EFFECTS OF SOUND ON SWARMING MALE *PSOROPHORA COLUMBIAE*[1]

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ABSTRACT. Male *Psorophora columbiae* were shown to respond to sound during swarming. The responses consisted of abrupt changes in flight speed and direction. Tones with frequencies of 200 to 425 Hz were attractive to males over a distance of at least 1 m. Male mosquitoes responded better to tones with sine waveforms than they did either to square waveforms or triangular waveforms. Swarming males became accommodated and no longer responded to sounds presented for 5 seconds or longer. Based on observations of field populations of swarming *Ps. columbiae,* it appears that males use sound waves to locate females, but additional factors seem to be required for males to initiate the actual copulatory behavior. Also, males appear to use sound to maintain their position and spatial relationship within the swarm.

INTRODUCTION

Several investigators have previously reported that male mosquitos respond to sound (Downes 1969, Nielsen and Haeger 1960, Nielsen and Neilsen 1962, Provost 1958, Nielsen and Greve 1950, Roth 1948). Laboratory studies by Roth (1948) showed that male *Aedes aegypti* (Linn.) responded to sound and that sounds are involved in the mating response of males to females of this species. Later, Nielsen and Greve (1950), Nielsen and Haeger (1960) and Provost (1956) all described movements of field populations of male mosquitoes toward sounds produced by human voices. However, the role of sound in the maintenance and organization of swarms in the field is still not fully understood.

Observations of male behavior in the massive marker swarms of *Psorophora columbiae* (Dyar and Knab) in East Texas ricelands (Peloquin and Olson 1985) led us to believe that sound plays an important role in the male swarming behavior of this species. Audio and video recording techniques were thus combined to investigate the role of sound in the organization and positioning behavior of swarming *Ps. columbiae* males.

MATERIALS AND METHODS

This investigation was part of the general study of male *Ps. columbiae* swarming behavior that was conducted in riceland areas of Chambers and Jefferson counties, TX from 1979 to 1983 (Peloquin and Olson 1985). Sources of sound were people singing and humming, the striking of objects and an electronic sound-producing system. The electronic equipment used to present controlled sound emissions to swarming male mosquitoes consisted of a 7.5 cm diam Gelco®[4] or Quam® loudspeaker (Radio Shack, Fort Worth, TX 76102) mounted on a 2 m fiberglass pole and driven by a Wavetek® model 180 solid state function (waveform) generator (Fisher Scientific Co., Pittsburgh, PA 15219). Responses of swarming mosquitoes to various sounds were video-recorded using equipment and methods described by Peloquin and Olson (1985).

The pole with the speaker was positioned adjacent to the edge of the artificial, 2 m × 2 m cloth swarming marker described by Peloquin and Olson (1985). The function generator was placed 15 m away from the marker on the card table supporting the other instruments used in video recording mosquito swarms. A coaxial cable connected the speaker to the function generator. The output of the function generator through the speaker was controlled by a field observer at the card table. Thus, the instruments and the observer were positioned far enough away from the mosquitoes swarming over the marker to minimize any distracting effects they might have on the mosquitoes.

Checks on the acoustic properties of the sound system were made to determine the linearity of response of the speaker to the output of the waveform generator. The sound pressure produced by the speaker in response to a given output of the waveform generator was measured in decibels (A), or dB(A), by a Fisher® sound level meter (Fisher Scientific) positioned 1 m from the speaker.

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Decibel (A) is the standard measurement used to describe sounds in the range audible to man. It is a dimensionless measure equal to 10 times the logarithm to the base 10 of the ratio of 2 powers, P^1 and P^2. With respect to acoustics, dB(A) is 20 times the common logarithm of the sound pressure ratio, with the reference pressure being 0.0002 dyne/cm^2 (Weast and Astle 1982). This statistic is weighted in accordance with the perceptive characteristics of the human ear (Schaudinischky 1976).

A Tektronix® oscilloscope (Tetronix, Inc., Beaverton, OR 97077) and an Ealing® frequency counter (Adcole Corp., Waltham, MA 02145) were used to verify the accuracy of the frequencies produced by the system. The frequency response of the system is shown in Table 1.

In the early evening (40–80 min after sunset) when swarming began over the artificial marker, the generator was turned on and a series of sound stimuli were presented to the mosquitoes. The series of tones presented ranged from 100 to 100,000 Hz. This was accomplished by setting the frequency generator to produce the desired frequency with the volume off. The volume was then suddenly increased to maximum. During observations of mosquito swarming, abrupt jumps or twists and changes in flight speed and/or flight direction by swarming males were taken as positive responses to sounds. On the basis of pilot studies on the length of time to which mosquitoes would elicit a response to a tone, a 5-second stimulus was considered enough to determine if a response was forthcoming. The response of the mosquitoes to a given tone was noted by the observer in his field notebook and recorded on videotape.

The range of tones which elicited the maximum mosquito response was determined by starting from the low frequency end of the sound spectrum, i.e., 100 Hz. The tone generator could produce square, sine and triangular (sawtooth) waveforms. Only sine waveforms were used in the main study to determine the frequency response of mosquitoes to sound. This was because results of pilot trials in which each of the 3 waveforms were presented to swarming male mosquitoes indicated that mosquitoes responded more actively to sine waveforms than to the other 2 waveforms.

Choice of frequency to be tested was based on the response of male mosquitoes to previous sound stimuli. Test frequencies were increased from the initial 100 Hz signal by $\log_{10}$ or half $\log_{10}$ increments. For example, after the 100 Hz test was made, and if no response was seen, the frequency was increased to 500 Hz. If no response was elicited at that frequency, 1000 Hz was tried and so on. If there was a response at 500 Hz, then frequencies between 100 and 500 Hz were tried until a range of sound frequencies to which the swarming males would respond was determined.

Table 1. Frequency response of speaker used to produce sounds presented to swarming *Psorophora columbiae* males in Texas ricelands.

Sound Frequency (Hz)	Loudness in decibels (A) for each waveform		
	Triangular	Square	Sine
100	53	82	43
250	61	84	63
265	66	86	63
275	66	85	62
300	64	84	61
500	72	87	67
1,000	72	84	71
10,000	60	63	61
100,000	47	47	46

RESULTS AND DISCUSSION

Swarming *Ps. columbiae* males were found in our study to respond preferentially to sounds with frequencies in the range of 200 to 500 Hz (Table 2). Responses to synthesized sounds were characterized by an abrupt change in flight speed and sometimes, direction of flight. If a sound stimulus within the range to which the mosquitoes were sensitive was continued

Table 2. Responses to synthesized sine waveform sound by swarming male *Psorophora columbiae* in Texas ricelands.

Sound frequency (Hz)	Number of observed responses by swarming mosquitoes (Responses/No response)	Percent responses for all observations
100	0/9	0
120	0/1	0
140	0/1	0
200	1/13	7
250	9/2	81
260	59/2	96
275	62/2	96
300	28/0	100
350	0/1	0
360	0/1	0
400	13/24	65
425	2/0	100
510	0/11	0
550	0/10	0

for a second or so, the mosquitoes would fly to the source of the sound and thus away from the center of the pre-existing swarm. The attracted males would closely approach the speaker (within 1–2 cm) and orbit it at seemingly maximum flight speed, but none were seen to actually alight on the speaker. After a synthesized tone was presented to the swarming males for more than 5 to 10 seconds, the number of mosquitoes flying towards and orbiting the speaker decreased.

These observations thus indicate that swarming *Ps. columbiae* males are sensitive to sounds originating at least 1 m away from the periphery of swarms and will leave their swarming stations to follow a tone of the proper frequency. Further, the responses of *Ps. columbiae* males to tones produced by the waveform generator suggest that swarming males of this species will approach a sound that has a pitch of 200 to 500 Hz, which is the range reported for female mosquito wingbeat noise (Roth 1948). Roth (1948) demonstrated that the sound of the wing beats of *Ae. aegypti* females is attractive to their male counterparts. It is likely that a similar situation exists for swarming *Ps. columbiae* males and that males of this species, at least in part, use sound for location of their mates. However, swarming *Ps. columbiae* males also appear to exhibit accommodation to sound stimuli; and since the attracted males did not land on the sound source even though they orbited in close proximity to it, this would indicate that some additional stimuli must be present for the males to land on or attempt to grasp the sound source.

As noted in the Methods section of this paper, results of our pilot studies indicated *Ps. columbiae* males to be more sensitive to sine waveform tones than to square and triangular waveforms. The output of the sound generating system was checked to ensure that relative volume at each frequency was similar. As shown in Table 1, the response within the range of 100 to 10,000 Hz is relatively flat. Square waveforms produced relatively louder sounds at a given frequency than did either triangular or sine waveforms. Triangular and sine waveforms were about equally loud in decibels at a given frequency. Thus, the lesser response of swarming *Ps. columbiae* males to square and triangular waveforms must be due to some factor of their sensory physiology and not due to sine waves being relatively louder under experimental conditions.

Percussive noises and human voice noises seemed to elicit a different male mosquito behavior than that observed for sounds from the electronic sound-producing system. Also, altering the pitch or tone and manner of speech or singing or humming altered the response of the mosquitoes. In response to the clink of cans or bottles or the rap of metal on a hard object, the swarming *Ps. columbiae* males would suddenly jump upward and away from the sound source. Human speech percussives, i.e. utterance of *p, b, k* and *t*, also elicited this same reaction. However, not all human voice sounds elicited such an abrupt jumping reaction. When a lower pitched tone was hummed or sung, mosquitoes would fly downward and towards the singer. Some mosquitoes would actually hit the face of the singer, but none landed for any length of time. If the singer sang at a pitch which was initially attractive to the swarming males, then suddenly raised the pitch of his voice, the mosquitoes quickly moved up and away from the singer. The tones which were attractive to the mosquitoes when sung or hummed sounded similar in pitch to the artificial sounds produced by the electronic sound generating system that were attractive to male *Ps. columbiae*. The reaction of the swarming males to changes in volume and pitch of the hummed sounds give indication that, in addition to using sound to locate potential mates, *Ps. columbiae* males may also use sound to maintain their distance and spatial relations within the swarm.

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