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THE AUDITORY (ULTRASONIC) RECEPTION AND
BEHAVIOR OF TWO STORED PRODUCTS PESTS:
THE ALMOND MOTH, CADRA CAUTELLA, AND THE
INDIAN MEAL MOTH, PLODIA INTERPUNCTELLA,
(LEPIDOPTERA, PYRALIDIDAE).

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PRODUCTS PESTS: THE ALMOND MOTH, CADRA CAUTELLA, AND THE INDIAN
MEAL MOTH, PLODIA INTERPUNCTELLA, (LEPIDOPTERA, PYRALIDIDAE)

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INTRODUCTION AND LITERATURE REVIEW

The large volume of literature in the field of insect acoustics is amply demonstrated by the bibliography of Frings and Frings (1960). The approximately 1800 references there have by now almost doubled. Haskell (1961) reviewed this literature on sound production and reception, and Roeder (1966c, 1970) surveyed recent literature, particularly regarding his research. Frings and Frings (1971) reviewed the literature on sound production and reception by insect pests of stored products.

Romanes (1876) noted that certain moths were sensitive to high pitched sounds, and White (1877) suggested that the moths might thus be able to hear bat predators and escape. Deegener, (1909) described and named paired structures on the metathorax of noctuid moths as "ears." However, Stobbe (1911) found that mutilation of these structures did not stop the moths from responding to the squeaking of a cork bottle stopper. Eggers (1923, 1925, 1928, and 1934) and Kennel and Eggers (1933) published a series of anatomical papers on tympanal organs of noctuids, arctiids, geometrids, and pyralidids. The tympanal organs in noctuids and arctiids are on the metathorax, while in geometrids and pyralidids they are on

base of the abdomen. In all, representatives of 13 families have tympanal organs on the base of the abdomen (Eggers, 1928). Morphological studies are lacking on the tympanal organs of Cadra and Plodia, the genera used in this study.

It was not until 1941 that Griffin and Galambos showed that bats make use of ultrasonic pulses in orientation. Schaller and Timm (1950) first reported evasive responses by moths to artificially generated ultrasonic sound or to the approach of bats, and Griffin (1953) demonstrated that bats use their ultrasonic pulses in prey capture. Treat (1955) reported that four species of moths (two of which were pyralidids), when flying, swerve abruptly at each stimulus with a Galton whistle. He also tethered moths on long silken strands and observed responses. He then tethered moths to a kymograph and demonstrated start and stop responses and changes in flight pattern. While unilateral tympanectomy caused no differences in this response, bilateral tympanectomy abolished it. If the chordotonal strings were detached in any way, the response was abolished. Destruction of structures around the tympanal membranes and perforation of counter-tympanal membranes had no effect. The counter-tympanal membranes in noctuids are membranes inside the counter-tympanal chambers. He could not get kymograph records with the delicate bodied pyralidids.

Haskell and Belton (1956) and Treat and Roeder (1956) later began a series of electrophysiological studies on ultrasonic reception in moths, most of which were noctuids. Belton (1962) has done the only electrophysiological studies on pyralidids. He reported electrical responses in the European corn borer, Ostrinia nubilalis,

and the wax moth, Galleria mellanella, at sound pressure levels (SPL) as low as 30 dB (hereafter all dB = deciBel are re 0.0002 dynes per sq. cm) and frequencies above 18 kHz (hereafter all kHz = kiloHertz or thousand cycles per second) at 90 dB.

His studies showed that four chordotonal organs are present in each tympanum in pyralidid moths. This study included the flour moth, Anagasta kuehniella, as well as the above-named two species which all responded behaviorally to high frequency sounds while tethered or immobilized, but apparently the flour moth was not successfully studied electrophysiologically.

Treat (1962) compared moths trapped in a sound trap (the moth had to pass through an ultrasonic sound field to get trapped) with those trapped in a silent light trap and found that the most effective frequency for moths with abdominal tympana was 75 kHz. In the latter case 82% of the moths trapped in both traps were trapped in the silent light trap. Photographs have been taken (Roeder, 1962) of wild moths, usually not identified, subjected to artificial ultrasonic pulses. They showed directional responses (moving away from sound sources) at low intensities, and non-directional responses (power dives, loops, rolls, or sharp turns) at high intensities. Sound pulses at 30/sec, 5 msec duration were usually used; pulses of 10/sec were equally effective. He found in this study that lacewings (Chrysopidae) respond similarly. Roeder (1965) tested moths, captured in the field and later identified, in an enclosure, but possibly because of their excited state the stimulus did not affect their behavior. Agee (1969) used a 50 by 50 ft. section of insect netting laid over the grass into which the moths

dived and were then captured. Thus, he was able to study for the first time evasive behavior of identified species of moths, including the bollworm moth, Heliothis zea, and ten other species of noctuids. Of the moths that attempted evasion of bats, only 8% were caught by the bats, but of the moths that did not attempt evasion, 39% were caught. The survival differential was therefore 4:1.

Roeder (1963) mounted moths with wax on insect pins and tested them while they were in stationary flight. The frequency he used was between 70 and 90 kHz. He found that maximum echo occurs when the wings are at right angles to the ultrasonic source --30 dB greater in this position than in the minimum echo position. Cessation of flight eliminates much of the moth's echo. Roeder (1966d, 1967a) devised a very sensitive anemometer for showing directional changes of moths in the presence of ultrasonic sounds. Turning behavior was elicited in response to a pulse rate of 10/sec but was absent or transient to single brief pulses, or to non-pulsed tones. Turning responses in noctuids, according to Roeder (1967b), result mainly from partial folding of the wings on the side away from the sound. He observed that the whole body also bends in the turn. Payne et al., (1966) suggested a possible mechanism for directional sensitivity for noctuids using the difference in intensity between the near side (with respect to the sound source) and the far side of the moth. As much as 40 dB difference in sensitivity was found depending on the position of the sound source relative to the moth's body axis and the position of the wings.

Roeder (1964, and 1966b) extended the earlier electrophysiological studies, seeking a neurological basis for turning or avoidance behavior of noctuids. He (1970) theorized that bat pulses elicit turning behavior until the moth turns away and the pulses are then unmodulated by its own wing beat. This happens when the moth's wings are not between the tympanal organs and the bat (body axis in line with the bat). The area of no modulation is larger with the moth moving away from rather than toward the sound source so by this method the moth can move away from the bat and evade capture. The erratic behavior (non-directional diving and looping) is probably caused by saturation of both the more sensitive and the less sensitive nerves (designated as A1 and A2 respectively) in both ears (Roeder, 1970).

For a ctenuchid moth, Frings and Frings (1957) reported inhibitory responses at high frequencies but other responses at low frequencies (below about 18 kHz). Roeder (1968) found four out of 19 sphingid moth species responsive to high pitched sounds. Both vigorous behavioral responses and responses detected electrophysiologically in interneurons originating in the head occur. The acoustic receptor appears to be in the labial palps. Arctiid and ctenuchid moths produce ultrasonic sounds as well as detect them (Blest et al., 1963; Dunning and Roeder, 1965). There is good evidence that this is a case of aposematic advertising (warning sounds) of the noxious arctiids (Dunning and Roeder, 1965; Dunning, 1968). Kay (1969) found that Heliothis zea (Noctuidae) emits 50 kHz bursts every 25 msec in synchrony with the wing beat. The bursts consist of two 185 microsec units. This indicated possible echo-

locating capabilities for this moth.

Cadra cautella is essentially a warehouse pest (Cotton, 1950). The Indian meal moth, Plodia interpunctella, however, is thoroughly established out-of-doors, in California at least. It is the main lepidopterous pest of many stored foods, and can be found in nearly all food processing warehouses and in most home kitchens in the U.S.A. Both species are cosmopolitan (Donohoe, 1946). References in the text to "Plodia" and "Cadra" refer to these species.

While these species are associated with man, perhaps they still retain sensitivity to bat sounds. Frings and Frings (1965) suggest that specific sounds might be found which would repel certain insect pests. Communication signals might be used, and they are not likely to injure man, as pesticides do. Robertson, (1944) used several stimuli to separate the saw-toothed grain beetle, Silvanus suranamensis from tea. As the tea passed by on a conveyor belt, heat, light, and mechanical agitation stimulated the insects to leave the tea. Frings (1948) and Frings and Frings (1962, 1963, and 1965) have reported the relatively few and disappointing attempts at insect control by sounds, but they also point out the future possibilities. If extremely intense sounds (160 dB) are used to physically kill the insect pests, the expense is prohibitive (Allen et al., 1947; Frings et al., 1948). Wojcik, 1968, 1969) searched for acoustical communication signals from ten species of insect pests of stored products including Ephestia elutella and Cadra cautella. He monitored sounds produced under various conditions--e.g., during stress or mating activity. No non-

incidental sounds were heard. He apparently considered the flight tones as incidental sounds, for these are clearly audible if a tethered moth is held close to the ear or one in free flight flies within a few inches of the ear. This can also be heard as the males court. Chemical communication signals (pheromones) have been reported for many of these insects (Brady and Smithwick, 1968).

The bollworm moth, Heliothis zea, and the tobacco budworm moth, H. virescens, show typical evasive behavior to ultrasonic sounds (Agee, 1967), but in a preliminary field test ultrasonic sounds (21-22 kHz, pulsed 10/sec) did not affect the infestation level of either species in cotton. Agee noted, however, that equipment failure could have caused the lack of control. Belton and Kempster (1962), in a field test with a pyralidid moth, the European corn borer, Ostrinia nubilalis, used an "artificial bat signal" (pulsed 50 kHz tone) that reduced the infestation in a corn field more than half. Kirkpatrick and Harein (1965) used low frequencies (120-200 Hz) with laboratory populations of Plodia interpunctella, exposing adults during oviposition to the sounds and then removing adults from the food stations. They counted the adults that emerged and found that the number was reduced to 74.8% that of controls. They suggested that higher mortality in the treated chambers might have caused the reduction in oviposition.

POTENTIAL ORGANS OF PHONORECEPTION

Among insects in general, the following organs may serve as phonoreceptors: tactile hairs, spines, hair plates, campaniform sensilla, muscle receptor organs, and chordotonal organs (Frings and Frings, 1970). The chordotonal organs may be in simple form (e.g., in appendages) or as units of complex sensilla (e.g., tympanal organs or Johnston's organs). Eggers (1928) showed that pyralidids have tympanal organs in the base of the abdomen. Belton (1962) showed that at least one pest of stored products in this family was receptive to sounds of ultrasonic frequencies. The phonoreceptors were the tympanal organs.

Treat (1953) noted that many drawings and diagrams of lepidopterous tympanal organs are found in the extensive literature dealing with morphological and taxonomic studies, but no photographs showing the true tympanal membrane or associated complex parts. He provided three photographs and one diagram of the noctuid tympanal organ. Since then, no other similar photographs have been published for any family of lepidopterous insects. Mullen (1969) has made scanning electron micrographs of the tympanal membranes, but these have not so far been published.

In the intact moths (Cadra cautella and Plodia interpunctella) the paired tympanal membranes face forward (Fig. 1) and are tilted

slightly laterally and ventrally. If the thorax and abdomen are drawn together dorsally (Fig. 2), the tympanal membranes can be viewed. The metathoracic coxae (Fig. 3) fit closely over the surfaces of the tympanal membranes. These membranes lie in a slit between the anterior margin of the first segment of the abdomen and the posterior margin of the metathoracic coxae.

In a whole mounted female specimen of Cadra (Fig. 1), the area of the tympanal chambers clears well, while the rest of the abdomen, which is filled with eggs, does not. Thus, the position of the tympanal chambers and (at the anterior margin) tympanal membranes is clearly demonstrated. The size is larger than appears in the figure, because the eggs and other tissue partially cover the rounded tympanal chambers, except in the center where the chambers almost touch the body wall. The position of the tympanal chamber can best be demonstrated, as in Figure 4, where all tissues of the abdomen have been dissected away except the anterior margin of the first abdominal segment and the tympanal organs. The relative size and shape of the tympanal organs can be seen in Figure 5, in which Cadra appears on the left and Plodia on the right. While Plodia is generally more robust than Cadra, the tympanal organs are smaller in Plodia.

The tympanal membrane (Fig. 6) is clear and brittle. It is lateral to the counter-tympanal membrane (Mullen, 1969) which is in contrast white and leathery. The tympanal membrane has a ridge surrounding the outer attachment of the chordotonal string. The inner attachment of this strand is on the inside wall of the tympanal

chambers where there is also a circular ridge surrounding the point of attachment.

The inner point of attachment can be seen either through the intact transparent tympanal membrane, or (Fig. 4) through the tympanal chamber dorsally when the tissue dorsal to it has been dissected away. If the counter-tympanal membrane is ripped away and the tympanal membrane is pulled out, the inner attachment of the chordotonal string breaks. The tympanal membrane can then be folded out (Fig. 7) so that the narrow chordotonal string is seen over most of its length.

Diagrams in Figure 8a show the approximate position that sections were cut from Cadra. Figure 9 is a cross sectional view of the tympanal organs represented by the vertical line in Figure 8a. Figure 10 is a longitudinal section of the tympanal organs and is represented by the horizontal line in Figure 8a. Figure 11 is a longitudinal section of one tympanal organ and is represented by the vertical line in Figure 8b. With the exception of the tympanal membranes, the tympanal cavities are enclosed within a thin but hardened capsule and are easily crushed when dissecting them out of the abdomen unless caution is exercised. There are two chambers in each tympanal organ with the membrane separating the two chambers running vertically and longitudinally from the junction of the counter-tympanal membrane and tympanal membrane posteriorly. Sections (Fig. 9 and 10) showing this separating membrane are difficult to cut and the membrane is also difficult to see in fresh specimens.

GENERAL MATERIALS AND METHODS

The major part of the experimental work was carried out at the University of Oklahoma in a laboratory with controlled temperature and humidity. No acoustic isolation of the room was attempted, and the ambient sound level was about 75 dB. The temperature was maintained at $79 \pm 2^{\circ}\text{F}$. and the relative humidity $40\% \pm 5\%$.

Living almond moths (Cadra cautella) were provided by the United States Department of Agriculture at Savannah, Georgia, and living Indian meal moths (Plodia interpunctella) were captured in and around Norman, Oklahoma. The culture media used for both species were as recommended by the U.S.D.A. for Cadra. The medium consisted of the following: (in parts by volume) whole wheat flour, 4; cornmeal, 4; Gaines dog food (ground fine), 2; bakers' yeast, 1; oatmeal, 1; wheat germ, 0.5; honey, 1; and glycerine, 1. For new cultures, several adults from at least four different cultures were placed in a widemouth 1 qt. jar on not more than six cm of culture media. When more than six cm of medium was used, excessive heat, moisture, and molds destroyed many of the cultures. Both species were cultured continuously from 1967 to 1971.

It was desirable to find a reasonably natural situation for auditory testing which would yield reliable and behaviorally observable responses. Initially a wide variety of sound generating equip-

ment was used and spot checks were made with various frequencies at high intensities. The moths were flying about in the laboratory, or crawling or perching on a variety of substrates such as wood, cloth, food media, etc. In other tests, the moths were restrained in the sound field by mounting them on glass and wooden rods with a paraffin ball. Very few "flew" under these circumstances and none responded to any of the sounds used.

After numerous modifications of insect mounting methods were tried, (Frings, 1945) one modification was adopted for all tethered flight experiments. Cotton thread (No. 50) was drawn through melted paraffin and, after it stiffened, was cut into 3 cm sections. One end was dabbed in a pool of melted paraffin and the paraffin drawn out until a very small ball remained on the end of the string. Moths were chilled and placed in a Petri dish on ice under a dissecting scope. The ball of paraffin was fused to the notum of the moth with a hot dissecting needle, with the moth positioned so that the body axis was perpendicular to the string. The tethered moths were sexed and given numbers by their position on an insect rack. Stiffening of the string prevented the moth from flying upward to perch on the upper part of the thread or clip.

The tethered moths were placed in one of four sound chambers (Fig. 13), with the abdomen pointing toward the center of the speaker diaphragm, 52.5 cm from it. Cadra tethered in this way flew periodically, and responses to the sound stimulus could be noted. Among the non-electronically generated sounds which elicited responses in flying tethered moths are the following: squeaking of ground-glass stoppers turned in bottles; clicking of electric

switches; slapping of flat objects; sound of pop-guns; finger snapping; hissing through the lips; or sounds produced by hand held bats. Usually the brief pulses that many of these sources produced did not elicit persistent responses.

Preliminary tests with pure tones were disappointing. An audio-oscillator (Hewlett-Packard Model 200AB) was used with either a coaxial speaker (Utah coaxial-Model D15PXC-3) or with a tweeter (Mustang Model MS Sphericon Super Tweeter). This equipment was not capable of producing high intensity signals in the high frequency, or ultrasonic, range (above 15 kHz). Responses similar to those given to the noises were observed, but they were usually not duplicatable at the same frequencies and intensities. The responses observed at low frequencies were found to be due to the click or noise produced by the electric switch rather than to the particular signal that was being used as the stimulus. Many of these tests, however, were performed on tethered but non-flying moths, and later results showed that non-flying moths are not very responsive.

Indications were that the few reactions observed were the result of reception of ultrasonic sounds like those produced by bats. New equipment for production of sounds of known frequencies and intensities was therefore obtained (Fig. 12). An audio-oscillator (Hewlett-Packard Model 202CR) induced signal was reduced (shorted) by a potentiometer in order to prevent overloading the amplifier (McIntosh Model MC 30). Switching was done without an audible sound or electrical transient by the use of a photoresistor (Clair-ex Photo Conductive Cell CL 603) controlled by a silent push button switch powering a 6 v incandescent light. The amplifier boosted

the signal to a maximum of 15.0 volts peak-to-peak in order to have sufficient sound levels but not to overload the speaker (Listening Inc. Model EL 9-1). Pulsing was accomplished by using a laboratory stimulator (Grass 6 Stimulator, Model SM 6 C) which controlled a 6 v DC relay (Potter and Brumfield Type K5DY). The relay was acoustically isolated in a box because of the noise it produced. The pulse mode produced a click in the speaker each time a pulse occurred, but it was hardly audible. Intensity changes were controlled by the oscillator attenuator which was calibrated to allow selection at appropriate peak-to-peak speaker voltages. A Tektronix (Model 502A) oscilloscope was used to calibrate attenuator settings and as a monitor for wave form, peak-to-peak voltages, pulse rate, and pulse duration. Sound levels in dB were determined by using the factory speaker output calibration (dB to peak-to-peak voltages) and the peak-to-peak voltage readings of the attenuator. These two voltages V_1 and V_0 respectively) were used in the formula (dB difference = $20 \log \left(\frac{V_1}{V_0} \right)$). The dB difference was added to or subtracted from the dB output on the factory calibration curve for the frequency under consideration.

Preliminary results indicated that moths adapt to persistent sounds, so four separate but identical chambers were constructed and used. Since four moths were set up for simultaneous testing, and only one test was made with each in succession, a time lag was provided of four to eight minutes before a given moth was retested. The stimulus duration was kept minimal (0.5 to 3.0 sec), but long enough to observe whether a response occurred or not. The chambers were made from heavy corrugated cardboard boxes, 40 cm by 40 cm by

62.5 cm with a 1 cm thick layer of cotton batting on the inside surfaces (Fig. 13). Windows 15 cm sq. were cut in the front of each chamber for introducing moths and for observation. Windows of the same size were cut in the ends and covered with filter paper to admit diffuse light from 100 watt bulbs on the outside of the chambers. A layer of cotton surrounded the chambers at any point that the chambers touched a solid support. A plywood support was placed between the two lower and two upper chambers and a foam plastic block was placed between the chambers at each level to support the speaker as it was moved from one chamber to another as different tests were made. Holes 10 cm in diameter were cut to allow the sound to enter the chambers. A heavy wire hanger was placed 52.5 cm from the diaphragm of the speaker, and a strip of lead fused to a hair clip was hooked over this to hold a tethered moth. Thus, the final position of the moth was 52.5 cm from the center of the speaker diaphragm (the distance at which the speaker output was calibrated). A tolerance of ± 1 cm and 30° in pitch, yaw, and roll was allowed. If a moth ceased tethered flight, it could be stimulated to continue flying by placing and withdrawing a wooden support under it, or by gently blowing on it, or both.

Testing procedures largely developed under University of Oklahoma Research Institute Project 1621 (Frings and Lollis, 1971) were employed to gather data for the audiogram tests. These involve finding at least five frequencies over the range from highest to the lowest near the sensitivity limits of the animals. For each of these frequencies, a series of at least five SPL's are found by trial which yield about 5% response at the lowest, to about 25%,

50%, 75%, and finally 95% response at the highest. Using probit methods (Finney, 1952), one can find the median effective intensities for each of the five frequencies and develop an audiogram.

A five by five testing regimen was used with five frequencies, in this case 20 kHz, 40 kHz, 60 kHz, 80 kHz, and 100 kHz in that order for each of the runs at five intensities (Fig. 14). Preliminary tests showed that 20 kHz was about the lowest that clear-cut reactions could be seen, and the equipment could not operate above 100 kHz without modifications. The first test was made with an approximated median effective intensity for each frequency; the second and the third were two consecutively higher intensities; and the fourth and fifth were lower. No tests were performed above the first intensity to which a moth responded, and none below an intensity to which a moth did not respond. This was helpful in avoiding possible effects of adaptation.

So much difference was noted between responses of flying and non-flying tethered moths that a test series was run using the above five frequencies. Non-flying tethered Cadra (25) were tested at a SPL to which about 90% flying moths usually responded. Each of the five frequencies evoked very low percentages of response, the highest being 16%. Cadra had lapses when a response could be induced, if at all, at only the highest of intensities at the frequencies of greatest sensitivity (40-60 kHz). These moths were tested at a later time, as were those which did not fly, and they often responded normally during their retest.

The lowest frequency at which Cadra and Plodia responded was the same (15 kHz at 94 dB). Responses were noted consistently

down to 10 kHz on the pulse mode, but this was probably an artifact caused by the noise the speaker produced on the pulse mode, as has been noted before.

I have classified the observed responses as did Treat (1955), with certain modifications, as follows: 1, non-flight responses (any body movement such as a jerk of the wings, legs, or abdomen but not associated with flight); 2, flight start (flight is initiated when the stimulus is presented); 3, flight stop (flight ceases soon after the stimulus is presented); 4, transient flight change (a change in flight pattern lasting probably less than 0.1 sec); and 5, persistent flight change (a change in flight pattern lasting longer than the transient and often as long as the stimulus is presented). In the last two responses the change is in speed of one or both wings, and in the last only is often associated with multiple directional changes. Also in the last response at higher intensities, the abdomen is at times jerked up and down vigorously, or twisted around and around.

Most of these responses have been photographed, using a Bolex H16 movie camera with an indicator light in the background to show when the ultrasonic signal was presented. Streak photography was used on moths in free flight in the laboratory with a 35 mm camera, as was done by Roeder and Treat (1961) on moths against the night sky. In streak photography, the shutter of the camera is opened for several seconds while the moths fly across the field of view. The light reflected mainly from the wings imprint the flight path of the moth on the film. A dark background is used to increase the contrast, and precise focusing is not necessary.

EXPERIMENTS AND OBSERVATIONS ON TETHERED MOTHS

Audiograms

Audiograms for sounds between 20 and 100 kHz were determined for male and female Cadra and Plodia for both non-pulsed and pulsed sounds. A high proportion of Cadra did not fly well while tethered, so many attempts had to be made to test the required number of moths. Plodia flew well and rarely had a lapse of sensitivity. A pulse pattern of 30 per sec with a 10 msec pulse duration was chosen arbitrarily, but later data indicated that a different pulse pattern probably would not have made much difference. The rise and fall times of the pulses were 2.0 and 0.5 msec respectively, but became longer as the relay became worn.

Tables 1A through 1H present the results of these tests. A typical probit graph of the data from one of these tables (Table 1E) is shown in Figure 15. The median effective intensities derived by examination from these probit graphs as shown in Figure 15 are plotted in Figures 16 and 17 against frequencies.

In the audiogram (Fig. 17 - marked "Stopping") derived from a probit graph of Table 2, the behavioral response used as an assay was the "flight stop response" described earlier. Many other responses were observed usually at a lower SPL than the flight stop responses, but were classed as non-responders. Thus, Table 2 in-

TABLE 1

AUDIOGRAM DATA FOR CADRA CAUTELLA AND PLODIA INTERPUNCTELLA OF BOTH SEXES TO NON-PULSED AND PULSED ULTRASOUND USING ANY FLIGHT RESPONSE

TABLE 1A CADRA CAUTELLA, FEMALE, NON-PULSED, N = 50

Frequency (kHz)	Intensities in dB -- Percent responding					
20	74.6-- 12	77.0-- 34	80.5-- 72	81.9-- 90	83.1-- 90	
40	52.0-- 2	58.0-- 12	67.6-- 54	72.0-- 90	81.6-- 98	
60	53.0-- 2	65.0-- 10	68.6-- 46	73.0-- 62	79.0-- 84	
80	64.6-- 16	75.0-- 42	81.0-- 64	84.6-- 92	89.0-- 98	
100	67.0-- 12	76.6-- 32	79.1-- 50	80.1-- 66	81.0-- 78	

TABLE 1B CADRA CAUTELLA, MALE, NON-PULSED, N = 25

20	65.0-- 4	77.0-- 12	80.6-- 44	81.9-- 52	83.1-- 72	
40	52.0-- 8	58.0-- 20	67.6-- 60	72.0-- 84	81.6-- 92	
60	53.0-- 16	65.0-- 36	67.6-- 44	72.0-- 68	79.0-- 84	
80	64.7-- 8	75.0-- 36	81.0-- 80	84.6-- 92	89.0-- 100	
100	67.0-- 8	76.6-- 28	79.1-- 52	80.1-- 64	81.0-- 84	

TABLE 1C CADRA CAUTELLA, FEMALE, PULSED, N = 50

20	74.6-- 14	77.0-- 40	80.6-- 78	81.9-- 84	83.1-- 86	
40	52.0-- 0	58.0-- 10	67.6-- 50	72.0-- 76	81.6-- 98	
60	53.0-- 2	65.0-- 20	68.6-- 58	73.0-- 70	79.0-- 80	
80	64.6-- 12	75.0-- 40	81.0-- 76	84.6-- 98	89.0-- 100	
100	67.0-- 12	76.6-- 52	79.1-- 76	80.1-- 84	81.0-- 92	

TABLE 1 continued

TABLE 1D CADRA CAUTELLA, MALE, PULSED, N = 25

Frequency (kHz)	Intensities in dB -- Percent responding									
20	74.6--	4	77.0--	32	80.6--	52	81.9--	68	83.1--	80
40	52.0--	0	58.0--	4	67.6--	44	72.0--	76	81.6--	100
60	53.0--	0	65.0--	24	68.6--	36	73.0--	64	79.0--	76
80	64.6--	16	75.0--	40	81.0--	64	84.6--	96	89.0--	100
100	67.0--	12	76.6--	52	79.0--	72	80.0--	80	81.0--	96

TABLE 1E PLODIA INTERPUNCTELLA, FEMALE, NON-PULSED, N = 50

20	71.0--	10	74.6--	28	77.0--	46	80.6--	60	81.9--	86
40	64.0--	12	67.6--	26	72.0--	50	75.0--	72	78.0--	82
60	65.0--	8	73.0--	38	79.0--	66	82.6--	82	85.0--	98
80	75.0--	12	81.0--	20	85.9--	56	87.1--	80	89.0--	90
100	76.6--	2	81.0--	22	85.0--	50	87.0--	64	88.6--	80

TABLE 1F PLODIA INTERPUNCTELLA, MALE, NON-PULSED, N = 25

20	71.0--	4	74.6--	12	77.0--	24	80.6--	60	81.9--	80
40	64.0--	0	67.6--	12	72.0--	40	75.0--	68	78.0--	80
60	65.0--	0	73.0--	12	79.0--	72	82.6--	88	85.0--	92
80	71.9--	4	75.0--	12	81.0--	40	84.6--	60	87.1--	68
100	79.1--	4	81.0--	12	85.0--	32	87.0--	64	88.6--	76

TABLE 1 continued

TABLE 1G PLODIA INTERPUNCTELLA, FEMALE, PULSED, N = 50

Frequency (kHz)	Intensities in dB -- Percent responding							
20	67.9--	14	71.0--	34	74.6--	56	77.0--	80 81.9-- 88
40	58.0--	2	64.0--	28	67.6--	34	72.0--	80 78.0-- 98
60	59.0--	6	65.0--	36	68.6--	46	78.9--	90 79.0-- 98
80	71.9--	18	75.0--	28	78.6--	48	81.0--	82 83.0-- 84
100	73.4--	38	76.0--	48	77.9--	58	80.1--	80 81.0-- 88

TABLE 1H PLODIA INTERPUNCTELLA, MALE, PULSED, N = 25

20	67.9--	8	74.6--	40	77.0--	64	81.9--	76 83.1-- 92
40	58.0--	0	67.6--	36	72.0--	64	78.0--	92 81.6--100
60	59.0--	0	73.0--	40	75.9--	60	79.0--	96 82.6-- 96
80	71.9--	4	78.6--	16	81.0--	40	83.0--	72 85.9-- 88
100	73.4--	16	77.9--	28	79.1--	52	80.0--	64 81.0-- 80

TABLE 2
 AUDIOGRAM DATA FOR PLODIA INTERPUNCTELLA
 USING ONLY THE FLIGHT STOP RESPONSE
 FEMALES, N-20, NON-PULSED

Frequency (kHz)	Intensities in dB -- Percent responding				
20	89.0-- 5	91.0--20	92.5--50	94.0--55	95.0--55
40	52.0--30	78.0--20	84.0--35	98.0--70	98.0--80
60	79.0-- 5	79.0--10	85.0--35	93.0--70	99.0--70
80	81.0-- 0	89.0--25	89.0--30	93.0--30	96.5--50
100	85.0-- 0	87.0-- 0	89.0--15	80.0--25	91.0--35

cludes only flight stop responses while Table 1 includes any behavioral response, many of which were transient responses. While the transient responses did not inhibit flight, flight stop responses stopped the flight and made it necessary to initiate flight each time the response occurred. After a few responses considerable difficulty in initiating flight was experienced as well as great loss of time. Many moths became untestable because they would not resume flight. One can see a pattern was emerging showing a threshold of about 15 dB higher for female Plodia than the corresponding audiograms using any behavioral response as an assay for hearing. This seems to correspond to results with noctuid moths in the switch from the lower sensitivity sense cell to the higher sensitivity sense cell (Roeder, 1970).

Pulse Rate and Duration

Common North American bats in searching for insect prey use an echolocation signal of 20 to 70 kHz at pulse rates of 8 - 10 per sec. The pulse duration is about 12 to 15 msec. However, as soon as the bats have located an insect, a shift occurs, the pulse rate is increased to over 100 per sec. and the duration is decreased to about 2 msec. (Griffin, 1958; Griffin, et al., 1960). One could hypothesize that the shift in pulse rate and duration could somehow be used by moths as an indication that their presence had been discovered. So moths in flight might alter their behavior to evasion or evasive attempts. In noctuids the tympanal organ is particularly sensitive to pulsed sounds in contrast to trains of non-pulsed sounds (Roeder, 1959). So, it seemed reasonable to think that the

relative sensitivity of pyralidids might be greater to certain pulse patterns than to others.

A test of relative responsiveness to various rates and durations of artificial pulses should show if the moth does distinguish different pulse patterns. At high intensities Cadra and Plodia respond to almost any pulse pattern, so there would be no differences in relative responsiveness to pulse rates and durations. Therefore, an intensity which I had determined to yield about 50% response (72 dB at 40 kHz) was chosen and pulses whose duration was set at 3 msec were used, with the pulse rate varied. The results (Table 3) show no obvious differences at different pulse rates. The percentage duty cycle is given to show the large differences in the percentage of time the sound was actually produced during trains of pulsed sounds.

TABLE 3
RESPONSE OF CADRA CAUTELLA TO PULSE RATES*

Rate (pulses per sec)	2	5	10	30	50	100
Percentage duty cycle	0.6	1.5	3.0	9.0	1.5	30.0
Percentage response	38	33	35	44	49	33

*The parameters held constant were pulse duration, 3 msec; frequency, 40 kHz; and intensity, 67 dB. N=45

Since pulse duration, as well as pulse rate, as pointed out above, may be important, a new test was run on both Cadra and Plodia varying both parameters. There were 50 females of each species tested in the order shown in Table 4.

TABLE 4

PERCENTAGE RESPONSE OF CADRA CAUTELLA AND PLODIA INTERPUNCTELLA TO PULSE RATES AND DURATIONS*

Duration (msec)	5	5	5	5	5	3	10	15
Rate (pulses per sec)	5	10	30	50	70	30	30	30
Percentage duty cycle	2.5	5	15	25	35	9	30	45
<u>Cadra</u> (67.5 dB)	50	50	50	50	48	44	58	60
<u>Cadra</u> (78.0 dB)	86	88	88	80	88	92	92	94
<u>Plodia</u> (72.0 dB)	44	48	54	46	36	42	48	48

*The number tested in each case was 50, and the frequency was 40 kHz.

Median effective intensities were used for each species, and one higher intensity was used with Cadra, in case this would make differences appear in the relative responsiveness to various pulse rates and durations. As can be seen (Table 4), no significant differences appeared. These negative data do not disprove the original hypothesis, but certainly do not support it.

Duration of Response

Throughout the above tests on thresholds (median effective intensities), every effort was made to reduce the effects of adaptation, and this eliminated the chance to observe a continuous (persistent) response. The observations did, however, suggest that a

pulsed signal might evoke a persistent response in contrast to the momentary response (transient) that was common as a reaction to a non-pulsed signal. A 40 kHz signal was selected and 20 moths tested. The non-pulsed signal produced many persistent responses, but some were transient responses. It seemed that the transient response was associated with intensities at near-threshold more often than with intensities well above threshold.

In a new test, intensities of 68 dB were selected for Cadra and 72 dB for Plodia as starting points. If the moth did not respond at that sound level, then the intensity was slightly increased until a response was observed in subsequent trials, which were run at least three minutes later. Since some moths are much more sensitive than others, this insured that the test with the first response was threshold or near threshold for the moth tested. A stopwatch was used to measure the duration of a persistent response, up to five seconds. A "flight stop response" was also considered persistent, since the change was "permanent." In these cases the sound was turned off, and the moth was later stimulated to flight to finish the remainder of the tests. A short response was recorded as "transient" (probably less than 0.1 sec in duration).

In the persistent response, moths changed their flight direction and speed several times before reaching an equilibrium (settling down to steady flight). Some did not settle down as long as the sound was on. Each of the moths in the chambers was tested with non-pulsed sounds, then with pulsed sounds (Table 5).

TABLE 5

TRANSIENT VERSUS PERSISTENT RESPONSE (to 40 kHz, near threshold SPL) FOR NON-PULSED AND PULSED SIGNALS* (30/sec; 10 msec)

	<u>Non-pulsed</u>		<u>Pulsed</u>	
	Transient	Persistent	Transient	Persistent
<u>Cadra</u> Percentage	88	12	28	68
<u>Plodia</u> Percentage	72	20	40	52
Pooled Percentage	80	16	34	60

*The number tested in each case was 25. A small percent of responses could not be classed with certainty as transient and persistent so the data do not add up to 100%.

These data support the hypothesis that a transient response is more likely to occur with non-pulsed than with pulsed signals. This may be true, however, only near threshold intensities. The moths may have rapidly adapted to the low intensities unless the low intensities were pulsed. In that case, the time between pulses may have allowed time for disadaptation. For example, with a much longer inter-pulse interval (pulse rate of 1/sec and duration of 10 msec), four specimens of Plodia responded (transient) each second for the duration of the test (four minutes).

Tympanectomy and Counter-tympanal Membrane Perforation

As expected, bilateral cutting of the chordotonal string in the tympanal organs completely abolished acoustic sensitivity. Both species flew normally after the operation, but, among 20 of

each species tested, none responded to any sonic or ultrasonic stimuli.

In preparation for a test to determine the importance, if any, of the counter-tympanal membrane, intact moths were tested for the lower frequency limits for non-pulsed and pulsed (standard 30/sec; 10 msec) sounds. The lower frequency limits for reception of pulsed sound was as low as "10 kHz" (the factory specifications recommended that the speaker not be driven below that frequency). The lower frequency limits for reception of non-pulsed sound were 15 kHz and 16 kHz respectively for Cadra and Plodia.

The moth was anaesthetized on ice and a perforation was made on each counter-tympanal membrane (Fig. 18), avoiding changes in the tension in the chordotonal string, or its disruption. The results (Table 6) show a great loss of sensitivity to all stimuli and complete loss of sensitivity to pulses at "10 to 13 kHz." This "low frequency reception" was, as noted before, probably the noise associated with the pulse. In the one discordant case of sensitivity to this noise, the moth was tested on the following day and examination indicated that a tanned regenerated area or darkened body fluid had resealed the counter-tympanal membrane.

TABLE 6

RESPONSE OF MOTHS TO PULSE AND NON-PULSE BEFORE AND AFTER COUNTER
TYMPANAL MEMBRANE PERFORATION*

<u>Cadra</u>	Before		After		
	Non-pulsed > 15 kHz	Pulsed "10-13 kHz"	Non-pulsed > 15 kHz	Pulsed "10-13 kHz"	Pulsed > 30 kHz
Number tested	23	22	22	22	22
Number responding	23	21	5	0	6
Percentage response	100	95	22	0	27
<u>Plodia</u>					
Number tested	24	23	20	20	12
Number responding	24	17	11	1	5
Percentage response	100	74	55	5	42

*The pulse rate was 30/sec and the duration was 10 msec.

EXPERIMENTS AND OBSERVATIONS ON MOTHS IN FREE FLIGHT

Pure Tones Above 15 kHz

The electrostatic speaker was hand-aimed at free flying moths in the laboratory and in a glass enclosure (Fig. 19). Non-pulsed and pulsed signals were used at 85 to 93 dB and at 95 to 102 dB sound levels. Frequencies between 40 and 100 kHz were effective in eliciting responses. The distance between the speaker and the flying moths varied, and the unpredictable effects of reflection and standing waves prevented a more accurate determination of actual intensities.

Evasive flying was elicited by lower intensities and diving by higher intensities. No differences could be detected between non-pulsed and pulsed signals, or between sexes or species, although no extensive series of tests was made. On several occasions moths fell out of the air onto the floor, then started flying upward, but with another train of ultrasonic sounds were put down again and again. Some of the moths seemed to be stunned for some time on the floor. A gust of air often stimulated them to further flight.

A glass chamber was constructed to house the moths while being photographed, but the moths did not fly well in it and under those conditions only very poor photographs resulted. One unique response was noted under these circumstances. Moths climbing up the glass,

when stimulated by ultrasound often dropped several inches, then resumed climbing the glass. The responses were photographed with a movie camera and a 35 mm still camera with tri-x film. Several techniques were tried, including use of a stroboscopic light, before a new method was found. In this, a black cloth was hung over the laboratory wall and three incandescent 100 watt bulbs with reflectors were aimed upward about 1.5 m from the black cloth. Shields were placed to shade the camera lens and the black cloth. This produced a "V" shaped trough of light perpendicular to the camera. This method, while developed independently, is similar to that used by Griffin et al. (1960). Fig. 20 shows typical flight without ultrasonic stimulation; Figs. 21, 22, and 23 show typical evasive patterns of flight with ultrasonic stimulation.

Noise

As in tethered flight, the response depends upon whether the source produces a single short pulse, as in a handclap, or a sound of some duration, such as a hiss. Moths respond to a noise pulse by "dipping" several inches at the time of the pulse. The same noise sources (squeaking of ground-glass stoppers turned in bottles; clicking of electric switches; slapping of flat objects; sound of pop-guns; finger snapping; hissing through the lips; and sounds produced by hand held bats) that were effective with tethered moths were effective with moths in free flight. The responses are much more pronounced after the moths have been released from the culture jars for several minutes and are then flying less erratically. Handclaps are effective from across the laboratory (five meters). If

the moths are flying undisturbed, the snapping of one's fingers elicits a dip (at 2 meters). In taking streak photography pictures, the camera noise occasionally elicited small dips (at 2 meters). Both species seem to be equally sensitive to this stimulation and "no response" is rare. A hiss from one's lips at close range elicits evasive flight.

I have also noted this "dipping" behavior in wild, unidentified moths under street lights at night. The response is identical to that of Cadra and Plodia in the laboratory. The simplest noise source found that elicited dips in moths was a child's pop-gun (Daisy No. 960). With that noise source at Weleetka, Oklahoma, I observed responses in 25 out of 37 tries, and on a different night 36 out of 50 tries. With a "handclap" as a noise, I observed responses in 31 out of 50 tries at the same location. At Lake Stanley Draper near Oklahoma City, I observed responses in only 13 out of 50 tries. It should be noted that I did not clap entirely unselectively, for it soon became obvious that it was useless to clap at certain insects that were recognized by their flight pattern and size. I simply wanted to know if moths that were sensitive to ultrasonic sounds would "dip" as do Cadra and Plodia in response to noise bursts. It is possible that some insects flew back into the darkness, reappeared and were tested more than one time. For the most part, all tries were on insects thought to be moths, and several moths were captured after they responded, and found to be tympanate. Lacewings (Neuroptera:Chrysopidae) were recognizable during flight, and at the Weleetka location 7 out of 12 responded in a similar manner (cf. Miller and MacLeod, 1966). Among lacewings

responding were Chrysomes nigricornis and C. oculatus.

Bats

Several bats were brought into the laboratory and hand held (with gloves) near moths in free flight. With two species of bats, the Free-Tailed Bat, Tadarida mexicana, and the Eastern Pipistrel, Pipistrellus flavus, mild evasive flight by the moths was observed as a response to the cries of the bats. With the one available specimen of the Red Bat, Lasiurus borealis, strong diving behavior of the moths was observed as a response to what seemed to be louder clicking sounds (known to accompany the ultrasonic component) (Griffin, 1958) produced by this species. In two tries two moths dived simultaneously and in one try three moths dived simultaneously as if turned into raindrops. In a number of tries with all species of bats named, no responses at all were observed, but the response to the Red Bat was better than to any other stimulus used.

A few experiments were done by releasing both bats and moths in the laboratory for free flight. No air-borne catches or evasive behavior were observed. The light intensity necessary for observation inhibited flight of the moths. Unless large numbers of insects are flying in a laboratory bats are not likely to begin active hunting (Griffin et al., 1960). Even then, Griffin found that at best only a small fraction of Myotis lucifugus undertake serious hunting. Perhaps with lower intensities of light and with more moths and bats, hunting and evasion could be observed.

PRELIMINARY TESTS ON ACOUSTICAL CONTROL OF MOTH PESTS OF STORED PRODUCTS

The vigorous responses in previous tests indicated that sound might interfere with some part of the normal behavior necessary for survival of the moths under study. Two test chambers were constructed such that a sound could be used in either one while the other alternately served as a control chamber. Two large (52 cm tall) plastic waste barrels lined with four layers of gauze cloth were used so observations could be made while the experiments were in progress (Fig. 24). Several types of food stations for oviposition were tried with variable success. The one adopted was a jar 10 cm tall and 3.8 cm in diameter with a 2.5 cm hole drilled in the center of its metal lid. The jar was filled with culture medium and a layer of gauze was placed between the medium and the lid. By tracing back and forth along the grid produced by the gauze, any eggs that were laid could be counted accurately. Tests lasting from one to several days were run using one of two types of equipment as sound sources. One system, designated as "electrostatic speaker," is diagrammed in Fig. 12. The other system, designated as "tweeter," was simply an oscillator (Hewlett-Packard Model 200AB) connected directly to a tweeter (Mustang Model MS Sphericon Super Tweeter). The sound was either continuous (non-pulsed) or pulsed with the pulsing apparatus shown in Fig. 12. Basically there were

four experimental situations: two sound sources each either pulsed or non-pulsed. During the tests either almond moths, Cadra cautella, or Indian meal moths, Plodia interpunctella, were studied and records were kept on flight, mating, mortality, and oviposition in the two chambers.

There were no apparent differences in the number of moths flying, mating, or dying in the two chambers. However, differences did occur in oviposition rate between the chambers (Table 7 and 8). Mortality data are included, because of the small but consistent difference found in most cases. In most tests the oviposition rate in the sound-exposed chamber was reduced and in one situation (non-pulse with tweeter) the reduction was quite large.

TABLE 7

EFFECTS OF ULTRASOUND UPON MORTALITY AND OVIPOSITION IN MIXED POPULATIONS OF CADRA CAUTELLA

Sound source	Mode	Pulse pattern	"N"	Frequency (kHz)	Duration of test (days)	Treated chamber	Oviposition		Mortality	
							Treated	Control	Treated	Control
Tweeter	non-pulse	none	≈100	40	2	2	169	224	38	33
"	"	"	"	"	2	2	57	160	41	45
						total =	226	384	79	78
"	pulse	10/sec 5 msec	75	30	2	1	14	25	8	4
"	"	"	37	"	2	2	41	50	-	-
						total =	55	75	8	4
Electrostatic speaker	non-pulse	none	≈100	40	1	1	33	56	-	-
						total =	33	56	-	-
"	pulse	30/sec 10 msec	78	60	5	2	250	192	19	16
"	"	"	"	"	3	1	197	98	31	27
						total =	447	290	50	43

TABLE 8

EFFECTS OF ULTRASOUND UPON MORTALITY AND OVIPOSITION IN MIXED POPULATIONS OF PLODIA INTERPUNCTELLA

Sound source	Mode	Pulse pattern	"N"	Frequency (kHz)	Duration of Test (days)	Treated chamber	Oviposition		Mortality	
							Treated	Control	Treated	Control
Tweeter	non-pulse	none	≈100	40	1	2	29	174	34	27
"	"	"	"	"	2	1	19	190	52	37
"	"	"	"	"	2	1	7	75	33	36
total =							55	439	119	100
Electrostatic speaker	"	"	"	"	1	1	33	56	-	-
"	"	"	"	"	1	1	66	67	-	-
total =							99	123	-	-

DISCUSSION

Ultrasonic sensitivity is now generally accepted as a mechanism which aids moths and other insects in evading bat predators (Roeder and Treat, 1961). However, one might wonder whether the insects here studied are actually preyed upon by bats in warehouses or other man-made structures. Griffin (1958) discussed bats inhabiting buildings, but his only comments were in regard to the buildings as roosts or cave substitutes. Plodia, at least, is established out-of-doors in some areas, but Cadra seems to be a warehouse pest in a fairly strict sense (Donohoe, 1946; Cotton, 1950). Certainly in colder climates, both species are probably confined to the indoors. In the current study, both species were reared through at least 30 generations during three years and presumably the stock from which they came had been reared for many years in the laboratory or in warehouses without selection pressure from bat predators. As well adapted to this niche as the moths are, one could wonder why they should still be sensitive to calls of bats or more specifically to ultrasonic sounds. It is possible that some other animal, such as a predatory insect or rodent living in their habitat, is a major element in maintaining this sensitivity. Rodents and shrews are known to emit ultrasound. (Tembrock, 1968).

On the other hand, evidence can be found that these moths are still targets for bat predation. Linsley (1942) discussed the high incidence of pests of stored products in nests of bees and wasps. Both species under study have been found in these non-man-made habitats. He suggested that these insect food caches serve as reservoirs and possibly as original sources in the evolution of this group of pests. He also pointed out that the food caches of rodents and other animals should be studied with the hypothesis in mind that the rodent habitat might be intermediate between the more open habitat of nests of bees and wasps and the more protected habitat of man's stored products.

If these food caches serve as reservoirs for small populations of moths, the moths must search for and travel to man's food stores. It is known that these moths are crepuscular in flight habits (Barnes, et al., 1939; Graham, 1970a). Therefore, they might be exposed to bats, and the ones that are successful in evading bats and so serve as the parent generation for new infestations would certainly be selected for each time a new infestation occurred by this means. New infestations also occur when man transports infested stored products to uninfested warehouses. Bat predation could have had great effects on moth evolution; among extant Lepidoptera there are more tympanate than non-tympanate species (Treat, 1955).

The ambient noise level in the laboratory in the ultrasonic range was not determined, but may have been high. This causes uncertainty in comparing intensity sensitivities in these studies with those reported earlier. The lowest total sound level

that produced a response in my studies (Table 1) was 52 dB. The corresponding value for noctuids was 40 dB (Roeder, 1967a) which was also the level arrived at from electrophysiological studies measuring the responses for the first interneuron in the acoustic system. This level was also used in determining that the hearing range for detecting the cruising cries of bats was about 36 m (Roeder, 1966a).

The stopping response of flying tethered moths would be equivalent to diving for those in free flight. In noctuids diving and looping occur only when high intensities are used (Roeder 1962). Intensities 40 dB above the minimal response level cause neural saturation of both sense cells (Roeder, 1969). In pyralidids the lowest level of response detected electrophysiologically is 30 dB and higher intensities cause more sense cells to fire (Belton, 1962). The stopping response may occur when additional sense cells are caused to fire or when all four sense cells are saturated at high sound pressure levels.

The sensitivity to ultrasonic frequencies in Cadra and Plodia is quite similar to that for other moths receptive to ultrasonic sounds and corresponds to the peak output that bats produce (Roeder, 1970). As Belton (1962) found, pyralidids are less sensitive at frequency ranges just below the human ultrasonic limit (15 kHz) than noctuids apparently are. This lack of sensitivity to low frequencies may mean that these species have no mechanism for reception of lower frequencies of airborne sounds, or that they simply do not show a behaviorally observable response at these frequencies, as do other species (e.g., Frings and Frings, 1957).

As to the lack of difference in sensitivity to various pulse rates and durations, and to pulsed and non-pulsed sounds, it should be remembered that any response at all was considered as a positive response. During the "audiogram" test and the "pulse rate and duration" test the only recorded differentiation of types of responses were "flight stop" and "responding but not stopping." If records had been kept for the other types of responses some trends may have emerged. After the first few milliseconds, sound may have little or no effect on the occurrence of a response. It did, however, affect the type of response. The duration of the response is very brief if the signal is non-pulsed and low in intensity. As in the persistent responses associated with pulsed signals found in this study, Roeder (1967a) found that a non-pulsed signal produces a transitory turn, while a pulsed signal causes a larger and sustained response. Electrophysiological data show that adaptation is slower in pyralidids than in noctuids (Belton, 1962), but there are weaknesses in comparing data from such diverse origins.

Nearest to what I have called "dipping behavior" was reported by Agee (1969). He found that noctuids respond to ultrasonic sounds by "bouncing," which was synchronized with a very slow pulse rate (less than 2 pulses per sec). Other reports of similar type are found in the literature, but no one has reported the use of a single brief burst of noise, such as a handclap, on free flying moths either in or out of a laboratory. Parenthetically, this is a very convenient method for demonstrating to a class this complex and fascinating behavioral adaptation without the use of complex electronic equipment.

Belton (1962) reports that the flour moth, (Anagasta kuehniella) and two other pyralidids, when immobilized, "often contract their musculature in such a way as to protrude the tympanal organs." I speculate that the functional significance of this abdominal motion is in causing very abrupt directional changes. Certainly if moths jerk the abdomen up or down, or twist it around during free flight, as they sometimes do when stimulated during tethered flight, one would believe that they would have a disturbed flight path. Roeder's (1967a) explanation that the moths turn by partially folding the wings on the side opposite to the sound source seems quite valid. He states that this might not, however, explain the little-studied tight turns, loops, and dives. He then speculates on an additional mechanism for these responses. He states that these responses could be due to "excessive feedback in the steering system accompanied by partial or complete suppression of the wing-flapping system" (Roeder, 1970). Possibly some combination of Roeder's and my speculation will be found to be the mechanism which produces the sharp turns and tight loops that moths sensitive to ultrasonic sounds exhibit when presented with such sounds.

Considering the profound behavioral changes induced by sounds in these insects (evasive flying, diving, and reduction of oviposition) it seems that a serious field study should be initiated in warehouses. Lum and Flaherty (1969) found that many more female P. interpunctella did not lay any eggs when they were mated with males that had been reared under continuous light (LL) than when mated with males reared under light-dark (LD) cycles. Spermatophores were transferred but these males (LL) did not provide adequate

stimulus for oviposition. Various phases of their biology are strongly affected by photoperiod and light intensity. Traynier (1970) learned that the response of males to female sex attractant was maximal at dawn and that fewer female Mediterranean flour moths, Anagasta kuhniella, "called" (sexual display associated with release of sex attractant) under continuous darkness. Dickens (1936) found that the sex attractant of A. kuhniella was attractive to several closely related species of moth pests of stored products, but interspecific matings were sterile. Brady and Smithwick (1938) reported that virgin female P. interpunctella released sex attractant almost continuously, but mating or certain anesthetics decreased this activity. The sex attractant common to both Cadra and Plodia has now been identified (Kawahara et al., 1971; Brady et al., 1971). It seems that the normal life cycle could be disturbed or completely disrupted by manipulation of photoperiods or release of excessive sex attractant. The latter might prevent males from finding the females or act as a repellent, or as Brady et al., (1971) found, as an inhibitor of behavioral responses.

There have been detailed ecological studies of both Cadra (Graham, 1970a, 1970b, 1970c, 1970d) and Plodia (Hamlin et al., 1931) where similar flight and mating cycles were found to be synchronized with light intensity and probably photoperiods. In bright light the moths exhibit little or no activity at all. There is good reason to believe that a non-pesticide control can be devised to control stored products moths. Ultrasonic sound stress, possibly combined with bright lights or pheromones might have profound effects on the moths in a warehouse.

The techniques developed in this study on tethered moths and controlled populations of free flying moths can be easily applied to several species of moths of stored products. These techniques are especially valuable if accompanying electrophysiological studies can be made of the same species. Roeder (1964) lamented the weaknesses in comparing neurological information from a few species with behavioral information from mixed populations of unidentified species. This problem has been tackled by Agee (1969) who did electrophysiological work and behavioral work in the field on the bollworm moth, Heliothis zea; moths of stored products, however, are adapted to living in large enclosures (warehouses) which would make them testable in large acoustic enclosures during free flight. Factors such as the population density and composition could be controlled. Physical factors such as weather would not interfere, and the time of flight could be controlled. The walls could be marked and cameras used to determine exact positions of moths and pursuing bats. Studies of this kind should yield comparative data of an especially significant nature.

SUMMARY

Two moths of stored products: the almond moth, Cadra cautella, and the Indian meal moth, Plodia interpunctella, were tested for responses to pulsed and non-pulsed pure tones, cries of bats, and various noises. The moths were restrained in the sound field by tethering so that they could fly in place. For this purpose, a three cm piece of cotton thread was fused to the notum of the moths with paraffin for tethered flight experiments.

Behavioral responses (changes in flight pattern) occurred from 15 kHz at 89 dB (re. 0.0002 dynes per sq. cm) to 100 kHz (the maximum frequency the equipment would produce) at 61 dB. Maximum sensitivities were in the 40 kHz to 60 kHz range, with median effective intensities for female Plodia interpunctella on non-pulsed sounds at 77.5 dB for 20 kHz, 72.7 dB for 40 kHz, 72.5 dB for 60 kHz, 83.5 dB for 80 kHz, and 87.7 dB for 100 kHz. Corresponding median effective intensities for female Cadra cautella were 78.2 dB for 20 kHz, 66.9 dB for 40 kHz, 70.9 dB for 60 kHz, 77.0 dB for 80 kHz, and 77.8 dB for 100 kHz. The minimum ultrasonic sound pressure level (SPL) at which responses were observed was 52 dB; the ambient SPL (sonic and ultrasonic) was about 75 dB.

Differences in thresholds between sexes, species, or non-pulsed and pulsed sounds were minor. At low SPL's pulsed sounds evoke

mainly persistent responses while non-pulsed sounds evoke mainly transient responses. The insects responded with patterns like those induced by pure tones, to the cries of bats, and to almost any source of noise. Bilateral counter-tympanal membrane perforation reduced sensitivity to ultrasound.

Both species of moths in free flight in the laboratory showed vigorous evasive flying and diving as a response to pure tones (about 20 kHz), to cries of hand held bats, and to bursts (single pulses of noise. Single bursts of noise caused these moths in flight in the laboratory and moths in the field to dip. Photographs and motion pictures of responses showing tight turns, loops and dives are included. Photographs and descriptions of the tympanal organs are included.

The sensitivity to ultrasonic frequencies and responses of Cadra and Plodia are similar to those of other moths receptive to the ultrasonic calls of bats. This probably lends a degree of protection from bat predation when Cadra and Plodia are flying at night in search of the stored products of insects, rodents, or man. Ultrasound reduced oviposition of moths to 10% of that by controls in the laboratory so an acoustical pest control system might possibly be devised for these insects. The methods are yet to be worked out for controlling these serious pests in practical situations.

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LEGENDS FOR FIGURES

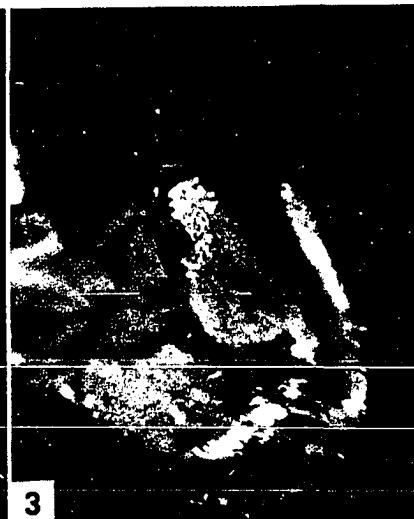
1. Cadra - Clearing is poor in the abdomen of highly gravid females causing the location of the tympanal chambers to show clearly. The arrow points toward the tympanal organ.
2. Plodia - By pinning the abdomen to the notum, the previously hidden tympanal membranes are shown clearly. Anterior is to the left. The arrow points toward the tympanal membranes.
3. Cadra - The posterior surfaces of the metathoracic coxae fit closely over the tympanal membranes.
4. Plodia - Removal of tissue above the tympanal chambers in this dorsal aspect demonstrates the relatively large size of the chambers.
5. Cadra (Left) and Plodia (Right) - The tympanal organs completely removed showing the larger tympanal organs in Cadra (scale=1 mm).



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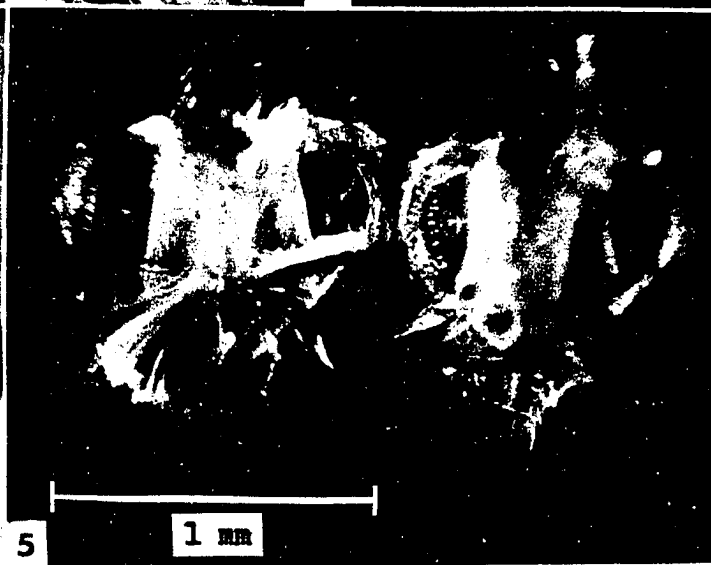
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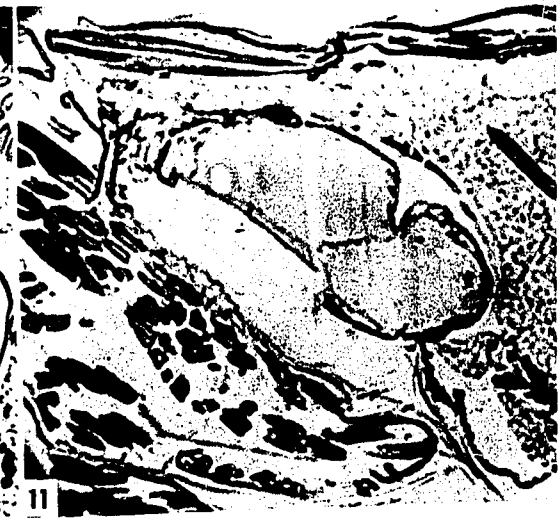
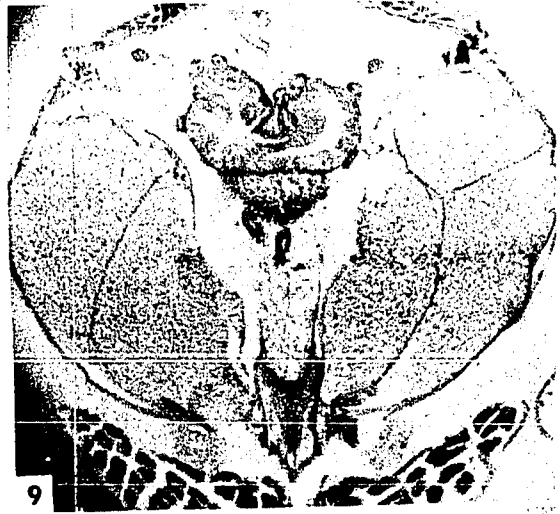
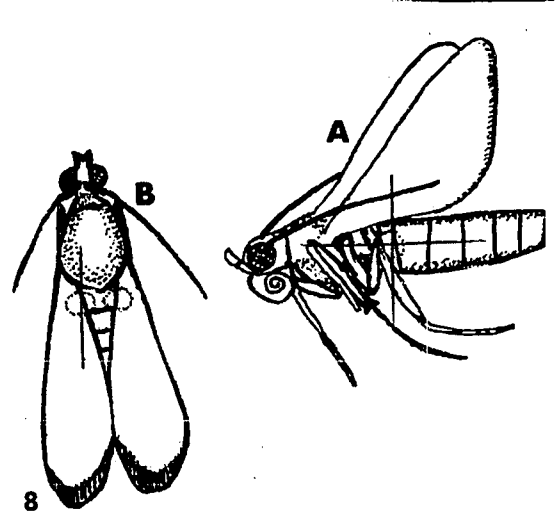
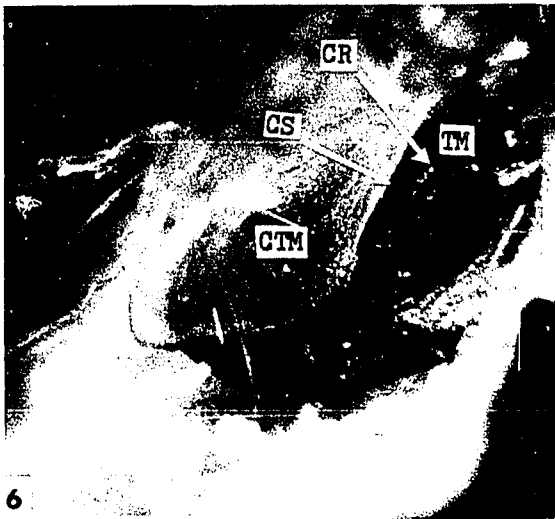


5

1 mm

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6. Plodia - The counter-tympanal membrane is medial to the tympanal membrane, it appears cloudy and leathery. In the center of the tympanal membrane is a circular ridge with the chordotonal string attached. CR, circular ridge; CS, chordotonal string; CTM, counter-tympanal membrane; TM, tympanal membrane.
7. Plodia - The chordotonal string is seen in its entire length with the innermost attachment broken.
8. Cadra - Diagram showing where the following sections were taken (a. lateral aspect, b. dorsal aspect).
9. Cadra - Cross section of the tympanal cavities (Fig. 8a, vertical line).
10. Cadra - Longitudinal (frontal plane) section of the tympanal organs (Fig. 8a, horizontal line).
11. Cadra - Longitudinal (sagittal plane) section of a tympanal chamber (Fig. 8b, vertical line).



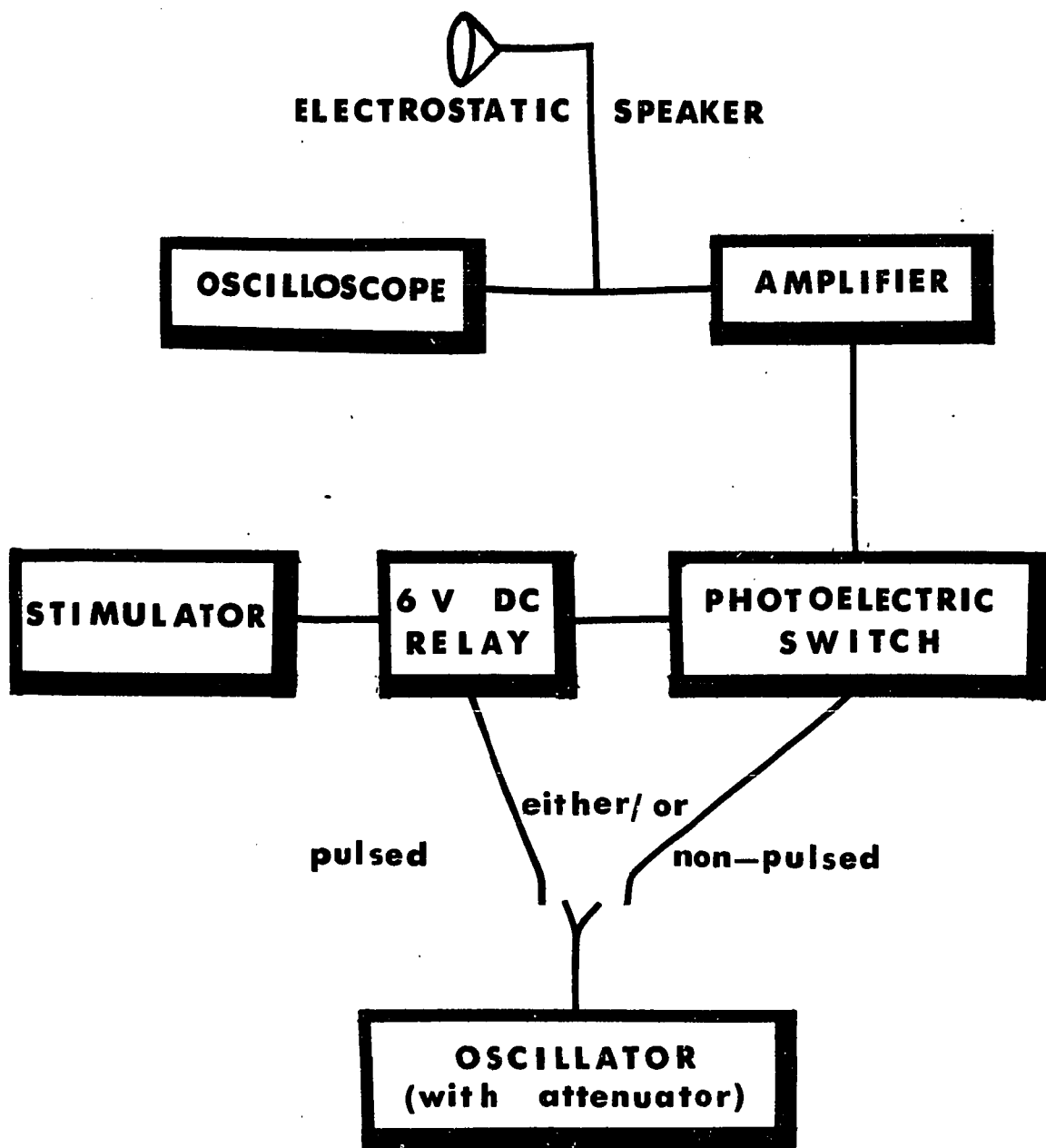


Fig. 12 Block diagram of electronic system for producing pulsed and non-pulsed high frequency sound used in studies of tethered and free flying moths.

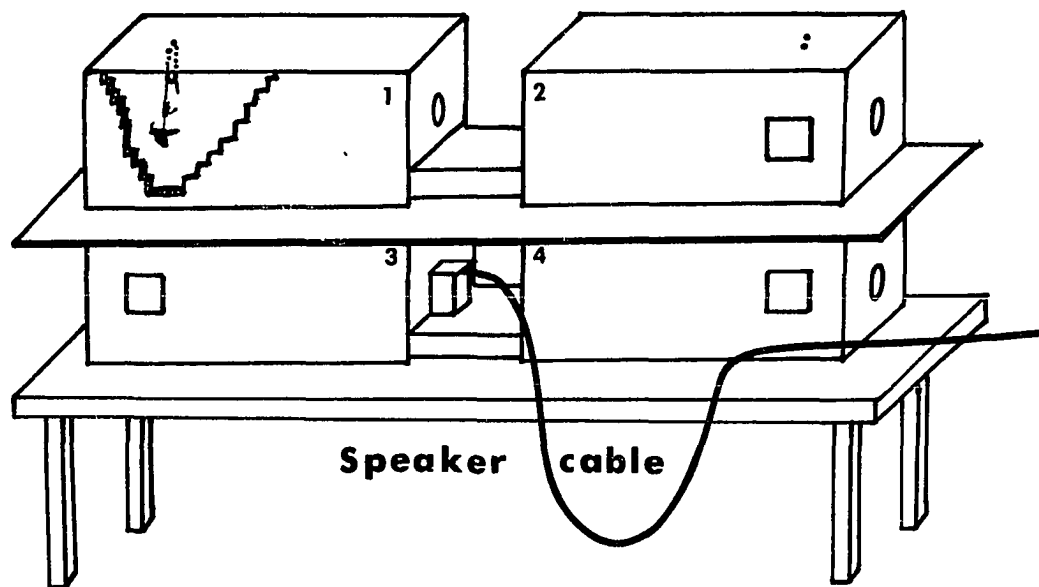


Fig. 13-Four sound testing chambers and one speaker.

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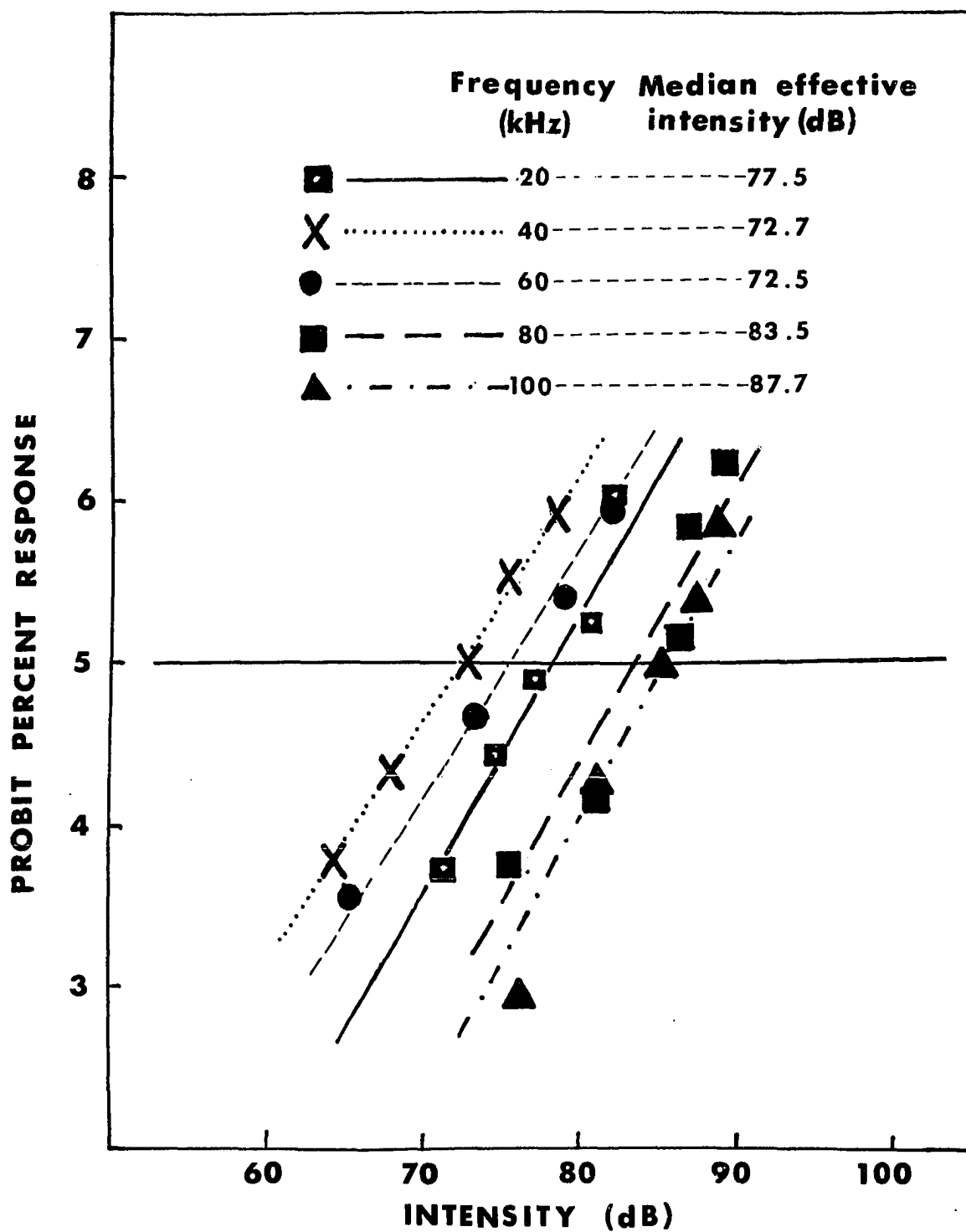


Fig. 15 A typical probit graph showing the median effective intensities derived from it. This one was for female Plodia interpunctella.

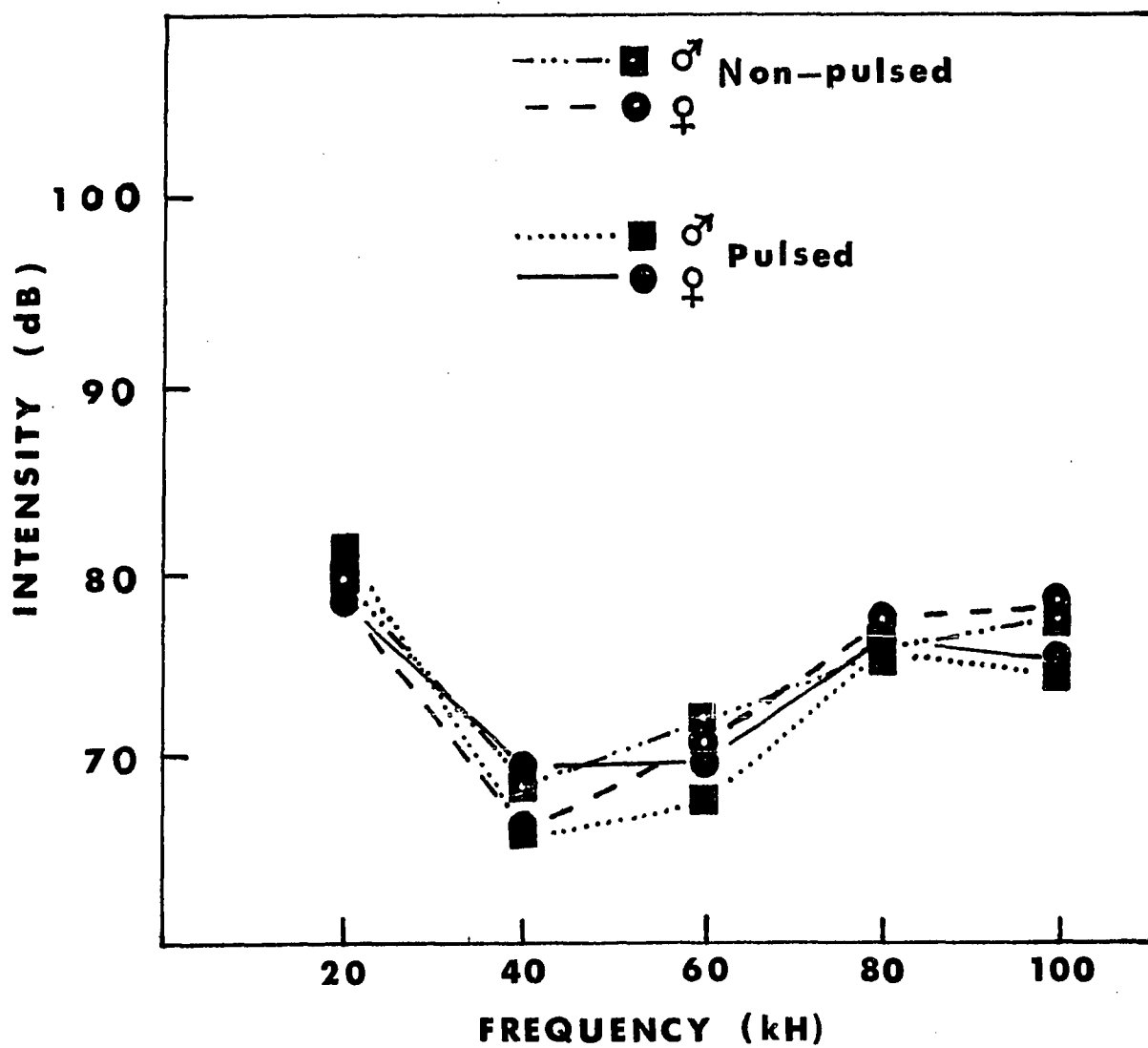


Fig. 16 Audiograms for Cadra cautella showing the median effective intensities for any response.

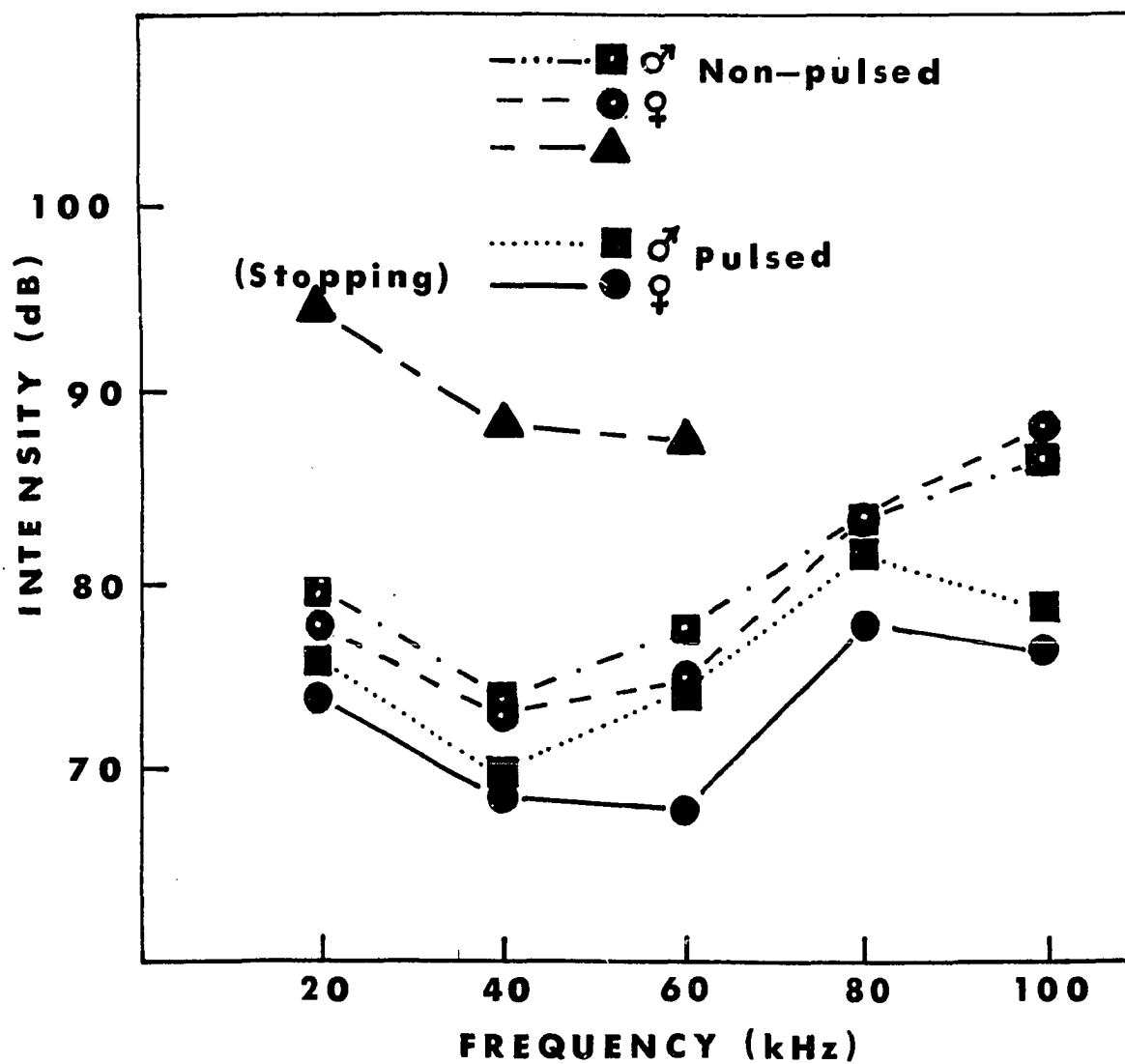
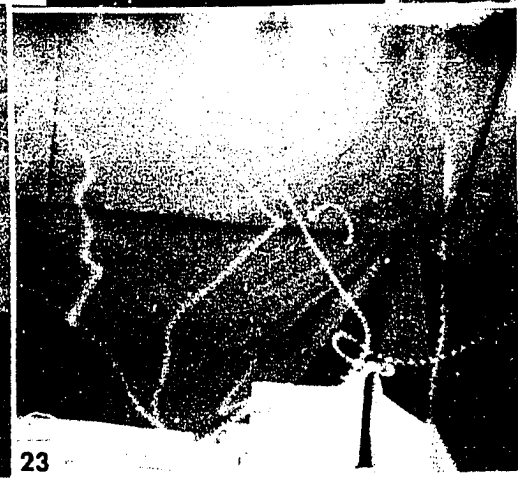
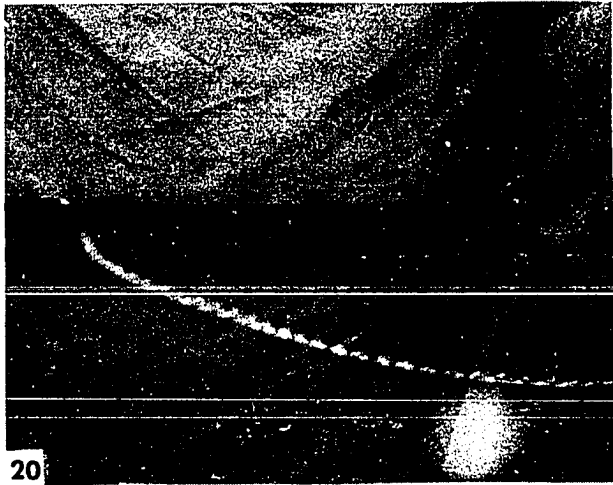


Fig. 17 Audiograms for *Plodia interpunctella* showing median effective intensities. "Flight stop response" was used for "Stopping."

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18. Plodia - The counter-tympanal membranes are shown here perforated.
19. Cadra - the moths (white spots on glass) are not flying in this photographic chamber probably because of inhibition by light.
20. Plodia - Streak pattern showing typical flight without ultrasonic stimulation.
21. Plodia - Typical evasive flying observed in the laboratory.
22. Cadra - Streak pattern showing typical flight with ultrasonic stimulation.
23. Plodia - Numerous streak patterns showing evasive flying. The camera shutter was left open about 20 seconds to get several tracks.



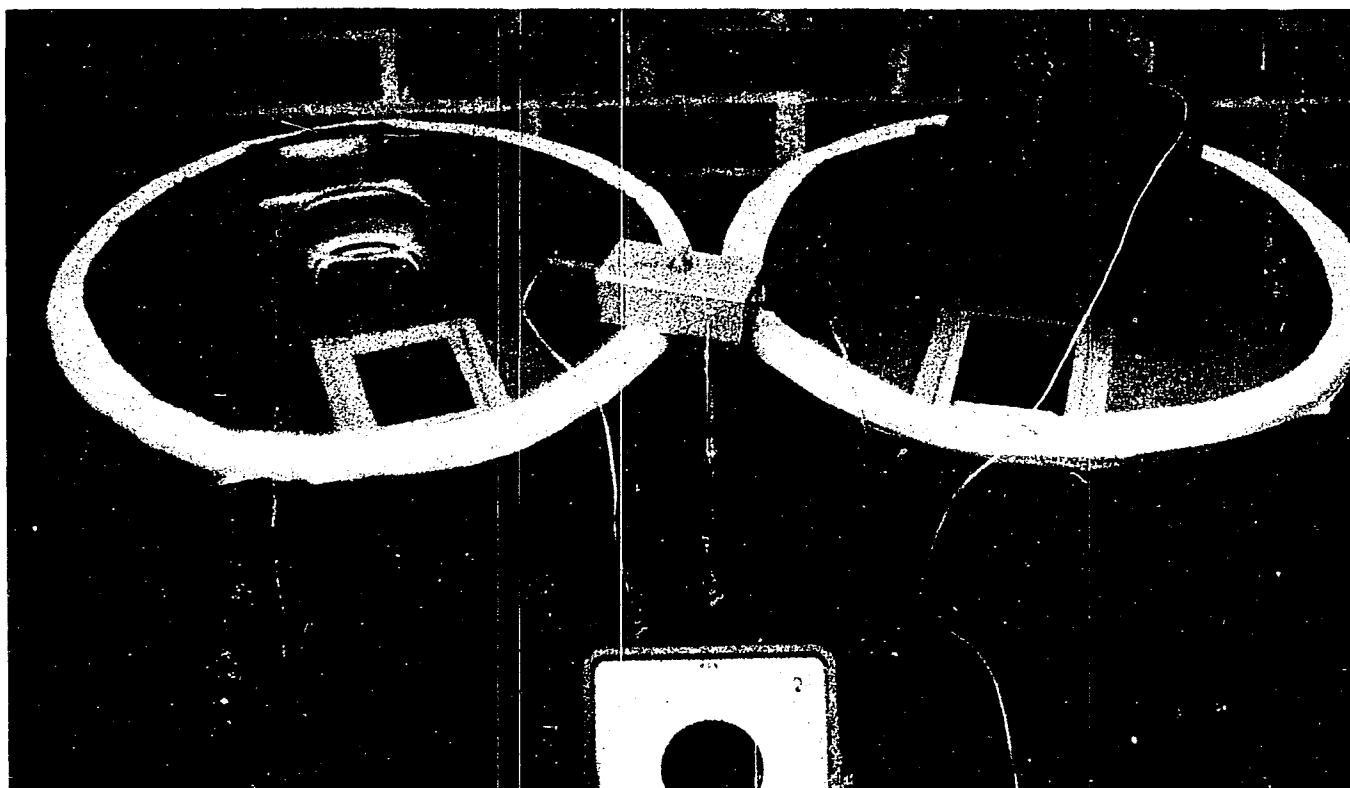


Fig.24 Two modified plastic waste barrels used to study mortality and oviposition habits of moths exposed to various forms of ultrasound.