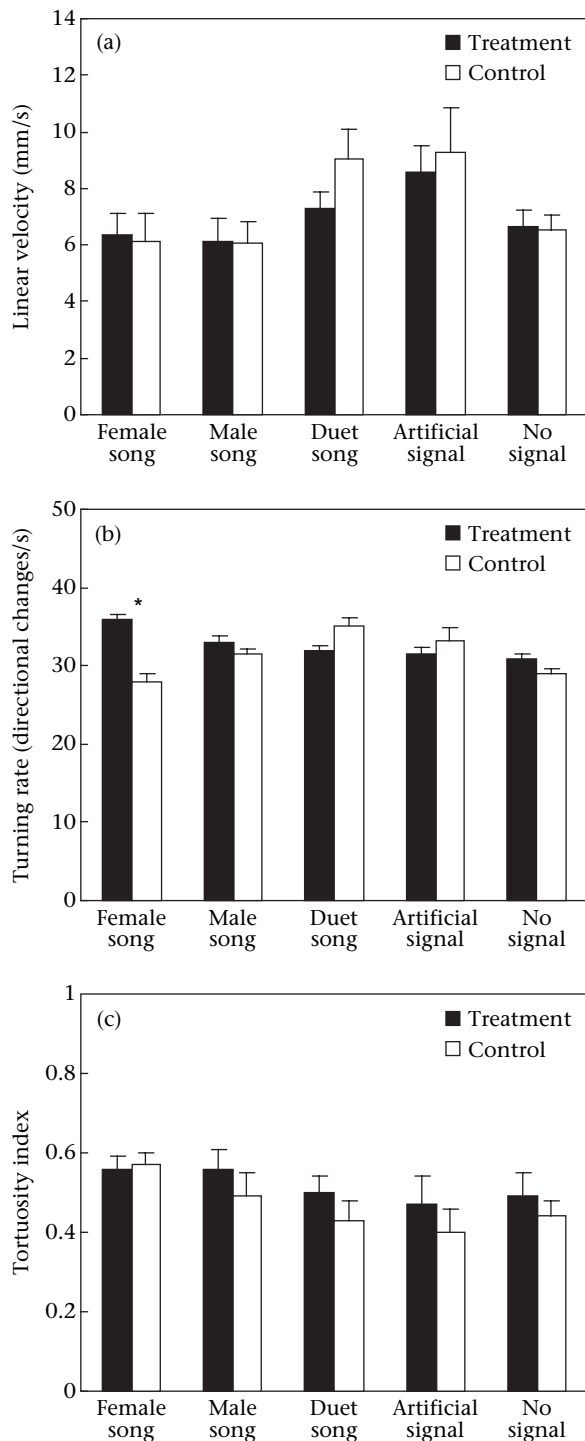
The experiments described here were not designed to test the preference for a particular song and it was not possible to conclude that *T. podisi* females preferred female vibratory songs over other *E. heros* songs. On the other hand, our results demonstrated a clear influence of *E. heros* female songs on the searching behaviour of *T. podisi* females. However, because of our experimental design

and the limited power of the statistical analyses, the influence of other *E. heros* songs cannot be discarded.

The underlying mechanism used by *T. podisi* females is not clear and requires further investigation. The use of vibratory signals for oriented movements (positive or negative taxis) has been described for various arthropods, including spiders (Barth 1998), fiddler crabs (Aicher & Tautz 1990), nocturnal scorpions (Brownell & Farley 1979) and insects such as stink bugs (Čokl et al. 1999). In the latter case, mate location mediated by substrate-borne signals was first demonstrated in *N. viridula* (Ota & Čokl 1991; Čokl et al. 1999). Pfannenstiel et al. (1995) reported that the predator *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae) can locate prey by the vibratory signals produced by chewing.

Movement towards the source of vibrations can be estimated by analysing the signal intensity and the time or phase difference of signal transmission through a substrate, from one spatially located receptor to another. The propagation of 100-Hz signals (such as those of *E. heros* and other pentatomid songs) in plants occurs at speeds of 10–100 m/s (Barth 1998). At this low velocity of propagation, the time delay between two points separated by a distance shorter than 1 mm, as in the case of *T. podisi* legs, would be well below the threshold of behaviourally determined responses in arthropods such as scorpions (Brownell & Farley 1979).

One way to find the source of vibrations is to follow the track of increasing signal intensity. This mechanism could work on a completely artificial substrate such as polyester film ( $\sim 6$  dB velocity difference per cm) or on plant parts such as the lamina of big leaves. But the mechanism cannot work in rod-like structures, such as plant stems and stalks, where the intensity of vibratory signals increases and decreases regularly with increasing distance (Čokl &



**Figure 5.** Behavioural parameters (mean  $\pm$  SE) for *T. podisi* females when searching the arms of an arena with (treatment) and without (control) a stimulus. (a) Linear velocity, (b) turning rate and (c) tortuosity index. \*Indicates a significant difference between the control and treatment (Student's paired *t* test:  $P < 0.05$ ).  $N_{\text{Female song}} = 24$ ,  $N_{\text{Male song}} = 16$ ,  $N_{\text{Duet song}} = 24$ ,  $N_{\text{Artificial signal}} = 18$ ,  $N_{\text{No signal}} = 11$ .

Virant-Doberlet 2003) because of the occurrence of standing waves (Michelsen et al. 1982). In addition, the mechanism of vibrational directionality described for the 9-mm-long treehopper *Umbonia crassicornis*, which

consists of a general vibration of the insect body (Crocoft et al. 2000), cannot be applied to 1-mm-long parasitoids. Despite the lack of an explanation for the underlying mechanism, *T. podisi* females may locate the source of vibration like some species of small insects (<1 cm) as Braconidae, *Choetospila elegans* (Pteromalidae) and *Leptopilina longipes* (Eucoilidae) that show taxis to vibratory stimuli (Meyhöfer & Casas 1999).

The anatomy of the vibrational sensory organs of parasitoids may be useful in understanding the underlying mechanism of vibrational directionality. The subgenual organ of hymenopteran parasitoids is more complex and contains more sensory cells than do subgenual organs of most other insects. In *Orussus* spp. (Hymenoptera: Orussidae), this organ is characterized by 400 scolopidia (Vilhelmsen et al. 2001), indicating that a precise analysis of vibratory signals can occur at the periphery of the sensory system. Sensitivity to substrate vibrations has also been described in five subfamilies of Ichneumonidae (Broad & Quicke 2000), but a subgenual organ with about 40 scolopidia has been described in only one species (Otten et al. 2002).

Variation in tissues and structures among plants of the same and different species could also affect the transmission of vibratory signals through the substrate and indirectly affect the parasitoid's ability to detect and use the stink bug vibratory signals. For example, *Pimpla turionellae*, a parasitoid that uses echolocation, is unable to locate its host in high-density substrates because of attenuation of vibrations (Fischer et al. 2003). In addition, since the transmission of signals through a plant may oscillate with minimal and maximal intensities, the position of a parasitoid on a given plant could also affect the parasitoid's ability to detect stink bug vibrations.

The adaptive value of eavesdropping on stink bug vibratory communication for *T. podisi* is unclear. Broad & Quicke (2000) suggested that the use of vibratory signals could allow parasitoids to locate concealed hosts, and similar reasoning could be applied to parasitoids that use host vibrations.

In *T. podisi*, the use of host vibrational signals does not appear to be directly adaptive since the parasitoids search for host eggs and vibratory signals are produced by adult female hosts. This behaviour does not fit with the model of host location proposed by Vet et al. (1990) in which the parasitoid should respond to the stimulus directly or in close association with the host. However, it does agree with the 'infochemical detour' hypothesis proposed by Vet & Dicke (1992), in this case cue detour, which involves mechanisms for overcoming the reliability-detectability problem.

For *T. podisi* and other Scelionidae (including *Trissolcus* spp.) that attack pentatomid eggs, plant synomones (Colazza et al. 2004; Moraes et al. 2005b) and host kairomones (components of sexual and alarm pheromones) (Mattiacci et al. 1993; Medeiros et al. 1997; Borges et al. 1998; Colazza et al. 1999; Conti et al. 2003) are used for habitat and host location during foraging behaviour. Other chemical and/or physical (visual and tactile) signals from eggs are used for host recognition and selection at short distances (<1 mm; Sales et al. 1980; Bin et al.

1993; Borges et al. 1999, 2003; Colazza et al. 1999; Conti et al. 2003).

The use of vibratory signals from *E. heros* females over intermediate distances (on the same plant) can be favoured because these cues are more conspicuous, and more detectable, than are chemical or visual cues from eggs. *Telenomus podisi* probably uses the vibratory signals of adult females to locate sites where there is a high probability of deposited eggs. This hypothesis may be particularly valid if stink bug females copulate and oviposit on the same plant, but it requires confirmation by field experiments.

Predation pressure can influence the evolution and modulation of mechanisms involved in propagation of airborne and substrate-borne signals used in communication. Possibly the best known cases are the anti-bat behaviour of moths and the emission of defensive sounds (Bailey 1991). The use of mechanical signals from the host for their location by parasitoids has been well documented for flies (Tachinidae) using cricket sounds (Cade 1975). In this case, song structure appears to be a decisive factor in the incidence of parasitism; crickets that produce longer pulses at the beginning of the song are parasitized more frequently than others (Zuk et al. 1998). In a more extensive study, Zuk et al. (2001) reported that populations of the cricket *Teleogryllus oceanicus* living on Pacific islands had songs with longer pulses than populations from the continent (Australia), and they associated this phenomenon with the reduced predation on the islands. A similar situation of natural enemy pressure may apply to relationships between stink bug and parasitoids since the calling songs of *E. heros* females have shorter pulses than do male songs (see Table 1). Although this is a plausible and valid hypothesis for some pentatomid species (McBrien et al. 2002; Moraes et al. 2005a), in several other species, such as *Nezara viridula*, the female calling song signals are significantly longer than those of males (Čokl et al. 2000).

In conclusion, the results of this investigation provide the first demonstration that parasitoids can orient to substrate-borne signals produced during sexual communication by the hosts. The effects of this pressure on the evolution of stink bug communication remains to be investigated.

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