Responses of *Diaphorina citri* (Hemiptera: Psyllidae) to Conspecific Vibrational Signals and Synthetic Mimics

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ABSTRACT   Mate-seeking in *Diaphorina citri* Kuwayama, a vector of the economically damaging huanglongbing citrus disease, typically includes male–female duetting behaviors. First, the male calls by beating his wings at ≈170–250 Hz, producing vibrations that are transmitted along the host tree branches to the female. If receptive, she immediately replies, helping to direct the searching male toward her. The duetting and searching continues until the male locates the female. Males and females are similar in size and produce wingbeat vibrations with similar temporal and spectral patterns. A study of male and female responses to playbacks of recorded and synthetic mimics of different vibrational signals on citrus plants was conducted to better understand the range of signals to which *D. citri* respond and potentially to co-opt or disrupt their vibrational communication. In general, both sexes responded well to a variety of 0.3–0.5-s signals that included multiple harmonics of ≈200-Hz wingbeat-frequency chirps up to ≈1,400 Hz (where a chirp is a sine wave tone that sweeps across a narrow range of frequencies). There were only minor differences in female responses to signals containing different relative amplitudes of such chirps, and males readily located sources that played these multiple-harmonic signals. The results are discussed in relation to mating-signal selectivity and the potential for developing automated methods to trap male *D. citri* by using vibrational signals.

KEY WORDS   Asian citrus psyllid, communication, citrus greening disease

Diaphorina citri Kuwayama (Hemiptera: Psyllidae) is a vector of huanglongbing, an economically devastating disease of citrus trees (Bové 2006). It causes additional harm by inducing malformation or abscission of new citrus flush (Michaud 2004). Consequently, scouting for *D. citri* and suppressing its populations is an important focus of citrus pest management programs (Halbert and Manjunath 2004, Rogers et al. 2012).

  Diaphorina citri can be sampled by aspiration, bagging, or tapping of an infested stem, or by hanging unbaited sticky traps of various colors near the exterior of the tree canopy (Hall et al. 2007, 2010; Hall 2009; Hall and Hentz 2010). Various costs and inefficiencies in these procedures, however, have led managers and researchers to search for alternative, complementary sampling methods (Wenninger et al. 2009b). Aspiration and stem tapping are rapid, but labor-intensive. Sticky traps are only weakly attractive to psyllids and

they capture many nontarget insects as well. It could be beneficial to incorporate intraspecific communication cues, such as vibrational signals (Wenninger et al. 2009a), into *D. citri* traps to enhance their capture efficacy.

  Like many psyllids (Tishechkin 2007) and other hemipterans (Drosopoulos and Claridge 2006), *D. citri* adults communicate with potential mating partners on their host plants by producing substrate-transmitted vibrations (Wenninger et al. 2009a). Both sexes produce low-amplitude vibrations by wing-fanning at frequencies of 170–250 Hz (Wenninger et al. 2009a). Male *D. citri* search for females by calling periodically while they crawl around in the tree canopy. If a female detects and replies to a call, the male moves toward her. A series of duetting calls and replies then ensues, helping to guide the male toward the female for mating (Wenninger et al. 2009a).

  Until now, there have been no reports where duetting behaviors have been co-opted for trapping of male *D. citri.* However, there have been several successful investigations to trap other hemipteran insects with vibrational signals, and efforts to manipulate or interfere with their communications (Saxena and Kumar 1980, Zhang et al. 1995, Hunt and Morton 2001, Polajnar and Čokl 2008, Čokl and Millar 2009, Mazzoni et al. 2009, Eriksson et al. 2012). Previously, differential responsiveness and mate-choice selectivity were observed in studies of vibrational communication in several other hemipteran species (Miklas et al. 2003).

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In addition, Percy et al. (2006) found that females of the psyllid species, *Schedotrioza multitudinea* Maskell, responded frequently to playbacks of conspecific male calls but only infrequently to playbacks of calls of other *Schedotrioza* species. We hypothesized that signals with temporal and spectral patterns near the midranges of those in replies reported previously from female *D. citri* (Wenninger et al. 2009a) might be of greatest effectiveness for trapping male *D. citri.* In addition, because vibrations in plants are least attenuated at frequencies below ≈500 Hz (Cocroft and Rodríguez 2005, Čokl and Millar 2009), it was of interest to consider potential signals that would attract males over the longest distances.

Wenninger et al. (2009a) found that *D. citri* male calls and female replies both are variable in amplitude and contain harmonics of ≈200-Hz wingbeat frequencies up to ≈2,000 Hz, with strong energy between 600 and 1,400 Hz. In signals from both sexes, the different harmonics usually were 5–10% higher during the middle of the signals than at the beginning and the end. To gain further information about male and female responses to signals that might be effective in attracting males to a vibrational trap, we explored responses of both sexes to recorded signals and also to synthetic signals containing chirps (swept sine wave tones [Weisstein 2012]) of ≈200-Hz harmonics at different relative amplitudes up to 1,400 Hz.

Materials and Methods

Insects and Experimental Arena. Nymphs of *D. citri* were obtained initially from a colony at the United States Department of Agriculture–Agricultural Research Service–United States Horticultural Research Laboratory (USDA–ARS–USHRL). Thereafter, a colony was maintained at the United States Department of Agriculture–Agricultural Research Service–Center for Medical, Agricultural, and Veterinary Entomology (USDA–ARS–CMAVE), supplemented as needed with additional groups of 200–300 nymphs reared by methods similar to those described in Wenninger and Hall (2007) and Wenninger et al. (2009a).

Because previous studies noted that mated female psyllids may be less responsive to male calls than virgin females (Taylor 1985, Percy et al. 2006), all bioassays were conducted with virgin psyllids that had been isolated as nymphs. Each nymph was released singly onto a citrus seedling in a small, 52-mm-height vial with four holes covered in screen near the top for ventilation, and the vial was capped with a foam plug. The isolated nymphs were maintained at 25–30°C, 60% RH, and a photoperiod of 14:10 (L:D) h. The sex of each adult was checked under a microscope ≈1 d after emergence, and the adults remained separate in their vials until testing, 3–9 d after emergence.

Bioassays of psyllid responses to vibrations were conducted 4–10 h after the beginning of photophase. As noted by Wenninger and Hall (2007), there did not appear to be a peak time for mating activity. The psyllids were released singly onto a small, ≈10-cm-height Duncan grapefruit plant (*Citrus paradisi* Mac-
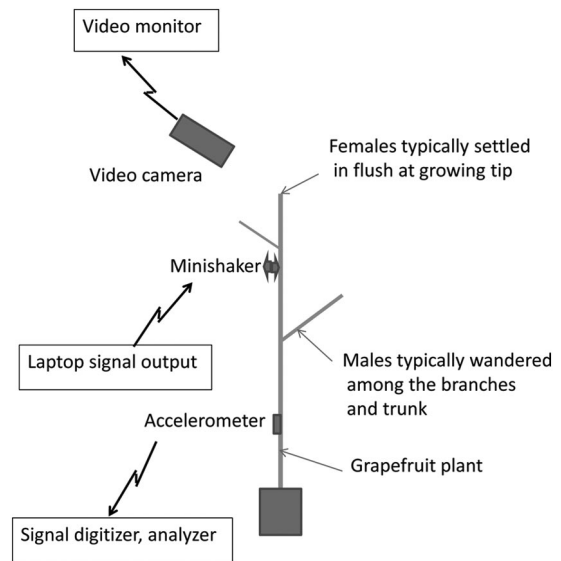

Fig. 1. Experimental arena inside the vibration-shielded anechoic chamber. Video monitor, laptop controller, and the vibration analysis and recording system were external to the chamber.

fadyen) (Fig. 1) inside a vibration-shielded anechoic chamber (Mankin et al. 1996). A 100-W floodlamp was set ≈1 m above the plant and a videocamera (model HDR-SR1, Sony Corp., New York, NY) was set ≈0.5 m to the side. Background noise interference was reduced by closing the anechoic chamber door after the psyllid was released onto the tree. Observations of the test were made on a monitor outside the chamber.

Signal Processing and Analysis. Vibrations were monitored continuously with an accelerometer (model 4371, Brüel and Kjær [B&K], Naerum, Denmark) attached to the base of the plant by an alligator-clip system (Mankin et al. 2004). The vibrations were amplified 40 dB with a charge amplifier (model 2635, B&K), band-pass filtered between 60 and 3,500 Hz, and fed externally to a signal analysis system (model 4300B, Kay Elemetrics Corp., Lincoln Park, NJ) where they were digitized, observed, and recorded. Temporal and spectral pattern analyses were performed on digitized recordings by using Raven 1.3 (Charif et al. 2008). Spectrograms were calculated using spectrum sizes of 4,096 samples for measurements of harmonic frequencies and spectrum sizes of 512 samples for measurements of signal intervals and durations.

Synthetic mimics of *D. citri* signals were constructed as combinations of multiple harmonics of ≈200 Hz, ranging up to 1,400 Hz, incorporating the findings in Wenninger et al. (2009a) that the harmonic frequencies in the middle of a call or reply are usually 5–10% higher than at the beginning or end. Each harmonic in the mimic was approximated as a combination of two chirps (sine wave sweeps) constructed using Matlab chirp functions (Matlab 7.11, MathWorks, Inc., Natick, MA). The first chirp in each harmonic was set to increase linearly from its initial frequency at the beginning of the signal to a 7.5%-higher

peak at the middle of the signal. Thereafter, the second chirp was set to decrease in frequency linearly from the peak down to the initial value at the ending of the signal. All the synthetic mimics were 0.45 s in duration.

Recorded or synthetic signals were played to psyllids through a minishaker (model 4810, B&K) connected to the plant with a small push rod that vibrated with signals generated by standard computer audio outputs. The minishaker was controlled by a remotely operated laptop computer running QuickTime (Apple, Inc., Cupertino, CA).

Measurements of Response and Attraction. In bioassays to measure female responses to vibrational signals, the minishaker was attached near the middle of the main stem and the psyllid was released onto a leaf near the top of the plant. Typically, she settled quickly on nearby flush and began feeding. Each test signal was played to her 10–20 times at intervals of 5–30 s, depending on the rapidity of responses. The order of the test signals was random. The proportional response to each test signal was measured as the fraction of playbacks to which the female replied.

In male attraction bioassays, the minishaker was attached near the top or bottom of the plant and the psyllid was released near the middle of the plant. When the male began crawling in the branches, the test signal was played at intervals of ≈1 min until he began to call. Then the test signal was triggered immediately. The test signal also was triggered after each subsequent call. Recording of vibrations continued until the male reached within 1 cm of the minishaker attachment to the plant, usually within 10 min after the initial call.

Because the responsiveness of the psyllids tended to increase with increasing signal amplitude, the playbacks were adjusted by eliciting several calls or replies at the beginning of each session and setting the playback amplitude at approximately the level detected from the live psyllid.

Statistical Analyses. In bioassays of female proportional response, nonparametric one-way repeated measures Friedman's tests (SAS Institute 2004), were conducted to estimate whether there were significant differences among responses to different signals. When Friedman's test was significant, female preference in comparisons of signal pairs was determined from the significance of the nonparametric Wilcoxon signed rank test (SAS Institute 2004). Four 3–5-d-old females were tested singly in an experiment that assessed the importance of low-frequency signals on response, and nine 4–8-d-old females were tested singly in an experiment that assessed the importance of the presence of multiple-harmonics of the wingbeat frequency on response.

In bioassays of male attraction, 10 males were tested singly with a recorded female reply and eight with a synthetic mimic. For control bioassays, 10 males were tested singly in 15-min sessions where the minishaker was attached but silent. These treatments were assessed using analysis of variance (ANOVA) followed by Tukey's studentized range (HSD) test (SAS Institute 2004).
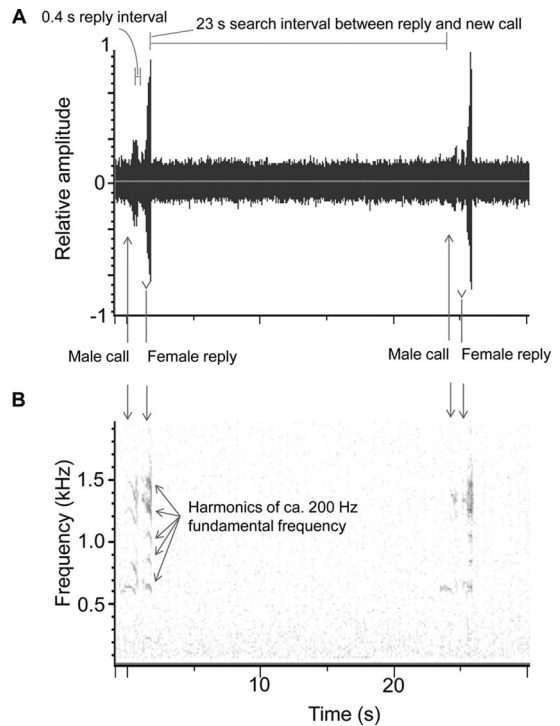

Fig. 2. Oscillogram (A) and spectrogram (B) of signals recorded from a duetting *D. citri* pair. Areas of darker shading in the spectrogram indicate higher relative energy at those frequencies and times.

Results

Characteristics of Recorded and Synthetic Signals used in Bioassays. The *D. citri* calls and replies recorded at the beginning of the study to obtain representative signals for playbacks were variable in amplitude and duration, with wingbeat (first harmonic) frequencies between 180 and 220 Hz, similar to signals observed in Wenninger et al. (2009a). Overall, the signal durations ranged from 0.2 to 1.5 s. A segment of one recording is shown in Fig. 2A, which displays two consecutive calls by a male, each followed by a female reply. In this example, the male searched along the branch for ≈23 s after the first female reply before calling again, longer than the mean of 8 ± 0.4 s found previously in Wenninger et al. (2009a), but within the range of durations they observed. The spectrogram in Fig. 2B shows several harmonics at intervals of ≈200 Hz in signals from both psyllids. As in Wenninger et al. (2009a), the frequencies with greatest energy ranged approximately from 600 to 1,400 Hz.

Two male calls and two female replies from four different recordings were selected for assessments of the range of *D. citri* responses to signals of different temporal and spectral patterns. One male signal contained harmonics with significant energy from 200 to 1,400 Hz (Fig. 3A), with the time of peak energy occurring near the middle of the call. The second male signal was similar except that minimal energy was present below 600 Hz. The temporal and spectral
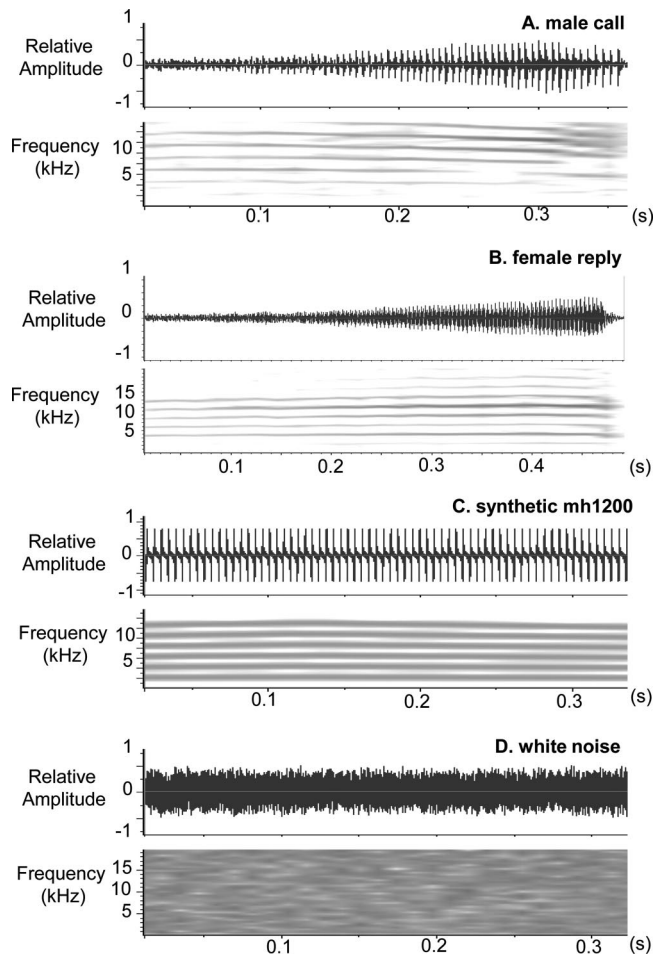
Fig. 3. Oscillograms and spectrograms of playback signals used in female response bioassays: A) 0.37 s of a male call, B) 0.5 s of a female reply, C) 0.35 s of the mh1200 synthetic mimic, D) 0.33 s of the white noise. Areas of darker shading in spectrograms indicate higher energy at those frequencies and times.

characteristics of this signal (rmc) are seen in Fig. 4A, which displays responses of two different females to multiple playbacks of rmc and a synthetic signal.

One of the recorded female signals selected for playbacks contained energy primarily between 600 and 1,200 Hz, with peak energy occurring ≈80% into the 0.5-s reply (Fig. 3B). The second female signal contained energy at harmonics from 200 to 1,200 Hz, with peak energy at the ending. The temporal and spectral characteristics of this signal (rfr) are seen in Fig. 5A, which displays responses of two different males in recorded sections containing multiple playbacks of rfr and a synthetic signal.

Five synthetic mimics were selected for use in playbacks to assess *D. citri* responses to different signals. One contained a chirp with a 200 Hz initial frequency, designated h200, and a second contained a chirp with a 400 Hz initial frequency, designated h400. These two signals were selected because they were approximately first- and second-harmonics of the *D. citri* wingbeat frequency and, because they were <500 Hz, had potential to be

detected over longer distances than signals of higher frequency (Čokl and Millar 2009).

A third, multiple-harmonic mimic, mh1200 (Fig. 3C), was constructed from chirps of equal amplitude at harmonics of 200-Hz between 200 and 1,200 Hz. Another multiple harmonic mimic, mh1400 (Fig. 4B), was identical to mh1200 except that the harmonic range was 200–1,400 Hz, and the amplitude at 1,200 Hz was three dB higher than for the other harmonics. A fifth mimic was constructed from white noise containing a random distribution of all frequencies between 0 and 20,000 Hz, but containing no harmonics (Fig. 3D). The multiple-harmonic and white noise mimics were constructed to consider whether the presence or absence of multiple harmonics affected *D. citri* responsiveness.

Responses of Females to Low-Frequency Signals. Results are presented in Table 1 from an experiment in which proportional responses of four females were examined to randomly presented series of h200-mimic, h400-mimic, white noise, and female call playbacks. Although females did reply to playbacks of the
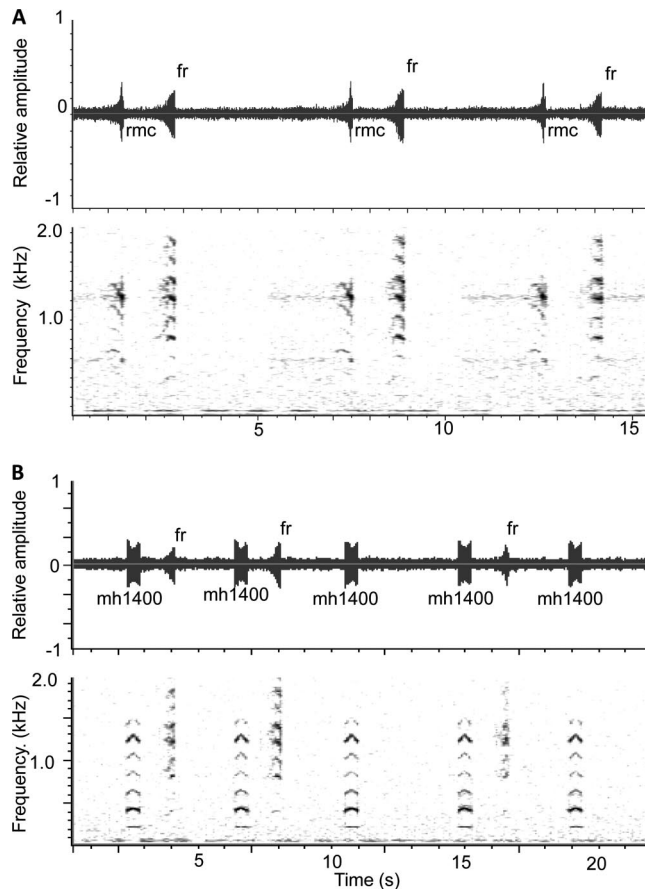
Fig. 4. Oscillograms and spectrograms of multiple female replies (fr) to playbacks of A) recorded male call (rmc), and B) synthetic mimic (mh1400). Areas of darker shading in spectrograms indicate higher energy at those frequencies and times.

two low-frequency signals and the white noise, the proportional responses were significantly lower than to the female signal. However, in preliminary testing leading to this experiment, higher levels of female responsiveness occurred when the amplitudes of the h200, h400, and white noise playbacks were increased to levels two to three times above the amplitudes of the live signals produced in the tests.

The female reply signal had been selected for testing in this experiment specifically because it contained relatively low energy below 600 Hz (Fig. 3C). The result that it elicited strong responses, even with low energy near the wingbeat frequency, suggested that a different signal feature, such as the presence of multiple harmonics, might increase the relative attractiveness of a playback signal.

Responses to Signals with Multiple Harmonics. There were no significant differences in the proportional responses of female *D. citri* to the mh1200 mimic, a male call, and a female reply in the experiment of Table 2 that considered signals with and without multiple harmonics of the 200-Hz wingbeat frequency. However, the proportional responses were significantly greater than to white noise. Females responded similarly to signals that maintained the same

amplitude throughout (the mh1200 mimic), and signals that rose from low- to high-amplitude during the playback (the male call and female reply). These results and other tests of male responses to different signals led us to select signals with energy at multiple harmonics from 200 to 1,200 Hz for an initial test of male attraction to playbacks.

Male Attraction Bioassays. Fig. 5 displays examples of a male response to a female reply signal, rfr, and of a second male to the mh1200 mimic. These two examples were representative of a series of tests conducted with 18 different males, 10 exposed to the rfr signal and 8 to the mh1200 mimic. All of the tested males began calling and, except for one test with the mh1200 mimic, each male moved within a 15-min period to within 1 cm of the minishaker attachment point. In the control, 10 additional males were observed for 15-min periods with the minishaker attached to the tree but silent. Only one male crawled within 1 cm of the minishaker attachment point. The fraction of tested males that reached the minishaker attachment point was significantly lower for the silent treatment than for the rfr and the mh1200-mimic treatments under ANOVA ($F = 75.89$; df = 2, 25; $P < 0.001$) followed by Tukey's studentized range (HSD) test ($P < 0.05$).
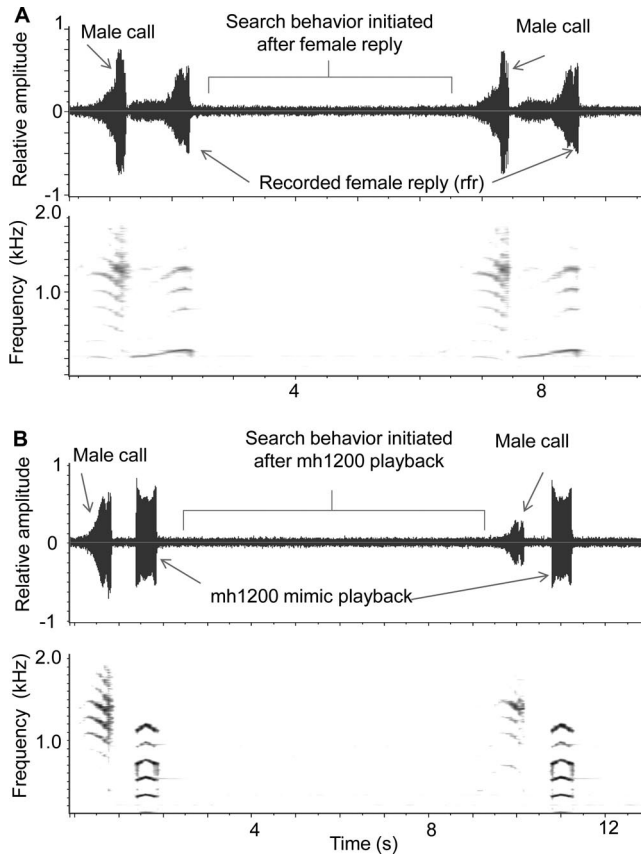
Fig. 5. Oscillograms and spectrograms of male calls during search behavior associated with playbacks of A) recorded female reply (rfr), and B) mh1200 synthetic mimic. Areas of darker shading in spectrograms indicate higher energy at those frequencies and times.

Discussion

In previous discussions of insect vibrational communication, it has been noted that the timing and the absolute and relative amplitudes of vibrations are modified significantly as they travel through a plant, and the signals can be easily masked by high levels of wind and other background noise (Cocroft and Rodríguez 2005, Cocroft et al. 2006, Mankin et al. 2011). Consequently, a duet between a *D. citri* male and female pair is likely to result in mating only when each psyllid can interpret their partner's low-amplitude signals correctly, focusing on the important species-specific signal features, although discounting background noise and unimportant substrate-induced temporal and spectral modifications.

Table 1. Means ± SE of female *D. citri* proportional responses in assessments of signals with and without low-frequency energy

Signal	Proportional response
Female reply (Fig. 3B)	0.58 ± 0.22a
400-Hz mimic (h400)	0.20 ± 0.200b
White noise (Fig. 3D)	0.17 ± 0.17b
200-Hz mimic (h200)	0.10 ± 0.10b

Significant differences occurred in the mean proportional response to different signals (Friedman's test statistic = 9.76, df = 3, $P = 0.02$). Mean proportional responses followed by the same letter are not significantly different at the $P < 0.05$ level under a Wilcoxon signed rank test. Specific comparisons were as follows: female reply ranked with h400, $T_s = 0$, $N = 4$ $P < 0.001$; female reply ranked with white noise, $T_s = 0$, $N = 4$ $P < 0.001$; female reply ranked with h200, $T_s = 0$, $N = 4$, $P < 0.001$; h400 ranked with white noise, $T_s = 0$, $N = 1$, $P > 0.2$; h400 ranked with h200, $T_s = 0$, $N = 1$, $P > 0.2$; white noise ranked with h200, $T_s = 0$, $N = 1$, $P > 0.2$.

Table 2. Means ± SE of female *D. citri* proportional responses in assessments of signals with and without multiple harmonics of the 200-Hz wingbeat frequency

Signal	Proportional response
Male call (Fig. 3A)	0.82 ± 0.07a
Mh1200 mimic (Fig. 3C)	0.61 ± 0.13a
Female reply (Fig 3B)	0.56 ± 0.13a
White noise (Fig. 3D)	0.01 ± 0.01b

Significant differences occurred in the mean proportional response to different signals (Friedman's test statistic = 13.57, df = 3, $P = 0.0036$). Mean proportional responses followed by the same letter are not significantly different at the $P < 0.05$ level under Wilcoxon signed rank test. Specific comparisons were as follows: male call ranked with white noise, $T_s = 0$, $N = 9$ $P < 0.001$; mh1200 mimic ranked with white noise, $T_s = 0$, $N = 8$, $P < 0.001$; female reply ranked with white noise, $T_s = 0$, $N = 8$, $P < 0.001$; male call ranked with female reply, $T_s = 5$, $N = 8$, $P > 0.05$; male call ranked with mh1200 mimic, $T_s = 5$, $N = 7$, $P > 0.1$; and female reply ranked with mh1200 mimic, $T_s = 16$, $N = 8$, $P > 0.2$.

Thus, it is of interest to consider which features of the *D. citri* and synthetic playback signals might be least affected by modifying influences of the plant substrate and background noise.

In considering three of the signals found to be successful in eliciting responses, Figs. 3A–C, we see that each signal was produced as a series of harmonics of a ≈200-Hz fundamental frequency, and the two recorded signals varied over time in the absolute and relative amplitudes of different harmonics between 200 and 2,000 Hz. In the laboratory (see Fig. 5 of Wenninger et al. 2009a), *D. citri* vibrations have the greatest signal to noise ratio between ≈600 and 2,000 Hz, whereas in field environments, wind noise becomes important at frequencies below 1,000 Hz (Cocroft and Rodríguez 2005) and can interfere with detection of low-frequency vibrations. In such environments, the occurrence of multiple harmonics of ≈200 Hz above 1,000 Hz may be the most reliable indicator that a signal is being produced by a conspecific. The results in Tables 1 and 2 combined with results from several other preliminary bioassays suggest that *D. citri* females do exhibit selectivity in response to different signals as has been found for other psyllids (Percy et al. 2006), but their preferences may be influenced more by the presence of multiple, ≈200-Hz harmonics than by temporal patterns or relative differences among harmonic amplitudes, in which case the production of such harmonics would be an important feature of an vibration trap.

For developing an automated vibration trap that plays back a reply immediately after detecting a male call, the ideal latency between call and reply has not been explored precisely, but examination of replies observed in Wenninger et al. (2009a) suggests that latencies of 0.3–1 s may be satisfactory. Preliminary studies with different delays between male calls and playback replies suggest that males rarely begin searching behavior unless the female replies are presented with a latency of 1 s or less. Ideally, an automated trap would be able to detect male calls reliably and produce immediate replies by use of a low-power, low-cost sensor-microcontroller system (Mankin et al. 2010).

Potentially, an automated trap could be a tool not only for sampling *D. citri* populations, but also for further exploration of *D. citri* biology and mating behavior, and for development of vibration-based methods that disrupt or otherwise interfere with mating behavior (Saxena and Kumar 1980, Polajnar and Čokl 2008, Čokl and Millar 2009, Eriksson et al. 2012). Further research also might combine vibrational attraction of male psyllids with chemical attractants for female psyllids (Mann et al. 2012), or with exposure to entomopathogenic fungi or other biopesticides (Hoy et al. 2010, Moran et al. 2011). Finally, parasitoids like *Tamarixia radiata* (Waterston) (McFarland and Hoy 2000, Gómez-Torres et al. 2012) might be attracted to the locations of *D. citri* vibrational signals, thereby augmenting rates of parasitization.

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