

Comparison of particle velocity and sound pressure measurements in anechoic and medfly bioassay chambers

J. B. Anderson and R. W. Mankin

USDA-ARS, Center for Medical, Agricultural, and Veterinary Entomology Gainesville, FL

ABSTRACT

Many insects without tympanal ears do not perceive the pressure component of sound, but instead have movement receptors (usually small hairs on body or antennae) that are sensitive to sound particle velocity -- oscillations of air particles in the sound field. In our laboratory, efforts to develop an acoustic trap for mate-seeking female medflies have centered on utilizing the particle velocity component of the male acoustic calling signal.

Bioassays in 61 x 61 x 152-cm chambers have demonstrated that traps reproducing male fruit fly calling songs capture virgin female fruit flies. In order to better understand the spatial dynamics of sound particle velocity in these bioassay chambers, simultaneous measurements /recordings of sound pressure and particle velocity were made and compared with recordings made inside an anechoic room. We also recorded particle velocities in the vicinity of a Multi-lure fruit fly trap. The results are discussed in relation to bioassay effectiveness.

INTRODUCTION

Particle velocity and sound pressure are both quantitative attributes of a sound wave. As the wave moves out and away from its source, air molecules bounce back and forth, jostled by others nearer the sound source, and small variations in ambient air pressure are produced. Most large animals have evolved specialized pressure transducers (a.k.a. ears or tympanae) by which they detect and extract information from these pressure fluctuations. Many small animals, such as ants or fruit flies, without tympanal ears, apparently do not perceive the pressure component of sound, but instead have specialized movement receptors (usually small hairs on body or antennae) that detect sound particle velocity -- the oscillations of air molecules in a sound field (Ewing, 1978; Fletcher, 1978; Tautz, 1979; Towne and Kirchner, 1989; Kämper and Kleindienst, 1990; Humphrey, et al., 1993; Shaw, 1994; Tschuch and Brothers, 1999; Göpfert, 1999; Hickling and Brown, 2000). Although particle velocity and sound pressure are both attributes of the same sound wave, it is possible that each of these different sensory modalities or 'perspectives' on

sound might convey somewhat different subsets of information or possess unique qualities, particularly near the sound source.

In our laboratory, efforts to develop an acoustic trap for mate-seeking female Mediterranean fruit flies have centered on utilizing the particle velocity component of the male acoustic calling signal. The mating system of this major pest insect is complex, involving the formation of male leks, or non-resource-based mating aggregations (Yuval and Hendrichs, 2000) and the use of chemical, acoustic and visual signals to allure and seduce females. Typically, small leks (3-5 males) form in mid-morning on the sunny side of particular trees (Whittier et al., 1992; Shelly et al., 1994). Each male positions himself on the underside of a separate leaf, and everts his balloon-like rectal epithelial sac to release sex pheromone (Prokopy and Hendrichs, 1979; Arita and Kaneshiro, 1989). Males also generate a long, droning, wing vibration or 'calling song' at a mean fundamental frequency of ~ 350 Hz (Webb et al., 1983; Sivinski et al., 1989). When a female approaches by landing on the top of his leaf, the male orients to her shadow, and continues calling until she comes underneath. He then switches to a pulsing 'approach song' (lower in pitch: fundamental frequency ~ 195 Hz.) consisting of short bursts of 'wing fanning', during which gusts of pheromone are directed toward the female (Arita and Kaneshiro, 1989), and moves toward the female, displaying visual signals such as his white 'capitata' (orbital bristles) and 'head rocking' (Holbrook et al., 1970; Landolt et al., 1992). If the female remains receptive, the male leaps onto her back and attempts copulation (which, to be successful in transferring sperm, must last 1-2 hours) (Seo et al., 1990). Female choice is evidently always possible; females can and do walk away at any stage (Shelly, 2000).

Courtship in this species has been studied intensively, as the entire success of the SIT (Sterile Insect Technique) program rests on the sexual prowess of the released (sterile) males. Although some studies have found released males less successful at mating than wild males, the authors could identify no single element of behavior to account for this difference (Liimatainen et al., 1997). They concluded that the timing and correct sequence of behaviors was less organized in mass released males, but some of their findings could be interpreted differently. For example, they found that females did not respond to calling by (unsuccessful) mass released males by approaching (as they did for successful wild males) but only by standing where they happened to be (Liimatainen et al., 1997). The quality of the male's calling sound could very well be critical in this matter.

We made recordings of male calling songs, and discovered that unmated female medflies were attracted when these were played back through a plastic funnel that was free to vibrate. We have done extensive bioassays in 61 x 61 x 152-cm bioassay chambers to demonstrate that virgin females are captured by fruit fly traps that reproduce male calling song in this manner. In order to better understand the particle velocity patterns to which the females were exposed in this context, we made several simultaneous measurements /recordings of sound pressure levels (SPL) and particle velocity levels (PVL) inside an anechoic room and, within the Plexiglas bioassay chambers. We also made both types of measurements around a Multi-Lure fruit fly Trap (Better World Manufacturing, Fresno, CA).

METHODS

We conducted three types of comparative measurements of both particle velocity and sound pressure: **1.** Sound level vs. distance within an anechoic room **2.** Sound level at different locations in the medfly bioassay chambers, and, **3.** Measurements 1 cm from the top opening of a Multi-Lure fruit fly Trap (MLT) in the anechoic room, positioned over a meter from the sound source.

As a sound source, we used a simple tone at ~ 350 Hz. generated with either a function generator (Leader Model LFG1300S) or an “acoustic laser” (small thermoacoustic engine) (Garrett and Chen, 2000; Garrett and Backhaus, 2000, or we used a recording of the male calling song (e, g., <http://cmave.usda.ufl.edu/~rmankin/soundlibrary.html>). Sound pressure levels (SPL) were measured with a B&K model 4145 microphone, and particle velocity levels (PVL) were measured with a Microflown half-inch ICP© probe (Microflown Technologies, Eisenstraat, The Netherlands). These signals were recorded with a B&K Model 2639 preamplifier, and a digital audio tape recorder (DAT) ((TEAC model DA-P1, Montebello, CA; input level = 5), subsequently digitized at 25 kHz and analyzed using the DAVIS insect sound analysis program (Mankin, et al., 2000a, b), as well as a speech analysis system (CSL Model 4300B) (Kay Elemetrics Corp., Lincoln Park, NJ).

RESULTS AND DISCUSSION

Anechoic room: attenuation with distance

We found that, under simple conditions (i.e., far field, no echoes), simultaneous measurements of sound pressure levels (SPL) and particle velocity levels (PVL) are very equivalent. The two types of measurements in the anechoic room matched almost exactly except at near field distances, where the PVL component, as expected, showed increasingly higher values closer to the sound source (Figure 1.). Outside the near field, both measurements showed attenuation proportional to (distance)² that was expected.

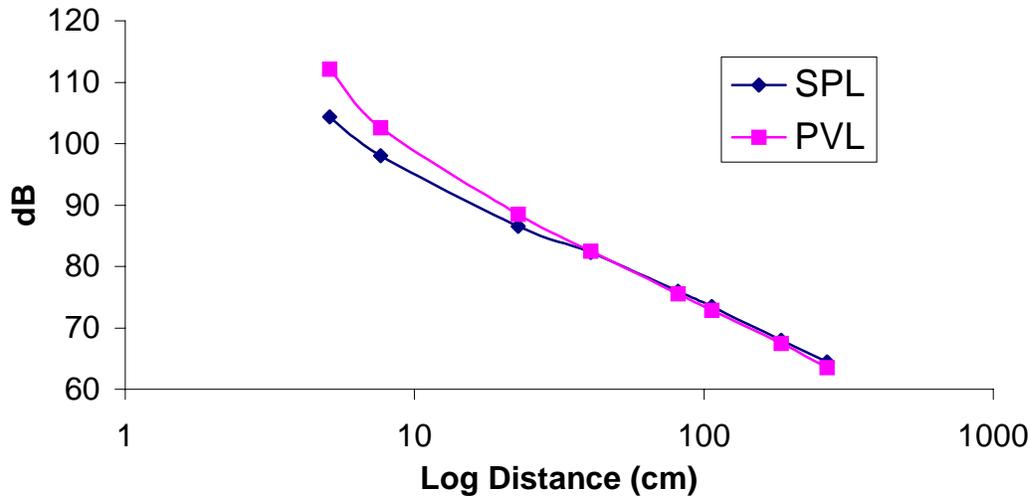


Figure 1. Measurements of sound pressure levels (SPL) and particle velocity levels (PVL) at different distances from a single sound source (350 Hz. tone) in an anechoic room

The fact that PVL attenuates more rapidly than SPL in the near field has led to the common assumption that, as an effective sensory modality, particle velocity is limited to short distances. However, as our results clarify, outside the near field, PVL attenuates at the same rate as SPL and is, at least potentially, discernable by insects with movement receptors specialized to detect it. The addition of the funnel to the speaker amplified the sound of a 350 Hz. tone about 10 dB (at a sound level of ~65 dB) for both SPL and PVL.

Bioassay chambers: spatial variation in sound levels

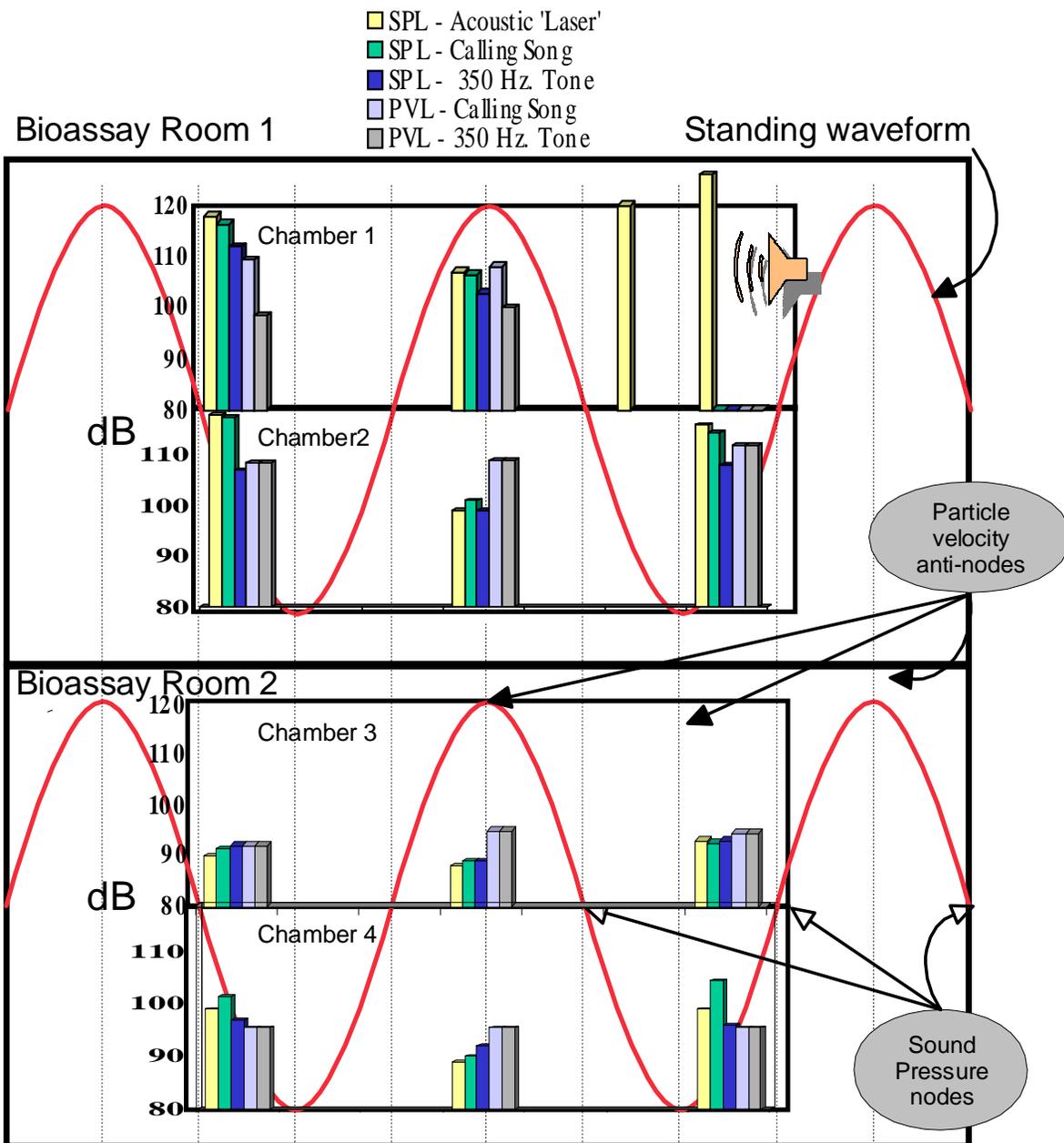


Figure 2. Sound Pressure Levels (SPL) and Particle Velocity Levels (PVL) in Medfly bioassay arena with two chambers stacked on each other in two adjacent rooms. The 350 Hz standing wave is drawn to scale and predicted zones of high and low SPL and PVL are identified.

Inside the Plexiglas bioassay chambers, neither of the types of measurement showed much attenuation with distance (Figure 2.) Even within chamber #1 containing the sound apparatus, both measurements were relatively uniform across the chamber, especially in the case of PVL, with SPL showing a pattern of lower values in the center of each chamber. The room

length was 2.44 m, almost exactly 2.5 times the wavelength of the 350 Hz. signal, (0.984m) which could lead to a strong standing wave resonance effect within each room, and account for the uniformity of the sound level measurements. Because of the spatial uniformity of the signal, the females did not have good spatial cues to identify the location of the sound except where the sound was most intense, within a few cm of the source.

The sound pressure levels and the pressure velocities had different spatial distributions in the chambers. This difference derives partly from the fact that sound pressure and particle velocity are 90° out of phase, and under resonant conditions the spatial variations in each of these parameters caused by wave interference would be segregated by a quarter wavelength (with a 350 Hz. tone, this is 24.57 cm).

Multi-lure fruit fly trap: resonance near upper opening

The largest divergence in our comparisons of sound pressure levels (SPL) and particle velocity levels (PVL) occurred at the small, upper opening of the Multi-Lure Trap (MLT). Both parameters were measured 1cm from this opening when either a 350 Hz. tone or Medfly song was played from a speaker over a meter away. Figure 3 shows the surprising results: a large increase in PVL but almost no change in SPL. Figure 3, A & B shows recordings made while the spherical plastic trap, hanging from a string, was made to rotate so that the upper opening at each revolution passed 1 cm from the B & K microphone (SPL) and the Microflown (PVL). The SPL hardly changed as the opening rotated past, whereas the PVL increased more than 2-fold. Figure 3D shows a frequency scan (from 280 - 380 Hz. over ten seconds) with the trap stationary and both sensors positioned 0.5 cm from the opening. The frequency of highest PVL resonance is around 300 Hz., but somewhat lower with respect to SPL (~ 290 Hz.).

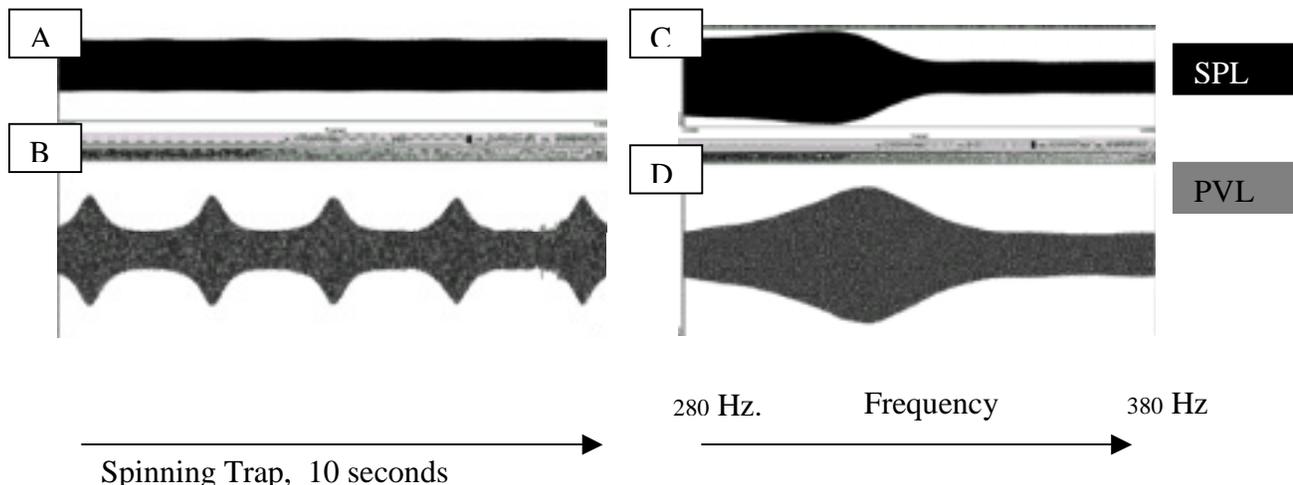


Figure 3. Measurement of SPL (3.A&C) and PVL (3.B&D) recorded near the upper opening of a MultiLure fruit fly trap in an anechoic room 107 cm from a sound source (350 Hz. tone). 3A and B were measured 1 cm from a spinning trap during a 10-s interval. 3C and D were recorded 0.5 cm from the opening of a stationary trap, during a frequency scan (sound source changing from 280 to 380 Hz. over 10 seconds).

This is another example of the spatial segregation of sound pressure (nodes) and particle velocity (anti-nodes) under standing wave conditions. In the presence of an ambient 350 Hz. tone, the area around the trap opening showed a high standing PVL, with the air oscillating back and forth out of the opening. Zones of high SPL should exist inside (with denser accumulations of molecules and not much air movement), where maximum air compression occurs at each cycle of vibration. These sound pressure nodes, locations of standing sound pressure maxima, like those mapped out in the bioassay room (Figure 2), will be loud to animals with eardrums. On the other hand, to insects having movement receptors for 'hearing' sound particle velocity, the opening of a resonator (a PVL anti-node) must also have a 'loud' or unusual sound.

ACKNOWLEDGEMENTS

This study was funded in part by a BARD Research Grant (No. IS-3137-99), to Amos Mizrach, Principal Investigator, Israel, and Richard Mankin, USA) We are grateful to our cooperating investigators in Israel (Amos Mizrach and Michele Mazor) for valuable feedback, and we thank Stephen Garrett for the custom built, 'acoustic laser'. We appreciate the expert technical assistance of Everett Foreman, as well as aid and use of facilities from others at the Center for Medical and Veterinary Entomology (CMAVE) Gainesville, FL.

REFERENCES

- Arita, L. H., and K. Y. Kaneshiro (1989). Sexual selection and lek behavior in the Mediterranean fruit fly, *Ceratitidis capitata* (Diptera: Tephritidae). *Pac.Sc.* 43: 135-143.
- Ewing, A. W. (1978). The antenna of *Drosophila* as a 'love song' receptor. *Physiol. Entomol.* 3: 33-36.
- Fletcher, N. H., 1978. Acoustical response of hair receptors in insects. *J. Comp. Physiol. A.* 127:185-189.
- Fletcher, B.S. (1989). Movements of tephritid fruit flies. In A.S. Robinson and G. Hooper (eds): Fruit flies; their biology, natural enemies and control. Amsterdam: Elsevier, pp. 209-219.
- Garrett, S.L., and R. Chen. (2000). Build an "Acoustic Laser" *Echoes.* 10, 3. p.4-5.
- Garrett, S.L., and S. Backhaus. (2000). The Power of Sound. *American Scientist.* 88, 516-525.
- Göpfert, M.C. H. Briegel, and D. Robert (1999). Mosquito hearing: Sound-induced antennal vibrations in male and female *Aedes aegypti*. *J. Exp. Biol.* 202: 2727-2738.
- Hendrichs, J. (1996) Action programs against fruit flies of economic importance: session overview. In B.A. McPherson and G.J. Steck (eds): Fruit fly pests; a world assessment of their biology and management. Delray Beach: St. Lucie Press, pp. 513-519.
- Hickling, R., and R.L. Brown (2000). Analysis of acoustic communication by ants, with particular application to *Solenopsis richteri*. *J. Acoust. Soc. Amer.* 108: 1920-1929.
- Holbrook, F. R., L. F. Steiner, and M. S. Fujimoto. (1970). Mating competitiveness of Mediterranean fruit flies marked with fluorescent powers. *J. Econ. Entomol.* 63: 454-455
- Humphrey, J.A.C., R. Devarakonda, I. Iglesias, and F.G. Barth. (1993). Dynamics of arthropod filiform hairs. I. Mathematical modeling of the hair and air motions. *Phil. Trans. R. Soc. Lond. B.* 340: 423-444.
- Kämper, G., and H.-U Kleindienst (1990). Oscillation of cricket sensory hairs in a low-frequency sound field. *J. Comp. Physiol.* 167: 193-200.
- Landolt, P.J., R.R. Heath, and D.L. Chambers. (1992) Oriented flight responses of female Mediterranean fruit flies to calling males, odor of calling males, and a synthetic pheromone blend. *Entomol. Exp. Appl.* 65: 259-266.
- Liimatainen, J., A. Hoikkala, and T. Shelly. (1997). Courtship behavior in *Ceratitidis capitata* (Diptera, Tephritidae) Comparison of Wild and Mass-Reared Males. *Ann. Entomol. Soc. Am.* 90: 836-843.
- Mankin, R. W., J. Brandhorst-Hubbard, K. L. Flanders, M. Zhang, R. L. Crocker, S. L. Lapointe, C. W. McCoy, J. R. Fisher, and D. K. Weaver. (2000a) Eavesdropping on insects hidden in soil and interior structures of plants. *J. Econ. Entomol.* 93: 1173-1182.
- Mankin, R. W., E. Petersson, N. D. Epsky, R. R. Heath, and J. Sivinski. (2000b) Exposure to male pheromones enhances *Anastrepha suspensa* (Diptera: Tephritidae) female response to male calling song. *Fla. Entomol.* 83: 411-421.

- Penrose, R. (1993) The 1989/1990 Mediterranean fruit fly eradication program in California. In M. Aluja and P. Liedo (eds): Fruit flies; biology and management. New York Berlin Heidelberg London Paris Tokyo Hong-Kong Barcelona Budapest: Springer-Verlag, pp. 401-406.
- Penrose, D. (1996) California's 1993/1994 Mediterranean fruit fly eradication program. In B.A. McPherson and G.J. Steck (eds): Fruit fly pests; a world assessment of their biology and management. Delray Beach: St. Lucie Press, pp. 551-554.
- Prokopy, R. J. and J. Hendrichs (1979). Mating behavior of *Ceratitidis capitata* on a field-caged tree. *Ann. Entomol. Soc. Amer.* 72: 642-648.
- Rössler, Y. (1989). Insecticidal bait and cover sprays. Reprinted from: World Crop Pests, Volume 3B, Fruit Flies, their Biology, Natural Enemies and Control, Robinson and Hooper (eds.). Elsevier Sci. Publishers B.V., Amsterdam. 329-336.
- Seo, S. T., R. I. Vargas, J. E. Gilmore, R. Kurashima, and M. S. Fugimoto. (1990). Sperm transfer in normal and gamma-irradiated laboratory-reared Mediterranean fruit flies (Diptera: Tephritidae). *J. Econ. Entom.* 83: 1949-1953.
- Shaw, S.R. (1994) Detection of airborne sound by a cockroach 'vibration detector': A possible missing link in insect auditory evolution. *J. Exp. Biol.* 193: 13-47.
- Shelly, T. E., T. S. Whittier, and K. Y. Kaneshiro. (1994). Sterile insect release and the natural mating system of the Mediterranean fruit fly *Ceratitidis capitata* (Diptera, Tephritidae). *Ann. Entom. Soc. Amer.*, 87: 470-481.
- Shelly, T. E.. (2000). Male signaling and lek attractiveness in the Mediterranean fruit fly. *Anim. Behav.* 60: 245-251.
- Sivinski, J., C.O. Calkins, and J.C. Webb (1989). Comparisons of acoustic courtship signals in wild and laboratory reared Mediterranean fruit fly *Ceratitidis capitata*. *Fla Entomol.* 72: 212-214.
- Tautz, J. (1979) Reception of particle oscillation in a medium -- An unorthodox sensory capacity. *Naturwissenschaften* 66: 452-461.
- Towne, W.F., and W.H. Kirchner (1989) Hearing in honey bees: Detection of air-particle oscillations. *Science* 244: 686-688.
- Tschuch, G., and D. J. Brothers (1999) Modeling vibration and sound production in insects with nonstridulatory organs. *J. Acoust. Soc. Amer.* 106: .3706-3710.
- Webb, J.C., C.O. Calkins, D.L. Chambers, W. Schwienbacher, and K. Russ (1983) Acoustical aspects of behavior of Mediterranean fruit fly, *Ceratitidis capitata*: Analysis and identification of courtship sounds. *Entomol. Exp. & appl.* 33: 1-8.
- Whittier, T. S., F. Y. Nam, T. E. Shelly, and N. Y. Kaneshiro. (1994). Male courtship success and female discrimination in the Mediterranean fruit fly (Diptera: Tephritidae). *J. Insect Behav.*, 7: 159-170.
- Yuval, B., and J. Hendrichs, 2000. Behavior of flies in the genus *Ceratitidis* (Dacinae:Ceratitidini) In: Fruit flies in the genus *Anastrepha* (Tephritidae): phylogeny and evolution of behavior, M. Aluja and A.L. Norrbom [eds], CRC Press, Boca Raton, FL. Pp. 459-489.