Broadcasts of Wing-Fanning Vibrations Recorded from Calling Male *Ceratitis capitata* (Diptera: Tephritidae) Increase Captures of Females in Traps

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ABSTRACT Female Mediterranean fruit flies, *Ceratitis capitata* (Wiedemann), from the sterile-male rearing facility in El Pino, Guatemala, were exposed to broadcasts of wing-fanning vibrations recorded from males engaged in calling behavior to investigate the feasibility of developing a female-selective acoustic trap. The recorded signals had frequent amplitude fluctuations and peak frequencies ≈350 Hz, typical of signals observed in previous studies of Mediterranean fruit fly acoustic behavior. Females did not exhibit long-distance phonotaxis, but remained near a speaker significantly longer when the sounds were broadcast at 103–107 dB than when the speaker was silent. In addition, significantly higher percentages of females were captured by yellow adhesive traps next to a broadcasting speaker than by traps next to a silent mimic. Additional bioassays were conducted with synthetic, 350-Hz tones produced by a thermoacoustic tube as well as with silent mimics of the different sound sources to examine the relative responsiveness of female Mediterranean fruit flies to traps with different acoustic and visual features. The visual attributes of the different sound source assemblies significantly affected capture rates. The range over which the broadcast significantly increased the percentage of female captures was <0.5 m, which may limit the utility of these acoustic cues in large-scale trapping programs. However, the findings of this study do justify further testing of whether optimized short-range acoustic signals could be used to augment longer range pheromonal and visual cues to improve the efficacy of female-selective traps.

KEY WORDS arrestment, sound, monitoring

DEVELOPMENT OF EFFICIENT, SELECTIVE attractants for the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), is of high priority to industries and government agencies responsible for management programs targeting this international agricultural pest (Buchinger 1996). Currently, two types of synthetic olfactory attractant are commonly used as lures in Mediterranean fruit fly traps. The parapheromones trimedlure (Beroza et al. 1961), ceralure (McGovern and Cunningham 1988), and (−)-ceralure B1 (Jang et al. 2003) are potent attractants for male Mediterranean fruit fly, but they are only weakly or not at all attractive to females (Nakagawa et al. 1970). Food lures in which ammonia is an important component (Mazor et al. 1987, Heath et al. 1995) are potent baits for mated females. A three-component, food-based synthetic attractant has been developed for trapping mated female Mediterranean fruit flies (Heath et al. 1995, 1997). Selective attractants for female Mediterranean fruit flies (Epsky et al. 1999, Miranda et al. 2001) are of particular need where sterile males are released to eradicate incipient populations (Hendrichs et al. 1995), and for mass trapping of established populations (Gazit et al. 1998). However, only limited progress has been made in development of selective attractants for virgin female Mediterranean fruit flies.

Mediterranean fruit fly courtship has been studied intensively to identify communicatory signals that could be used for trapping (Burk and Calkins 1983, Eberhard 2000). Mediterranean fruit flies mate primarily in leks, where groups of males aggregate on the undersides of leaves in microclimatically favorable areas near the tops of host trees (Prokopy and Hendrichs 1979, Arita and Kaneshiro 1989, Kaspi and Yuval 1999). Males in leks attract females by emitting sex

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pheromone and fanning their wings in low-amplitude vibrations at ≈350 Hz (Webb et al. 1983b). The significance of wing-fanning behavior is not well established, although the sounds produced have been suspected to have a potential communicatory role in courtship (Briceño et al. 2002). When a female lands on a leaf and approaches a male, he begins a series of head-rocking displays and vibrates his wings in higher amplitude, ≈100-ms pulses at 185 Hz (Webb et al. 1983b) superimposed on the continuous 350-Hz vibration (we designate the 350-Hz vibrations as "male hum: hereafter, and the 185-Hz pulses as "buzzes"). If the female accepts the male's multimodal performance of pheromonal, visual, acoustic, and vibrational signals, he proceeds to subsequent stages of courtship (Briceño and Eberhard 2000).

Previous research on communication-based Mediterranean fruit fly attractants has focused primarily on the male-produced sex pheromone (Baker et al. 1985, Heath et al. 1991, Flath et al. 1993). Synthetic pheromone lures have proven attractive to females in laboratory trials (Heath and Epsky 1993, Light et al. 1999), but they were not as attractive in field trials (Heath et al. 1999). Because Mediterranean fruit fly courtship involves visual and acoustic displays in addition to pheromone emission, we hypothesized that one or more of these displays might be useful in a female-selective trap, alone or in combination with other courtship stimuli.

Female Mediterranean fruit flies have not been reported previously to exhibit long-distance phonotaxis (Cade 1975, Spangler and Hippenmeyer 1988), a behavior exhibited primarily by insects with tympanic organs (Michelsen and Larsen 1985, Robert et al. 1992), and until now, there have been no reported attempts to develop a female-selective acoustic trap. However, a wing-fanning insect (or a broadcasting speaker) produces mechanical vibrations in air that can be detected over short distances by vibration sensors on the antennae of many insects (Michelsen and Larsen 1985). Airborne vibrations set up by wing fanning could be involved in Mediterranean fruit fly courtship at short range. Briceño and Eberhard (2002) have reported, for example, that a female Mediterranean fruit fly has an increased likelihood of moving toward and directly facing a male that produces humming and buzzing vibrations in her presence, which increases the likelihood that a mounting attempt will result in successful copulation.

Wing-fanning vibrations have been implicated previously in the courtship of various insects, including parasitic Hymenoptera (Sivinski and Webb 1989), drosophilids (Tauber and Eberl 2002, and references therein), and other tephritids (Sivinski and Burk 1989, Mankin et al. 1996a). Sivinski et al. (1984) reported, for example, that *Anastrepha suspensa* (Loew) females are more active in the presence of broadcast wing-buzzing vibrations recorded from calling males, as indicated by rates at which females crossed a bisecting line in a bioassay arena. Significantly higher percentages of females in large cages were captured in Jackson traps next to speakers broadcasting male buzzes than were captured with silent speakers (Webb et al. 1983a). Mankin et al. (2000b) found that the proportions of *A. suspensa* females standing under speakers broadcasting male buzzes were greater than under silent speakers if the females had been exposed previously to male pheromone. Sivinski and Webb (1985) found that virgin *Toxotrypana curvicauda* (Gerstäcker) females, but not males, became less active in the presence of male wing-fanning sounds broadcast at a sound pressure level (SPL) of 90 dB (where dB = 20 $\log_{10}$[P/20 μPa], and P is the pressure in Pascals [Pa]; Mankin et al. 2000a).

In several drosophilids, male wing-fanning vibrations do not elicit phonotaxis and function primarily to enhance intraspecific courtship or reduce mating between closely related species (Ritchie et al. 1999, Tauber and Eberl 2002). The rhythmicity of the male "sine song" and "pulse song" wing vibrations has been implicated in species recognition (Ritchie et al. 1999). *Drosophila* females have responded to broadcasts between 72 and 95 dB (Eberl et al. 1997), as well as between 78 and 108 dB (Crossley et al. 1995) in bioassays with playback of male song.

Several mosquito (Ikeshoji et al. 1985, Ikeshoji and Ogawa 1988) and midge (Ogawa 1992, Hirabayashi and Ogawa 1999) species have been captured in short-range acoustic traps. Males initially attracted to a swarm marker were captured in adhesive or other traps next to speakers broadcasting recorded wingbeats or synthetic mimics of sounds produced by flying conspecific females. These species do not have tympanal organs, and they do not exhibit long-distance phonotaxis (Ogawa 1992).

The short-range responses of these dipterans to conspecific sounds are considerably different from the long-distance phonotaxis observed with many insects that have tympanic organs. Male-produced calls have been recorded or synthesized and then broadcast over loudspeakers near different trapping devices (Walker 1988) to capture females of various field cricket species. Bucket and electrical traps broadcasting calls by male *Scapteriscus borellii* (=*acletus*) Giglio-Tos and *Scapteriscus vicinus* Scudder captured large numbers of both males and female conspecifics (Walker 1982, 1988). In general, the rate of capture and the distances over which the broadcast calls influenced insect behavior (i.e., the active space) increased with SPL up to the limits of the speaker output (Walker 1982, 1988). Such results led us to include broadcasts of sounds at high SPL in our initial explorations of female Mediterranean fruit fly responses to male wing-fanning vibrations.

To explore the feasibility of developing a female-targeted Mediterranean fruit fly acoustic trap, we observed females in the presence and absence of broadcast recordings of the 350-Hz wing-fanning hums produced by pheromone-emitting males. As expected from previous studies of tephritids and drosophilids, females did not exhibit phonotaxis in these preliminary bioassays. However, in tests where humming was broadcast at high SPL, females remained significantly longer at sites near broadcasting speakers than at sites

Table 1. Acoustic and visual treatments, SPLs, and numbers of female Mediterranean fruit flies tested in bioassays

Bioassay	Treatment description	SPL (dB)	n^a	No./test[b]
Resting time	25-cm speaker, silent[c] or w/hum	55–107[d]	10	25
Hum, 1 trap	8.9-cm speaker, silent or w/hum[e]	57–107[d]	40	29
Hum, 2 traps	8.9-cm speaker, silent or w/hum[f]	57–107[d]	45	41
Hum, 3 traps	8.9-cm speaker, silent or w/hum[g]	57–107[d]	45	41
Tone, 1 trap	Thermoacoustic tube, silent or w/350-Hz tone[h]	57–109[d]	16	65
Aural/visual	Comparisons among acoustic/visual cues[i]	57–107[d]	60	32

[a] Number of separate tests in bioassay.
[b] Mean No. females per test (total no. in bioassay/n).
[c] 10-min periods of silence used as controls.
[d] These tests were not conducted in an anechoic chamber. The background noise level was measured between 315 and 400 Hz in tests with silent control.
[e] Sound source assembly contained an 8.9-cm speaker and attached white funnel supported on laboratory stand. Control was an identical, silent assembly.
[f] Configuration as in Hum, 1 trap with an additional adhesive trap at far end of chamber.
[g] Configuration as in Hum, 2 trap with an additional adhesive trap in middle of chamber.
[h] 26.2-cm glass tube w/thermoacoustic source, supported horizontally on laboratory stand. Control was an identical tube assembly w/o thermoacoustic source.
[i] Configuration as in Hum, 2 trap. Treatment was an 8.9-cm speaker assembly, silent or w/hum; silent glass tube assembly; or an adhesive trap.

near silent mimics. The results were similar to those of Cade (1975), who reported that *Ormia ochracea* (Bigot) female parasitoids remained significantly longer on speakers during broadcast of male *Gryllus integer* Scudder cricket calling song. Such results prompted several additional bioassays, first to determine whether high-SPL male hum increased the rate of capture of females in visually attractive, e.g., yellow (Epsky et al. 1996), adhesive traps and then to consider the active space of the broadcast, i.e., the effective distance over which the broadcast increased the percentages of females trapped. Bioassays also were conducted to determine whether a high-SPL, synthesized sound could be used as a replacement for broadcast male hum as has been found previously with male-produced sounds of several crickets, mole crickets, tachinids, and midges. Finally, observations that different acoustic assemblies seemed to have different levels of visual attractiveness led us to conduct tests on the relative effectiveness of different visual and acoustic stimuli.

Materials and Methods

Insects. Mediterranean fruit fly pupae were obtained from the Moscamed Modular Mediterranean Fruit Fly Rearing Facility, El Pino, Guatemala (normal strain, sterilized under 145-Gy radiation). The pupae were placed in 30 by 30 by 30-cm screened cages on a photoperiod of 12:12 (L:D) h. Males and females were removed from the cage once each day during the 1–3-d period of emergence and thereafter kept in separate rooms at temperatures of 24–26°C and relative humidities of 50–60%. The flies were fed water and a mixture of sucrose and yeast hydrolyzate (3:1 by volume) ad libitum. Sexually mature virgin females (4–8-d after emergence) were used in bioassays.

Male Mediterranean Fruit Fly Acoustic Recording Procedures and SPL Measurements. Wing-fanning hums produced during calling behavior by 3-d-old, sexually mature male Mediterranean fruit flies were monitored during the first 4 h of photophase. A Brüel and Kjær (B&K, Naerum, Denmark) model 4145 microphone was positioned 2–5 mm above a 10 by 10 by 7-cm screen cage containing three to five males. The microphone was connected to a B&K measuring amplifier (model 2610). The output was stored on a digital audio tape recorder (model DA-P1, TEAC, Montebello, CA). All recordings were made in an anechoic chamber (Mankin et al. 1996b) at the USDA–ARS Center for Medical, Agricultural, and Veterinary Entomology (Gainesville, FL). The recordings were conditioned with a 0.1–10-kHz bandpass filter (model 3100, Krohn-Hite, Avon, MA) and digitized at 25 kHz. The spectral and temporal patterns of the hums were analyzed using the DAVIS sound analysis program previously described in Mankin et al. (2000a, b). The Mediterranean fruit fly wing-fanning SPLs (instantaneous, peak to peak measurements) were calibrated by attaching a 124-dB, 250-Hz standard sound source (B&K type 4228) to the microphone. The standard signal was analyzed in DAVIS, and the dB-offset parameter was adjusted to match the SPL of the power spectrum with the SPL measured by the B&K model 2610 amplifier.

Eleven recordings of male hum were obtained from cages of different pheromone-calling males on different days. Because studies by Burk and Webb (1983) with other tephritids suggested that males with louder and lower frequency wing-fanning vibrations had relatively greater sexual success, we selected an 8-s segment of one of the relatively loudest and lowest frequency records for an initial study of female Mediterranean fruit fly responses to acoustic stimuli. The success of the preliminary bioassays led to the continued use of the same recording in subsequent, adhesive trap bioassays in four larger chambers (Table 1; Fig. 1).

Sound Production Systems. Three different sound production systems were used in bioassays of female Mediterranean fruit fly responses to male hum or synthetic tones broadcast at high amplitude. The sound

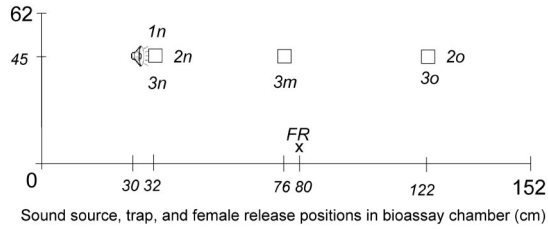

Fig. 1. Side view of 61 by 61 by 152-cm chamber showing positions of sound source or silent mimic, female release point (*FR*), and horizontal distances from bottom corner for traps in the Hum 1-trap and Tone 1-trap (*1n*) bioassays (see Table 1), Hum 2-trap and Aural/visual (*2n*, *2o*) bioassays, and Hum 3-trap (*3n*, *3m*, *3o*) bioassays, where *n* denotes near, *m*, mid-chamber, and *o*, opposite.

system for the initial, Resting time bioassays (Table 1) used a Targa model SSW-100 (Etronics, Seoul, Korea) 25-cm-diameter speaker designed for high-amplitude broadcasting at low frequencies. In preliminary experiments (see next section), the effects of sound on female behavior seemed most prominently at the highest SPLs tested. To increase the SPL by several dB immediately in front of the speaker, we attached a 20-cm-diameter by 20-cm-long plastic funnel at the front. Subsequently, we found that 8-cm-diameter, 5-cm-long plastic funnels attached to 8.9-cm-diameter speakers also increased the SPL at 350 Hz by 4–6 dB immediately in front of the funnel. Several assemblies of an 8.9-cm speaker (model AW-630SP, Circuit Warehouse, Springfield, MO) with a white 8-cm funnel were used later in the larger scale, adhesive trap bioassays (Hum, one trap; Hum, two traps; and Hum, three traps in Table 1).

A third sound source was tested in additional bioassays that considered whether a high-SPL synthetic tone at the male hum frequency would produce similar trapping increases (Tone, one trap in Table 1). Based on previous research with other tephritids (Sivinski et al. 1984, Sivinski and Webb 1985), we did not expect that white noise or synthetic tones at frequencies greatly different from the male-produced sounds would elicit a behavioral response. The source contained a thermoacoustic engine (Garrett and Backhaus 2000) inside a 26.2-cm-long, 2-cm-diameter resonant tube. It produced a continuous, 350-Hz, 109-dB tone when 6.4 V at 5.3 Amp was supplied to the heater through a DC power supply (Anderson and Mankin 2002).

Resting Time Bioassay. In a preliminary search for measurable behavioral responses to broadcast male hum, virgin females were observed for 10-min periods in a 38 by 38 by 46-cm screened cage before and during broadcasts. The tests were videotaped with a model VC8 3612T camera (Sanyo, Richmond, IN) during morning and early afternoon periods of peak sexual activity (Arita and Kaneshiro 1989). A 5-cm-diameter sheet of white filter paper was placed vertically, perpendicular to the face of the speaker. The speaker broadcast an 8-s recording of male hum played in a continuous loop by a Creative Wave Studio (Creative Labs, Milpitas, CA) program operating on a Pentium II personal computer. The computer output was amplified with a B&K model 2610 signal amplifier and a Realistic model SA-102 (Radio Shack, Ft. Worth, TX) speaker amplifier.

Initially, small numbers of preliminary tests were conducted with broadcasts between 75 and 95 dB. SPLs were measured after each bioassay with the sound level meter positioned 10 cm from the speaker. Because no behavioral effects of sound were observed until the SPLs exceeded 93 dB, we conducted additional testing at high SPLs. During 10 tests with different groups of 20–50 females (Table 1), landing behaviors were observed in 10-min periods before and during broadcast of male hum at high SPL (103–107 dB). Mean resting time was calculated as the total time in seconds spent by all flies on the filter paper during the 10-min observation period divided by the number of flies in the cage.

Adhesive Trap Bioassays. When the preliminary bioassay indicated that females remained near sound sources longer in the presence than in the absence of broadcast male hum, we conducted a larger scale experiment to assess the practical implications of such results. A trapping assembly was configured to attract female Mediterranean fruit flies to the location of a sound source by using a visually attractive, yellow surface (Epsky et al. 1996). We hypothesized that the behavioral arrestment observed in the resting time bioassay might result in a decreased tendency to fly away from the area where the male hum was broadcast and an increased rate of capture by a sticky surface nearby. Female Mediterranean fruit fly responses to sound were evaluated in bioassays with five different acoustic and visual treatments described below (see also Table 1).

In all five bioassays, sound sources or silent mimics were placed at ≈45-cm height, 30 cm from the ends of four Plexiglas chambers, screened on the front and back (Fig. 1). The chambers were centered under two 124 by 61-cm, 240-Watt fluorescent lights. The sound sources faced the main part of the chamber (see Anderson and Mankin 2002 for spatial distribution of SPL in chambers). SPLs in the bioassay chambers were measured with the B&K microphone-amplifier system (also see Anderson and Mankin 2002). Background noise levels were measured with a CEL-593 sound level meter (CEL Instruments, Milford, NH). The SPLs were highest within 3–5-cm distances from the speakers, but were 5–10 dB higher near the walls than in the centers of the chambers because of constructive and destructive interferences with sound reflections (Anderson and Mankin 2002). The frequencies of the emitted sounds were not altered by the walls.

Double-sided traps were constructed from 7 by 7-cm sheets of yellow adhesive paper (Atlantic Paste and Glue Company, Brooklyn, NY) to capture Mediterranean fruit flies. The traps were clipped to a 1-cm-diameter pole suspended end to end along the midline of the chamber, 58 cm above the floor. The traps were positioned vertically, parallel to the sides of the cham-

ber and perpendicular to the sound source assemblies. Tests with 20–60 virgin females (depending on availability) were run for 5–7 h, beginning 2 h after the start of the 12-h photophase. The females were released at *FR*, near a side entry door, 50 cm laterally from the speaker assembly (Fig. 1), and provided an ≈30-min free-movement period before the test began. Under these conditions, most females were distributed at the ceiling or upper walls when the traps were placed into the chamber, and there was no consistent preference for either end of the chamber. The percentage captured in each trap was calculated by dividing the final count of females in that trap by the sum of all females trapped and all females remaining in the chamber at the end of the test. The total percentage captured in the chamber was the sum of the percentages captured in all traps.

Male Hum Bioassay, One Trap per Chamber. Females were released simultaneously into two separate chambers, each containing a yellow adhesive trap adjacent to an 8.9-cm speaker assembly (Table 1, 1*n* in Fig. 1). Recorded male hum was broadcast from one of the two assemblies, and the broadcast was alternated daily between chambers. The expected result was that the mean percentage of captured females would be greater in tests with traps next to broadcast male hum than in tests with traps next to silent mimics.

Male Hum Bioassays, Multiple Traps per Chamber. Two multiple-trap bioassays were conducted to consider the distances over which broadcast male hum affected female captures. In one chamber, a trap was adjacent to the 8.9-cm speaker assembly (2*n* or 3*n* in Fig. 1), as in the hum, one trap bioassay. A second, untreated trap without a speaker assembly was set 30 cm from the opposite end of the chamber (2*o* or 3*o* in Fig. 1).

Our hypothesis for the two-trap bioassays was that the total mean percentage of captured females would be greater in chambers where sound was broadcast than in chambers with silent mimics. If no sound was broadcast, we expected there would be no significant differences in the mean percentages captured in the two traps. In chambers with broadcast hum, the percentages captured were expected to depend on whether the sound had a short- or long-range effect. Anticipating a short-range effect, we predicted the mean percentage captured in the trap next to the broadcasting speaker (2*n* in Fig. 1) would be greater than the mean percentage captured in the opposite trap (2*o* in Fig. 1). If the effect of the sound was long-range, however, both traps in the chamber with broadcast hum might capture greater percentages of females than traps in a silent chamber.

In the three-trap bioassays, an untreated trap was set in the center of the chamber, 76 cm from either end, ≈45 cm from the female release area (3*m* in Fig. 1). A second chamber was set up identically, and the sound playback was alternated daily between chambers. For tests with broadcast hum, we expected the percentages captured in the center trap to be similar to the percentages in the opposite trap (3*o* in Fig. 1) if the effect of the sound was short range because the only effect would be at the trap nearest the sound source. We expected the percentage captured to decrease with distance from the sound source if the effect of the sound was long-range because the effect of the sound would be increasingly greater as the female approached the source.

350-Hz Tone Bioassay, One Trap per Chamber. These tests were conducted to determine whether a loud tone at the fundamental frequency of the male wing-fanning hum elicited female responses similar to those observed with broadcast hum. Individual yellow adhesive paper traps (*1n* in Fig. 1) were set adjacent to 26.2-cm, 350-Hz resonant tube assemblies in separate chambers (Table 1). One tube contained a thermoacoustic source that produced a 109-dB tone under power. The source was alternated daily between chambers. The expected result was that the mean percentage of captured females would be greater in tests with traps next to synthetic tones than in tests with silent mimics.

Aural versus Visual Bioassay. The male hum, two-trap bioassay was expanded by adding two treatments for comparisons of female Mediterranean fruit fly trap captures in the presence of different acoustic and visual stimuli (Table 1). One treatment evaluated the visual attractiveness of the thermoacoustic source mimic because higher percentages of females were trapped at such assemblies in the 350-Hz tone bioassay than at silent speaker assemblies in the male hum bioassays. In the second treatment, the acoustic and visual assemblies were replaced with an untreated yellow adhesive trap. The four treatments were rotated daily among the four chambers. Based on the results of the previous bioassays, we expected the silent thermoacoustic source assembly, but not the silent speaker assembly to be more visually attractive than the adhesive trap alone.

Statistical Analyses. In the resting time bioassay, the mean difference in resting time before and after broadcasts of male hum at high SPL were analyzed with Student's *t*-test. The percentages of females captured in different adhesive trap and aural/visual bioassays were arcsine transformed before analysis with the Student's *t*-test or PROC GLM (SAS Institute 1988), and the resultant means and standard errors were reconverted to percentages in the tables and figures. In post hoc multiple comparison tests, the mean percentages captured in different treatments were compared using the Waller–Duncan k-ratio *t*-test (SAS Institute 1988).

Results and Discussion

Acoustic Characteristics of Male Hum Wing Vibrations. The recording posted at cmave.usda.ufl.edu/~rmankin/medfly11.wav.is a representative example of signals obtained in 11 recordings of wing vibrations from 3-d-old male Mediterranean fruit flies. The magnitudes and variations of the fundamental frequencies were within the range reported previously by Webb et al. (1983b) for "calling songs" of wild males and Sivinski et al. (1989) for wild and sterile males. The 48-dB

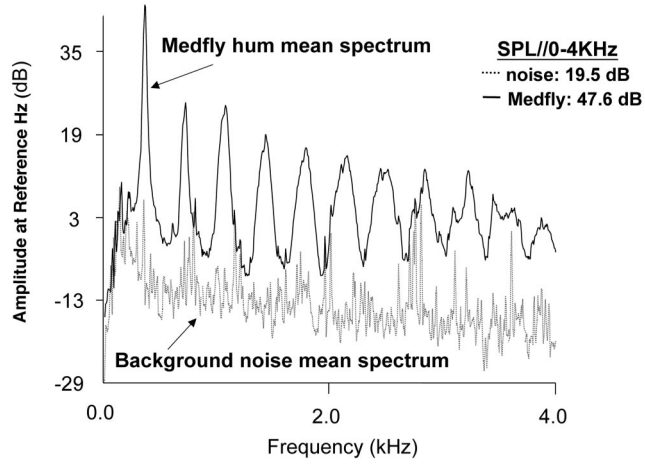

Fig. 2. A 520-point mean spectrum of a 10-s recording of wing-fanning hum from a male Mediterranean fruit fly compared with the background noise in the anechoic chamber. SPL was measured at a 1–2-cm distance from the fly.

SPL of the vibrations, recorded at ≈1-cm distance from the male, was slightly lower than the 50–54-dB levels reported by Webb et al. (1983a) for a larger tephritid, *A. suspensa.*

The power spectrum of a 10-s sample of hum from a different calling male is shown in Fig. 2. The peak at 355 Hz is the fundamental frequency, and the subsequent peaks at multiples of 355 Hz are lower amplitude harmonics. Figure 3 compares the spectrogram of the 8-s recording of male hum used in the resting time and adhesive trap bioassays with the spectrogram of the tone produced by the thermoacoustic source. The fundamental frequencies were similar, but the fluctuations in amplitude at the fundamental frequency and the relative amplitudes of higher frequency harmonics were greater for the male hum than for the thermoacoustic source.

Resting Time Bioassay. Virgin female Mediterranean fruit flies did not exhibit phonotaxis toward speakers broadcasting male hum at any tested SPL from 75 to 107 dB. However, when a female landed on the filter paper near the speaker, she remained longer (5.82 ± 0.84 s per fly per 10-min observation period) when male hum was broadcast at 103–107 dB than during the immediately preceding silent period (0.42 ± 0.12 s per fly per 10 min). The mean difference in resting time between silent and broadcast periods, 5.4 s, was statistically significant ($t = -5.78$, df = 9, $P < 0.0003$).

An increased duration of resting time in the presence of broadcast male hum is consistent with observations that a female Mediterranean fruit fly often stops walking and remains close to a male (Liimatainen et al. 1997) or turns to face a male (Briceño and Eberhard 2002) that begins to vibrate his wings during courtship. On several occasions when multiple females landed on the filter paper next to the broadcasting speaker, we observed them moving around and

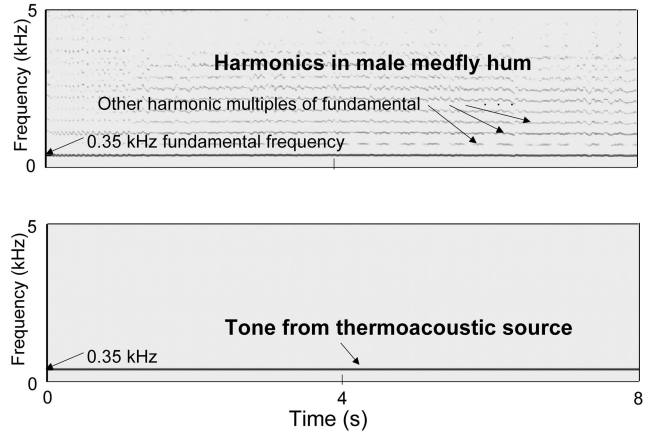

Fig. 3. Spectrograms of the continuous 8-s loop of broadcast male Mediterranean fruit fly hum and the signal produced by the thermoacoustic source. Higher relative signal amplitude is indicated by darker shading, frequency is displayed on the vertical axis, and time on the horizontal axis.

facing each other, occasionally touching, without immediately flying away.

Male Hum and 350-Hz Tone Bioassays, One Trap per Chamber. The results of the resting time bioassay suggested that male-produced sound would not be useful as a long-distance trapping cue, but it might indirectly increase trapping effectiveness by increasing the tendency of a female to land and remain on a sticky surface long enough to be captured if other cues had already attracted her within the sound detection range. Furthermore, if the most important feature of the signal was the presence of high-amplitude sound at the 350-Hz wing vibration frequency, the observed effect of broadcast male hum might be reproduced by using a synthetic tone. A second possibility was that the observed behavioral effect might be a generalized response to any loud signal, in which case it might be reproduced by broadcast of high-amplitude white noise. We did not test the latter hypothesis in depth, but there are no reports in the literature of such behavior in tephritids. The effects of 350-Hz signals were tested in a 40-trial bioassay comparing trap captures in the presence and absence of male hum broadcast at 107 dB SPL, and in a 16-trial bioassay comparing trap captures in the presence and absence of the synthetic tone broadcast at 109-dB SPL. To increase the likelihood that females would fly within range of the sound source in the larger bioassay chamber, we selected yellow adhesive paper as the trapping surface because it had been visually attractive to female Mediterranean fruit flies in previous field studies (Epsky et al. 1996).

Partly as expected, the 60.0 ± 3.4 (mean % ± SE) capture of females in traps near the assembly with broadcast male hum was significantly higher than the 34.4 ± 4.6 capture in control traps near the silent mimic ($t = -4.08$, df = 38, $P < 0.0002$). This result led to additional tests to evaluate the range over which the sound had a behavioral effect (two- and three-trap bioassays below). It should be noted also that, although similar behavioral mechanisms could have resulted in an increased resting time in the small-cage bioassay and in an increased percentage of captured females in the trapping bioassay, this study did not demonstrate equivalence between the female behaviors in the two bioassays.

The results in bioassays using a synthetic, 350-Hz tone were different from those with broadcast male hum. The 61.4 ± 2.1% of females captured in traps near the 350-Hz tone was not significantly different from 58.2 ± 2.4% captured in traps near silent mimics ($t = 1.34$, df = 7, $P = 0.12$). The differences in the results of the two bioassays possibly were due to female preferences for frequency or amplitude fluctuations that were present in the recorded hum but not in the synthetic tone. However, the two sound sources had different colors and shapes, and the effects of different visual and acoustic features may not contribute additively to trap capture. The addition of a sound stimulus might increase trap captures when the trap color and shape are somewhat attractive to Mediterranean fruit fly females but might have no effect when the color and shape are either highly attractive or unattractive. We suspected, for example, that the visual features of the thermoacoustic assembly were more attractive to females than those of the speaker assembly or an untreated adhesive trap, which could confound interpretation of comparisons between the male hum and synthetic tone bioassays. For this reason, the effect of sound assembly shape and color on trap capture was explored further in a subsequent *Aural/Visual* bioassay (see below).

Male Hum Bioassays, Two Traps per Chamber. As expected, the total percentage of females captured in both traps in chambers with broadcast male hum (90.1 ± 1.5) was significantly different from the percentage captured in chambers with silent mimics (77.5 ± 2.3) ($t = -2.81$, df = 43, $P = 0.0075$). In addition, the distribution of captures within the chambers was supportive of the hypothesis that the broadcasts had only a short-range effect (Fig. 4). The mean percentage captured next to the broadcasting speaker, 63.2 ± 2.7, was significantly higher than the mean captured at the silent mimic, 40 ± 2.5. In the tests without broadcast hum, the percentage captured in the trap next to the silent mimic was not significantly different from the mean of 37.8 ± 3.9 in the untreated adhesive trap at the opposite end of the chamber.

Originally, we had expected also that the mean percentage of females captured in the untreated trap opposite the acoustic source (*2o* in Fig. 1) in chambers with broadcast sound would be similar to the percentage captured opposite the silent mimic. However, the mean percentage, 26.8 ± 3.7, was significantly lower than for the silent mimic, 39.7 ± 3.9%. The decrease likely occurred because the increased numbers of females captured in traps near the broadcast sound reduced the overall density of females in the chamber,

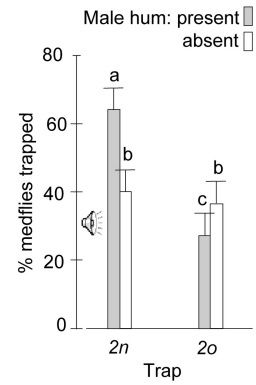

Fig. 4. Comparisons of percentages of virgin female Mediterranean fruit flies captured in yellow adhesive traps positioned 1 and 92 cm from speaker-funnel assembly in bioassay chamber (see *2n* and *2o* in Fig. 1). Solid bars indicate means in tests where speaker broadcast male hum. Open bars indicate means in tests where speaker was silent. Minimum significant difference (MSD) is indicated by error marker at top of bar. Means marked with same letter are not significantly different by Waller–Duncan k-ratio *t*-test ($F = 15.6$; df = 3, 86; $P < 0.0001$).

consequently reducing the numbers of females available for capture at the opposite end. In that case, we expected the percentage captured in an additional untreated adhesive trap elsewhere in the chamber also would be lower when sound was broadcast than when no sound was broadcast (see next section).

Male Hum Bioassays, Three Traps per Chamber. As expected, the total percentage of females captured in chambers with broadcast male hum, 83.9 ± 2.2, was significantly different from the total percentage captured in chambers with silent mimics, 73.6 ± 3.8 ($t = -2.74$, df = 43, $P = 0.0089$). Similarly, as in the tests with two traps per chamber, the distribution of trap captures was supportive of the hypothesis that the effect of the broadcast was short rather than long range (Fig. 5). The 34.3 ± 2% of females captured in traps next to broadcast hum remained significantly above the mean of 22.6 ± 3.1 at the silent mimics. If the broadcast had a long-range effect, we would expect that the middle (*3m*) and opposite (*3o*) traps would have captured a greater percentage of females in chambers with broadcast hum than in chambers with silent mimics. However, the 19.9 ± 1.8% captured in untreated traps opposite the broadcast hum (*3o* in Fig. 1) was not significantly different from the mean of 17.8 ± 2.7 in traps opposite the silent mimic. Likewise, the 29.7 ± 2.2% captured in the center trap with broadcast sound (*3m* in Fig. 1) was not significantly different from the 33.1 ± 4.0% captured in chambers with a silent mimic.

It was initially unexpected that the percentage captured in the trap near broadcast sound would be similar to the percentages captured in the center trap, with or without broadcast sound. We suspect that this result was due primarily to the initially skewed distribution of females in the chamber. Even after a 30-min period of free movement before broadcast began, many Mediterranean fruit flies had remained closer to the center trap than to the trap with the broadcast sound, 67 cm away. If the Mediterranean fruit flies entered the visually attractive range of the center trap (see next section) before they entered the acoustic range of the broadcast, they might be unaffected by the sound.

The results of both the two- and three-trap bioassays suggest that the active space of the broadcast hum was less than the 0.5-m distance from the speaker to the Mediterranean fruit fly release area, even at a 107-dB SPL. Indeed, a short range of acoustic detection may be a general rule for insects like the Mediterranean fruit fly that detect sound with particle velocity sensors by using antennal flagellar or Johnston's organs (Tautz 1979). A <1-m active space has been reported in mosquitoes (Ikeshoji et al. 1985, Ikeshoji and Ogawa 1988), midges (Ogawa 1992, Hirabayashi and Ogawa 1999), ants (Hickling and Brown 2000), honey bees (Towne and Kirchner 1989), and caterpillars (Tautz and Markl 1978).

Aural/Visual Bioassay. There were statistically significant differences in the total percentages of females captured in chambers with a broadcasting speaker, silent mimic, silent thermoacoustic source, or untreated adhesive trap at one end (*2n* in Fig. 1) and an untreated adhesive trap at the opposite end (*2o* in Fig. 1) ($F = 3.33$; df = 3, 56; $P = 0.026$). As expected, the mean percentages captured in traps at the silent tube and broadcasting speaker (Table 2) were significantly greater than at all other traps. The silent speaker assembly next to an adhesive trap captured significantly lower percentages of females than the broadcasting speaker and the silent tube, but significantly greater percentages than an untreated adhesive trap in the same chamber. There were no significant differences in the mean percentages captured in untreated traps at opposite ends of a chamber (see Source = None in Table 2).

These results provide some perspective on the relative significance of the visual and acoustic stimuli used for trapping female Mediterranean fruit flies in these studies. Clearly, the visual characteristics of the traps had a strong effect on percentage capture. The primary role of the broadcast male hum in increasing the percentage captured at the speaker assemblies used in these bioassays may have been to increase the

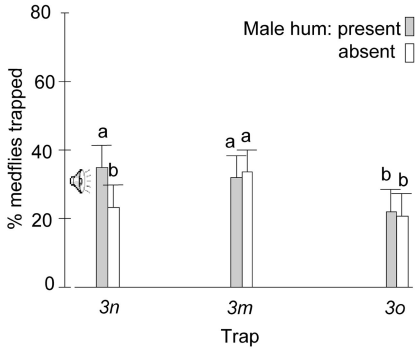

Fig. 5. Comparisons of percentages of virgin female Mediterranean fruit flies captured in yellow adhesive traps positioned 1, 46, and 92 cm from speaker-funnel assembly in bioassay chamber (see *3n*, *3m*, and 3o in Fig. 1). Solid bars indicate means in tests where speaker broadcast male hum. Open bars indicate means in tests where speaker was silent. MSD is indicated by error marker at top of bar. Means marked with same letter are not significantly different by Waller–Duncan k-ratio *t*-test ($F = 8.13$; df = 5, 129; $P < 0.0001$).

Table 2. Percentages (mean ± SE) of females captured in adhesive traps with different acoustic and visual stimuli, arranged in descending order of percentage captured at stimulus source

Stimulus source	Position of trap relative to source	
	Near	Opposite
Thermoacoustic tube, silent	67.5 ± 4.1a	14.3 ± 2.4e
8.9-cm speaker, male hum	62.8 ± 2.1a	25.9 ± 2.0d
8.9-cm speaker, silent	45.3 ± 3.7b	33.2 ± 3.3cd
None	35.6 ± 4.2c	41.0 ± 3.7bc

Means followed by the same letter are not significantly different by the Waller–Duncan k-ratio *t*-test ($F = 26.1$; df = 7, 112; $P < 0.0001$, and MSD = 8.3 by using the Waller–Duncan k-ratio *t*-test (SAS Institute 1988).

percentage of females landing secondarily after they had been attracted from long-range by visual cues. Other combinations of visual cues and broadcast male hum might yield different results, depending on the visual attractiveness of the trapping assemblies. Such an effect makes it difficult to compare the female responses to the broadcast male hum directly with the responses to synthetic 350-Hz tone in this study.

Relative Selectivity and Range of Acoustic Traps. A primary goal of developing an acoustic trap for Mediterranean fruit flies was to capture wild females selectively in areas where releases of sterile males would interfere with interpretation of trap catches (Epsky et al. 1996, Miranda et al. 2001). The laboratory studies reported here are an initial step in that process, but the ultimate potential of acoustic technology as a practical tool for Mediterranean fruit fly detection and monitoring remains uncertain. Broadcast male hum significantly affected female Mediterranean fruit fly behavior. However, the tested broadcast did not induce phonotaxis, and it affected female behavior over a relatively short distance (<0.5 m), even at high SPL. Large numbers of acoustic traps would be needed to monitor extended areas in field studies. In addition, sterile, laboratory-reared insects do not necessarily exhibit the same sexual behaviors as wild insects (Shelly et al. 1994, Liimatainen et al. 1997), and other studies are in progress to examine the responses of wild female Mediterranean fruit flies to broadcast song from wild males.

One potential method to increase the active space of an acoustic trap is to identify combinations of acoustic, visual, and olfactory cues that are more attractive than the combinations tested in these initial studies. A single recording was selected for broadcast in the adhesive-trap bioassays because of its successful alteration of female behavior in the resting-time observations. The 350-Hz tone tested as a synthetic mimic of the male hum had an appropriate fundamental frequency but it had none of the amplitude or frequency fluctuations that occur in typical calling and courtship. It has not yet been established whether such fluctuations are of relevance to the females. The sounds were broadcast at high amplitude to maximize the range of detection, but they were not necessarily optimally attractive. In previous studies (Shelly et al. 1994, Liimatainen et al. 1997), sterile Mediterranean fruit fly males frequently have been inferior to wild males in sexual competition. In wild populations, some Mediterranean fruit fly males (e.g., large, protein-fed, symmetrical males) may achieve greater mating success than others (Hunt et al. 1998, Taylor and Yuval 1999, Kaspi et al. 2000). Recordings of wing humming or wing buzzing from such males may yield sounds with more effective frequency or amplitude fluctuation patterns. Further increases in capture efficacy also may result from addition of olfactory or visual attractants that mimic the environments where leks form most frequently (Prokopy and Hendrichs 1979, Kaspi and Yuval 1999). Otherwise, the benefits of high selectivity could be offset by higher costs compared with presently available, less selective traps. The use of pheromonal stimuli (Heath and Epsky 1993) also is being considered as a way to increase the range of the trap while maintaining selectivity.

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