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The love song of the fruit fly

The value of the fruit fly *Drosophila* in genetic research lies partly in its enormous multiplicity of species. Humans find it hard to distinguish them, but it now appears that the flies recognize suitable mates by sound

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Much of our present-day knowledge of heredity has been gained through the study of a little fly, *Drosophila melanogaster*, variously called a fruit fly, a vinegar fly, a pomace fly and a garbage fly. It is a harmless creature about two mm in length that breeds rapidly under laboratory conditions. It has a generation time of under two weeks and one fertilized female can produce up to two hundred offspring. Many easily identifiable mutant characters such as differences in eye colour have been described, which makes *Drosophila* an ideal organism to demonstrate Mendelian segregation. Also, these flies have in their salivary glands giant chromosomes containing dark bands which can be considered as indicating the positions of genes. Trans-

locations, inversions and deletions within the genetic material can easily be seen in these giant chromosomes.

Drosophila is usually cultured on a corn meal, molasses, yeast mixture in half-pint milk bottles which are plugged with cotton wool. A pair of flies can be placed in a bottle, allowed to mate and lay eggs. When this was done, originally, with flies caught in the wild a few pairs refused to breed and it was quickly discovered that there were many different species of *Drosophila* which were superficially very similar.

In America A. H. Sturtevant described 23 new species in a single paper in 1916, and since then perhaps some 2000 species have been recorded, almost 1000 of them from the island of Hawaii alone where evolution in the genus *Drosophila* appears to have run riot. Many species resemble one another so closely that they can only be separated by careful examination under a high-power microscope or even, in some cases, by dissection and comparison of internal features. Such closely related species are termed sibling species.

If this is the only way they can be separated how do the flies distinguish potential mates of their own species? It has been found that they do this partially by scent or taste but also we believe by the nature of their songs.

If you watch a pair of *Drosophila melanogaster* you will see that before copulating the male performs a courtship dance. During this he extends one wing and runs after the female vibrating this wing (Figure 1). If she has not previously mated and if she is mature, she will stop running and allow the male to lick her genitalia with his proboscis and then to mount her and copulate. Figure 2



Figure 1 Male *Drosophila melanogaster* courting a female by standing behind and to one side of her and waving one of his wings.



Figure 2 At a later stage of courtship, he protrudes his proboscis and curls up his abdomen, ready to mate. He is still waving one wing

shows a male approaching the female and preparing to lick. If the two flies are of different species the male will probably court but the female will jump or fly, or kick, or flick her wings at the male.

Thus the courtship is one where the male will display to a female and she determines whether or not he is a suitable mate from his display. The American zoologist Spieth, has described the courtship displays in about 40 species of *Drosophila* and he found that many different species had seemingly identical displays. It was unlikely therefore that the females could discriminate on the basis of visual stimuli. This was supported by the finding that the majority of species mate quite successfully, and without hybridizing, in the dark.

In 1964 one of us found that courtship success was related to the wing area of the male. A male with amputated wings mated more slowly and a specially selected large winged stock provided males that mated faster than normal flies. About his time H. H. Shorey found that male *Drosophila melanogaster* made a noise during courtship consisting of a series of pulses of regular duration and interval. We became interested in this as it seemed likely that the pulses were produced by the wing display and were a code that identified the male to the female.

The first part of our work was to build apparatus to record the courtship sounds. We quickly found that the sound was very low indeed—the wing is only about two mm long and beats through about 0.5 mm. A crystal microphone was sensitive enough to pick up the sound if the flies were placed directly on the microphone diaphragm but that 20 cm of plaster board and glass wool sandwich all round barely gave enough insulation.

The "song" of *Drosophila melanogaster* is a series of nearly pure single sinusoidal cycles of sound, (Figure 3A). At 25°C, the single cycle has a frequency of about 330 cps and is repeated 29 times a second. Its sibling species, *Drosophila simulans* produces the same sound pulse 20 times a

second. Here, then, were two closely related species with a similar display differing only in pulse repetition rate (Figure 3B).

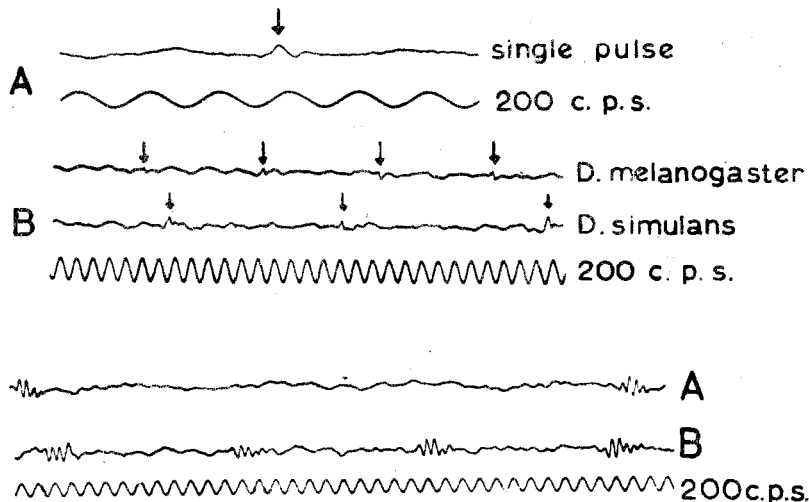
At this stage there was only circumstantial evidence that this sound was relevant in courtship, so we built an electronic circuit that produced an electrical analogue of the courtship sounds and used this to drive a loudspeaker.

The artificial courtship sound was played to groups of normal females and wingless males and these were induced to mate more rapidly than without the sound. When an air current was blown over them as well, the flies mated even more rapidly than the normal winged males. So it appears that the winged display provides tonic and phasic stimuli and, with the right sound, a female will accept an otherwise unattractive male.

Since then we have examined other species which are closely related to *D. melanogaster* and *D. simulans*. Most of these produce trains of single sine waves of sound repeated, as for example in *D. bipectinata*, as often as 110 a second. Another group of flies which are more closely related to one

Figure 3A Courtship sounds of two species of *Drosophila*. In A, a single sound pulse is shown, in B, *D. melanogaster* and *D. simulans* show similar pulses produced at different rates.

Figure 3B Courtship sounds of A, *D. pseudoobscura* and B, *D. persimilis* showing the same notes produced at different intervals



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continued

another than they are to *D. melanogaster* and its relatives, is the obscure species group. These tend to produce longer notes of up to seven sine waves with a higher frequency of about 500 cps. The repetition rates of these sounds varies from five per second in *D. pseudoobscura* to 20 per second in its sibling species *D. persimilis*, (Figure 4).

In *D. melanogaster* and *D. simulans* and a few other species, one wing is held out at right angles to the body during vibration while in most species including *D. persimilis* the wings are extended to a lesser extent. It is likely that by progressively unfolding the wing the fly can alter the extent to which the wing is coupled to the thoracic box thus changing the resonant frequency of the thorax and consequently of the sound produced.

The fly thorax and wing form a mechanical unit when the wing is fully extended. The thorax is an elastic box with the peculiar property of holding the wing in two stable positions, up or down, but not between the two. If the raised wing is pushed downwards it will suddenly click into the down position and vice versa. In flight this system is used to maintain wing oscillation by producing suitable mechanical loading for the large flight muscles. The

wing beat frequency during *Drosophila* flight is about 200 cps and recordings show that a fairly complex pattern of sound is produced. One of the components of this sound is virtually identical to the courtship note of *D. melanogaster* and *D. simulans*. We believe that the songs in these species are produced by repeated up and down movements of the wing, but with the main flight muscles unstimulated so that the entire resonant system does not go into oscillation. In *D. pseudoobscura* and *D. persimilis* which produce songs with their wings partially folded it appears that the main flight muscles are activated intermittently. The sounds produced, however, are of a higher frequency than in flight as the mechanical loading of the thorax by the wing is less when the wing is in the unextended position.

Unfortunately, the problem of insect flight is a very difficult one, especially with minute insects, and our study of this aspect of the problem has only just begun.

Various insects have organs that may be described as ears, with tympanic membranes. Grasshoppers have ears on the fore legs and, incidentally, have elaborate love songs and similar problems of finding the right mate as does *Drosophila*. Noctuid moths have thoracic ears used to detect the radar-like emissions of bats that prey on them. Flies, however, do not have ears with tympanic membranes.

Very recently a colleague, Aubrey Manning, has shown that if the feathery part of the fruit-fly's antenna, the arista (Figure 5), is removed or glued down, female *Drosophila* became unresponsive. We have watched the antennae of *Drosophila* when loud pure sounds are played and found that the arista and distal joint of the antenna vibrate with a natural resonance of about 200 cps. This suggests that the antenna is used to receive the love song.

Drosophila courtship is interesting at various levels. The love songs are produced by the wings in what appears to be a simple modification of the flight mechanism and the receptor system in females is adapted from one used in the control of flight. The sound language may have evolved from the buzzing noise that flies and other insects make when warming up before flight. A few species appear to have lost the ability to produce sounds and the wing displays provide visual stimuli.

Any language is restricted by the number of words in its vocabulary; this one is interesting in having only a very few words, but so far the only species with identical songs are two morphologically rather dissimilar species, *D. pseudoobscura* and *D. ambigua*. The former species is restricted to the North American continent and the latter to Europe and so are never likely to meet and hence need a language barrier. In contrast *D. pseudoobscura* and its sibling species *D. persimilis*, whose habitats overlap, have quite distinct songs. These two species are so similar morphologically that the most certain means of distinguishing between them is by listening to them courting.

The female fly also has a language but it consists of only one word; a long, very loud and very effective buzz. Its meaning to males of all species is "No".

Figure 5 Head of *Drosophila melanogaster* showing the compound eyes and the feathery arista of the antenna

