tion received from Herman Wessner. caretaker of the Woods Hole golf course for many years (6). He stated that only screened marine beach sand from Nobska had been placed in this particular trap for the past 15 years. This may be evidence that these animals have been there for a long time; they have not been found elsewhere in the Cape Cod area.

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- 27 March 1962

## Nature of the Sound Produced by Drosophila melanogaster during Courtship

Abstract. The wing vibrations of courting male Drosophila melanogaster Meigen produced pulsations of sound, with each pulse apparently caused by 1 to 2 cycles of wing movement. The average repetition rate at 25°C was 29.8 pulses per second. The rate was dependent on temperature, increasing at 1.4 pulses per additional degree Celsius.

A variety of overt male courtship behavior patterns is evident among the many species of Drosophila. For a given species, some or all of the following elements may be observed: tapping the female with the legs, posturing near the female, vibration or scissoring of the wings, and "licking" of the genitalia. Spieth (1) presents a comprehensive account of courtship and mating for 101 Drosophila species. These courtship behavior patterns have been intensively studied by researchers interested in the evolution of behavior and the development of sexual isolation between similar species.

The most obvious characteristic of courtship in D. melanogaster Meigen is the wing display, in which the male extends one wing to an angle of approximately 90 degrees to the side of the body and vibrates it. The wing extended is usually the one closest to the head of the female. The male ultimately assumes a position to the rear of the female and, in one coordinated series of movements, applies its proboscis to the female genitalia and attempts to copulate. If unsuccessful in this attempt, the male generally persists in its courtship-posturing at various angles to the female, vibrating a wing, and trying to mate.

There is at present no direct evidence that the wing vibrations of male Drosophila serve as an auditory stimulus to the female. Indirect evidence supporting (1, 2) or casting doubt on (3) the existence of such a stimulus is presented by various authors. My research was initiated in an attempt to characterize the wing vibrations of male D. melanogaster so that the function of this element of courtship behavior might be more thoroughly studied.

Virgin wild-strain adults which had been caged individually for 4 to 5 days after their emergence from puparia were used. For each trial, a male and female were anesthetized with carbon dioxide and were placed in a cylindrical cage constructed of 32-mesh plastic screen and measuring 12 mm in diameter by 10 mm in height. The bottom of the cage was mounted on the sensitive element of an Altec model 21 D condenser microphone, and the top was covered with a glass cover slip.

The microphone and attached cage were shielded from extraneous noise by an insulated box. The interior of the box, measuring 8 inches in height by 4 by 4 inches, was filled to a depth of 5 inches with rock wool insulation; the microphone was embedded in the insulation with only the cage exposed. Each side and the bottom of the box were constructed of two 2-inch-thick layers of glass wool placed alternately between three <sup>1</sup>/<sub>2</sub>-inch-thick layers of plaster board. The outer surface of plaster board was faced with 1/2inch-thick plywood. The top of the box was covered with five sheets of 1/2 -inchthick plexiglass which were separated from each other by 1-inch air spaces.

The microphone generated heat which increased the air temperature in the cage by 1/4° to 1/2°C per minute. Temperatures were measured with a Leeds and Northrup single range potentiometer connected to copper and



Fig. 1. Sound produced during courtship by a D. melanogaster male at 25.3°C. Top trace is a time marker at 200 cy/sec. Bottom trace shows sounds produced during two consecutive pulses of wing movement, with one pulse at each end of the trace.

constantan thermocouple leads. The leads were joined inside the cage.

Sounds produced by the males during wing vibration were transmitted from the microphone through an alternating current preamplifier to an oscilloscope. Photographs of the traces on the oscilloscope screen were obtained so that the nature of the sound could be accurately characterized.

The vibrations consist of series of discontinuous pulses of sound (Fig. 1). The pulses, each of which appears to correspond to between one and two complete cycles of up and down wing motion, occur at fairly regular repetition rates for any given temperature; the average rate at 25°C was 29.8 pulsa-



Fig. 2. Relationship between temperature and frequency of pulses of wing movement produced by male D. melanogaster during courtship. Correlation coefficient is 0.79, significant at 0.05 probability level.

tions per second. The frequency of wing-beat-induced sound within each pulse was quite variable, generally falling between 150 and 300 cy/sec. A significant correspondence between pulsation rate and temperature was manifested, with the rate increasing by approximately 1.4 pulses for each rise of  $1^{\circ}C$  (Fig. 2).

The sound produced was of such low magnitude as to approach the limits of sensitivity of the microphone and amplification equipment. In no known instance have these sounds been detected by the unaided human ear. The amplitude of wing excursion, which probably does not exceed 1 mm, appears to differ markedly among individual males. In most trials, interpretable signals were seen on the oscilloscope screen only when the male was oriented near the bottom of the cage with its vibrating wing close to the head of the microphone. A few males produced relatively strong sounds regardless of their location in the cage, and a few produced no discernible sounds at any time during their wing vibration behavior (4).

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## Oxygen-Motivated Behavior in the Goldfish, Carassius auratus

Abstract. Goldfish placed in deoxygenated water learned to interrupt a light beam in order to obtain brief exposure to aerated water. The training procedure brought this behavior under the control of arbitrary visual stimuli.

Swimming seems to be the obvious choice for studying the behavioral reactions of fish to variations in available oxygen. In two recent studies (1) investigators have exposed fish to spatial gradients of oxygen tension and have observed their locomotion. Although swimming may occur in nature as a reaction to a deficiency of oxygen, it is not necessarily an ideal dependent variable in behavioral studies. For ex-



Fig. 1. Experimental chamber. (a) General view and (b) plan.

ample, it is not clear to what extent swimming is an acquired or a reflexive response to oxygen deficit. If it is to any degree acquired, the learning process may go on outside as well as during the course of the experiment. Moreover, without some restriction on the direction of the fish's movement with respect to the oxygen gradients in the experimental chamber, swimming may become associated with both increases and decreases in available oxygen, thus creating an ambiguity in the relation between behavior and its consequences. To these difficulties must be added the problems of recording and quantifying swimming itself.

In the experiment described here a relatively arbitrary response of the fish was selected for study; the response is associated with temporal, rather than spatial, variations in oxygen tension, and the relation between the response and the changes in available oxygen is under the immediate and precise control of the experimenter.

The experimental chamber (Fig. 1) comprised a 4½-inch-long, clear plastic tube with a 1-inch internal diameter. Water flowed through this tube at a constant low rate (500 ml/min). The fish maintained its position in the tube by very slow and continuous swimming. A small perforated disk at the downstream end of the chamber prevented the fish's tail from lodging in the outflow tube.

Near the front end of the chamber was a small plastic constriction or bridge with an opening just large enough to admit the fish's head without contact. A light beam passed across the tube just upstream of this constriction. The interruption of this beam, which activated a photorelay, comprised the response. The goldfish learned to swim forward and back in a relatively stereotyped manner to break this light beam with its head. The bridge minimized chance interruptions of the beam resulting from general activity of the fish.

The water flowing through the chamber came from one of two sources. The first was equilibrated with air. The oxygen content of the second supply was reduced in a deoxygenating column through which nitrogen was forced. The modified Winkler test showed that this system produced almost complete deoxygenation. The water was recirculated, passing through a glass-wool and carbon filter. It was maintained at  $25^{\circ} \pm 0.5^{\circ}$ C by thermostatically controlled heaters.

Two electrically operated valves im-





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