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ATTRACTION OF MALE MOSQUITOES TO SOUND

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ABSTRACT. Early observations and experiments on the attraction of male mosquitoes are reviewed briefly. Our present inadequate knowledge of the physiology of sound receptors is summarized and some of the hypotheses to explain direction finding in flying male mosquitoes are discussed. Some of the field tests carried out to attract mosquitoes to traps with sound, alone or combined with other attractants, are described and the potential for using sounds in mass trapping or sterilizing and releasing mosquitoes is assessed.

The use of sound is an essential component in the mating behavior of most mosquitoes and many related flies with similarly adapted antennae. Because of the importance of the biting habits of females of these insects, both as pests and vectors of diseases, the potential for exploiting the attraction of the males to the sound of the female in flight has understandably been neglected. I hope to point out its relevance and describe our current knowledge of the subject in this paper.

Although swarming in mosquitoes was known to Réaumur (1738) at the beginning of the 18th century and described, probably in the same species, *Culex pipiens* Linn., by De Geer in 1776, the first reference to males being affected by sounds seems to be about a century later when Christopher Johnston, a Baltimore physician, described the elaborate hearing organs of mosquitoes (1855). He wrote: "That the male should be endowed with superior acuteness of the sense of hearing appears from the fact that he must seek the female for sexual union either in the dim twilight or the dark night where nothing but her sharp humming noise can serve him as a guide".

The first experiments to attract mosquitoes from swarms seem to be those of Landois (1874). Using tuning forks, he noted that the "voices" of the sexes were different and he attracted males by singing tones of d' or e' (between 300 and 350 Hz).

The difference in "voice" is because the males of almost all investigated species of mosquitoes and chironomid and ceratopogonid midges beat their wings at about twice the rate of their respective females. This results in a clearly audible difference between the sounds of the sexes, an obvious adaptation to the use of the sound of the female to attract the males. In species where large numbers of males swarm together they can evidently tune out the sounds of other males and detect the lower wingbeat of approaching females.

Species that do not use sound as a close range attractant, such as the crabhole mosquito, *Deinocerites cancer* Theobald, and the pitcher plant species, *Wyeomyia smithii* (Coq.), have little difference in wingbeat frequency between the sexes. Interestingly and perhaps significantly, the antennae of males and females of these species are similar in appearance, whereas the males that swarm and use sounds have whorls of long fibrils on the antennae giving them a bushy or feathery appearance very different from those of the females.

Soon after Landois's experiments, the famous Anglo-American inventor Sir Hiram Maxim wrote to the *London Times* of large numbers of mosquitoes being attracted by the humming of a newly installed electrical generator (Maxim 1901). As Service (1976) astutely pointed out, Maxim referred to the feathery antennae and smaller size of the males compared with females and may in fact have been describing the attraction of chironomids, which often occur in huge acoustically sensitive swarms in daylight.

At about the same time, Professor A. M. Mayer (1874), a physicist about whom I could discover little, was performing a series of experiments that are still described in some textbooks. They are worth discussing because the actual physical basis of the effect of sound on the antennae of males is still not well understood and, as many physicists point out, common sense very often does not apply to physical phenomena. Mayer had a set of 9 tuning forks, from about 128 to 1,024 Hz, with resonating boxes that amplified their output. He began his experiments "late in the fall" so probably used a *Culex* sp. He cemented a live male mosquito on a microscope slide with shellac and looked at the tips of several fibrils with a "⅕" objective, which probably had a magnification between 20 and 40×.

After experimenting with 12 mosquitoes, he concluded that their long fibrils were tuned to various frequencies between 250 and 1,000 Hz. He wrote that with a 512-Hz fork "certain of the fibrils enter into vigorous vibration while others remained comparatively at rest".

Mayer's experiments were repeated by Yagi and Taguti (1941) in Japan. Taguti found that male *Culex pipiens pallens* Coq. were strongly attracted by an electronically generated sound at 217 Hz. Observing the antennae of males under the microscope they found that when the sound source was perpendicular to an antenna, the flagellum and fibrils vibrated only at 217 Hz. When the sound was in line with the antenna, the fibrils were vibrated by frequencies between 193 and 870 Hz but vibration peaked at 217. They did not mention the tuning of individual fibrils and did not state the intensity of the sound. Belton and Costello (1979) pointed out the extremely wide range of wingbeat frequencies reported for *Cx. pipiens* (from 180 to 370 Hz). The attractive frequency reported by Yagi and Taguti (1941) is in the middle of this range but the vibration of the fibrils seen by Mayer (1874), perhaps because he glued the flagellum to the microscope slide, is not.

L. M. Roth, in 1948, carried out a series of detailed experiments on sounds and mating of *Aedes aegypti* (Linn.). He noted that a volatile chemical (i.e., sex pheromone) was not involved but that pure (sinusoidal) sounds generated by tuning forks or audio oscillators were all that was needed to attract and initiate copulatory movements in males of this species that mates any time that both sexes are flying. He observed that amputating both antennae or cementing the flagellum to Johnston's organ (JO) so that it could not vibrate blocked these responses. On the other hand, removing the fibrils from the antennae only reduced the sensitivity and the males responded normally to tuning forks but not to quieter females. Vibration of the flagellum, which can potentially stimulate up to 15,000 sensory neurons in each JO in this species (Belton 1989), rather than the vibration of the fibrils, tuned or not, is evidently the trigger for attraction and mating.

The role of fibrils remains obscure. Their length decreases from the 2nd or 3rd basal to the apical segments of the flagellum but when the antenna is stimulated laterally by sound, my videotapes show fibrils vibrating only at the resonant frequency of the flagellum (i.e., about 350 Hz in mature male *Ae. aegypti* at 20°C). If individual fibrils are tuned to different frequencies as Mayer suggested, their amplitudes of vibration must be small compared with that of the flagellum and it seems very unlikely that this is related to the attraction of the male to the sound of the female. Individual males respond only to sounds within a few tens of hertz on either side of the wingbeat frequency of a female reared under the same conditions and of the same age.

Even before the publication of Roth's paper, Kahn et al. (1945), at Cornell University, were recording the sounds of female mosquitoes on acetate phonograph disks, claiming that, as well as the sound of the beating wings, other sounds inaudible to the unaided human ear were produced. In their subsequent field tests in Cuba they played 7-sec bursts of sound recorded from a single female *Anopheles albimanus* Wied. behind an electrocuting grid. They attracted mosquitoes after sunset but from the lack of actual counts or claims in their publications it is unlikely that significant numbers of mosquitoes were killed. They did not point out that because most of the mosquitoes were male there would be little immediate effect on the biting rate (see Wishart and Riordan 1959). Kahn and Offenhauser (1949) did find that the intensity of the sound was important and that playing it at high sound levels repelled flying mosquitoes but did not activate or attract males resting in vegetation.

By this time there was some confusion about how the sound was produced and its specificity and there was an obvious need for further investigation into the use of sound to attract mosquitoes in the field.

A few years before his retirement from Canada Agriculture, George Wishart with technical assistance from Derek Riordan (1959) began to investigate acoustic attraction. In a series of elegant experiments with *Ae. aegypti* using accurate signal generators and sound level meters for the first time, they showed that mature flying males were attracted by a point source of pure sine waves between 300 and 800 Hz at 23°C. They used a low-speed vacuum line, 50 cm/sec, to remove males that flew at the 2.5-cm aperture of a driver, the type of loudspeaker used for public address announcements but without the horn attached. With the most attractive frequency of about 440 Hz, approximately 80% of the flying mosquitoes in a cage of males were attracted within 5 sec. This technique was totally objective and yielded reproducible results. They showed that a sine wave was as attractive as the harmonic-laden natural sound of a female, that the sound pressure level of mature females at 1 cm was about 40 dB, and that males could hear this at a distance of about 25 cm. In other experiments Wishart showed unequivocally that males could detect the sound of a female through a background noise up to 10 times louder and, in preliminary tests, he suggested that Doppler shifts in frequency or changing amplitudes of sound, which would be expected when females fly towards or away from males, had little effect on their attractiveness. However, one of Wishart and Riordan's (1959) conclusions was that a sound decreasing from a high to a low intensity would probably attract males that would otherwise be repelled by a constant high-level sound.

About the same time in Tübingen, Germany, the physicist Tischner (1953) and his group were able to measure the electrical activity of JOs of males in response to sound that vibrated the flagellum. Tischner showed that the antennae of male and female mosquitoes were tuned mechanically to particular frequencies and that the JOs of male antennae produced their maximal electrical signal in response to the wingbeat frequency of most females of the same species. Tischner and Schief (1955) showed that wingbeat frequencies of males and females increase over the first few days after emergence, and this matches quite closely the response of males to higher frequencies as they age. They were unable to record electrical activity from the JO of a female although their figure shows that its flagellum vibrates mechanically in response to sound and might even be more sensitive than that of males. This contradicts the assumption of several researchers, now widely quoted in textbooks, that the long fibrils of a male antenna enhance its sensitivity over one with a relatively bare flagellum. Both Wishart and I recorded electrical activity from female JOs and I found that the antennae of females were as sensitive to sounds around their wingbeat frequency as those of males. Investigating the mechanical suspension of the flagellae of both sexes of *Ae. aegypti*, McVean (1991) came to similar conclusions. He showed that the suspension of males was stiffer than the female's and suggested that the greater surface area of the male antenna served to match the strain on the larger number of sense cells in JOs of that sex.

Besides the effect of age, mosquitoes also appear to compensate for changes of temperature. Females beat their wings faster at higher temperatures and the tuning of male antennae increases similarly. Other environmental factors such as air pressure and humidity have much less effect on flight sounds (Belton 1986). Another parameter that may have a significant effect on mating success is size. Rearing temperatures and the availability of food can affect the size of adult mosquitoes, but again the tuning of the antennae of small males seems to match the wingbeat frequency of small females. This has seldom been taken into account when, for example, reared sterilized males are released into the wild population.

More research into the way male mosquitoes orient to sound is needed. An early hypothesis of workers in Germany (Keppler 1958) proposed that the harmonic content of electrical activity in JO changed with the direction of sound, being highest as the source moved in line with the flagellum. But Wishart et al. (1962) showed that the electrical response from JO was minimal when the source was in line with the flagellum. It now seems clear that the toroid of sensillae in each JO is intrinsically directional, and that if, in its central nervous system, a male can compare the azimuth and phase of the vibration of both its flagella it could rapidly pinpoint the source of the sound of a female (Belton 1974). This raises an important consideration in the use of sound to attract males, that is: if the attractive sound is produced at some distance from males, or is generated by a transducer much larger than the mosquito, the signals in the 2 JOs will be similar. Several investigators have noted that a point source from which sound diverges, such as a tuning fork or the pursed lips forming the sound "ooo", is more attractive than a nondivergent source, such as a large loudspeaker.

With the increased sophistication and miniaturization of electronic components, the probability of being able to attract a significant number of males to sound in the field is improving. My preliminary tests in Ontario (Belton 1967) used a large axial suction fan and sounds from a vacuum-tube amplifier tuned by a reversing electric motor, a bulky assembly weighing about 10 kg and not readily portable. It was set up under a branch where *Aedes stimulans* (Walker) were swarming and it collected up to 100 males per night.

After detailed laboratory and small scale field experiments, Ikeshoji (1986) set up a much larger trial in a paddy field in Japan. His traps consisted of 30-cm-long polyethylene tubes with a speaker 9.3 cm in diameter at the center. The inside of the tubes was coated with adhesive and 14 of them were placed on tripods 1 m above the ground over a 1 × 2-m or 1 × 3-m rectangle of black cloth used as a swarm marker. Traps spaced 20–50 m apart emitting a 370-Hz sound at 100 or 110 dB for 20 min at sunset each collected up to 600 male *Culex tritaeniorhynchus* Giles.

In Malaysia, Kanda et al. (1987) used techniques similar to those of Ikeshoji to attract *Mansonia* species and *Aedes albopictus* (Skuse). Using 2 plastic tubes at right angles to each other, coated with adhesive and containing 9-cm loudspeakers, they played sounds using small portable tape recorders for about an hour at sunset. With the most attractive frequencies of 330 or 350 Hz, they were able to trap up to 900 male *Mansonia* in one night. In a different locality they collected up to 52 *Ae. albopictus* per night playing the sound at the much higher wingbeat frequency of females of this species, 480 Hz. They found that catches of male *Mansonia* were enhanced 100-fold if a guinea pig and dry ice were hung below the tubes, whereas no such synergistic effect was found for *Ae. albopictus.*

Similar trials in Thailand on the edge of a rice paddy (Thongrungkiat 1990) may indicate that, in addition to males, female *Culex tritaeniorhynchus* can be attracted to traps like those used by Ikeshoji if a hamster and dry ice are suspended below it or if the speaker is inside an adhesive-coated hamster cage. Over 6 nights, Thongrungkiat reported an average catch of 79 females in a trap with no sound compared with 135 with a sound of 530 Hz. Over the same period, an average of 18 males was caught in polyethylene tube traps with a sound at 350 Hz (closer to the female wingbeat frequency than the 530 Hz used in tests with females). He trapped for 21 days with 21 traps but found no change in population density or insemination rate.

It seems unlikely that any of the field trials, from those of Kahn and Offenhauser in the 1940's to the present, have attracted significant numbers from the large natural populations of mosquitoes in the area. Nevertheless, sound traps are highly selective and can be used, as Ikeshoji (1982) demonstrated, to sterilize and release male mosquitoes. I believe that sound traps can play a part in the integrated control of these intractable pests particularly in isolated environments such as tire dumps, parks or small marshes. It would be optimistic at present to expect any effect on the huge populations in the tundra or in extensive tropical or boreal forests.

Traps are becoming smaller and more efficient; the power consumption of fans and sound-storing integrated circuits should allow them to be operated from solar-charged batteries. Suction traps, or those with lethal grids would require less maintenance than designs based on adhesive surfaces, which are ineffective for many mosquito species. Recently, a light trap with a fan and mechanical device for killing mosquitoes was designed that could easily fit into a briefcase (Anon 1993). With a sound source and solar power, this could be a useful addition to many control programs.

I dedicate this paper to the memory of George Wishart and Derek Riordan, Canadian enthusiasts, innovators and above all, scientists.

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