AMRL-TR-67-192

EXPERIMENTAL STUDIES ON ECHOLOCATION MECHANISMS IN BATS

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FOREWORD

These studies of the pursuit performance of echolocating bats and associated areas of investigation were carried out under Contract AF 33(615)-2964, Project No. 7233, "Biological Information Handling Systems and their Functional Analogs," Task No. 723302, "Biological Servomechanisms." The contract was monitored by Lt. Colonel J. E. Steele and Mr. Mark Cannon, Aerospace Medical Research Laboratories, Aerospace Medical Division, Wright-Patterson Air Force Base, Ohio 45433. Work on the research was chiefly carried out by Frederic A. Webster, principal investigator, and Oliver G. Brazier in Cambridge and Lincoln, Massachusetts. This study began in July 1965 and was completed in July 1967.

Additional field work was carried out in the vicinity of Tucson, Arizona, and the Gulf of California in conjunction with Howard A. Baldwin, J. L. Stewart, and D. W. Batteau, who have contributed to the program as consultants. Their research is reported in AMRL-TR-68-40, Analog Simulation Studies in Echoranging.

This technical report has been reviewed and is approved.

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ABSTRACT

Comparative pursuit studies carried out on three species (Myotis lucifugus, Eptesicus fuscus and Lasiurus borealis) revealed similar tactics of pursuit and capture in Myotis and Eptesicus. Detection and localization capacities of Eptesicus appeared equal to the other species, but discrimination between spheres and mealworms proved highly variable, and the capacity to capture small targets inferior. Though the measured pursuit signals of the three species had definable differences, the phases of pursuit exhibited common characteristics, adequate for real-time machine identification, and thus usable for pursuit-controlled triggering of stimuli or recording equipment. Echoes returned by objects discriminated by bats have been studied by oscilloscope and human listening. Due to the number of relatively nonfluctuating echoes from mealworms (projected into a sound field of ultrasonic pulses), other details must provide essential clues for the bats' observed discriminations. Human listeners could not discriminate clearly between echo categories clearly discriminated by bats, even with slow-down ratios up to 128X. Methods for accentuating significant echo properties are under development. Studies of the fishing bat Pizonyx vivesi suggest adaptation to both aerial pursuit and surface fishing. Symbiotic communication between these bats and the petrels that share the same roosts has been conjectured.

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SECTION I

GENERAL INTRODUCTION

The present study represents a continuation and further development of previously reported studies (ref 12, 14,16,35-42) which focused on the interception performance of echolocating bats, and a number of associated aspects. The studies were initiated in 1958 in conjunction with D. R. Griffin at the Harvard University Biological Laboratories. Sponsorship was taken over by MIT Lincoln Laboratory in 1959 and continued until the general curtailment of its research program in 1963. Since that time the project has been administered by Sensory Systems Laboratory, Tucson, Arizona. The main long range lines of interest have been as follows:

(1) to measure the performance capabilities of echolocating bats, chiefly in relation to the detection, identification, localization, trajectory-prediction and interception of airborne targets (including pursuit performance in the presence of various kinds of interference);

(2) to derive clues as to the kinds of methods or

mechanisms different bats may be using to achieve the observed performances; and

(3) to link the findings of numbers 1 and 2 above to neurophysiological observations and to synthetic or theoretical models with potential usefulness in engineering theory or the implementation of echolocation applications.

Inevitably, there have been collateral interests; for example,

(4) to explore the possible ways in which clues derived from such studies of animal echolocation might be applied in human acoustical orientation--with particular reference to object localization, recognition and evaluation, most especially in situations calling for rapidity of oriented response;

(5) to gain clues for improving man-machine linkages in various dynamic situations where acoustical interactions might be involved;

(6) to relate the methods and mechanisms of bats to those of other primary echolocators, such as cetaceans; and

(7) to develop improved methods and instruments (such as telemetering devices) which promise to enhance the effectiveness of echolocation studies.

While these collateral interests have been of secondary concern in carrying out the present program, they nevertheless constitute significant motivations for its existence.

The previous research (ref 40) focused primarily on meaningful definition of the interception system capabilities of selected bats. In the present study certain of these performance measures have been extended. However, the major concern has been to make further analyses of the emitted signals and to initiate exploration of clues used in echo utilization; also to consider features of the bats' systems that may adapt them to effective echo evaluations, particularly in comparison with human audition. These considerations will constitute the main context of the present study.

The chief extension of previously reported performance measures relates to target discrimination capacities of the big brown bat _Eptesicus_ _fuscus_. Comparisons have also been made of certain distinctive properties of the pursuit signals of several kinds of bats; and in addition, an attempt has been made to evaluate the usable information in the echoes from various configurations and objects when these objects or configurations were radiated with pulses having properties akin to the pulses of bats. Finally, certain field observations have been made on additional bats, notably the fishing bat _Pizonyx_ _vivesi_.

SECTION II

PERFORMANCE MEASURES RELATED TO TARGET PURSUIT

A. Introduction

Sections II and III of the previous report (ref 40) were concerned with distances of target detection, accuracies of localization, effectiveness of trajectory prediction, reliability of target capture, capacity to identify airborne objects, speed of pursuit responses and some of the conditions that affect such aspects of performance. The findings dealt almost exclusively with two species of bats: Myotis lucifugus (little brown bat) and Lasiurus borealis (red bat), mostly the former. In the present study a number of measures have been repeated on Eptesicus fuscus (big brown bat). These are presented below along with relevant material on the techniques of pursuit and capture used by Myotis, certain additional comparative data on other bats being also included.

B. Target Detection, Interception and Capture by Eptesicus fuscus

1. Introductory Comment

Prior to the availability of an outdoor cage for preliminary training, a large number of efforts to train

Eptesicus for catching targets in the laboratory had been unsuccessful. Out of an extensive variety of targets presented, the only interest previously elicited had been occasional flight deflections toward flying moths, but no moths had been hit or caught. Only when tested with targets in a large outdoor cage[1] did these bats initiate successful pursuits under captive conditions. Relative to the laboratory situation, there appeared to be at least three factors favoring the initiation of pursuit in the outdoor cage: (1) greater flight space (roughly 18 X 11 X 9 meters outdoors, as against 11 X 4-3/4 X 4-3/4 meters indoors), (2) lack of wall echoes (since the outdoor cage had only a light enclosing mesh), and (3) the presence of a variety of natural targets.

In most instances, once a bat began spontaneous pursuits of natural targets, it would soon begin to catch mealworms that were tossed into its approximate flight path. Transfer of this catching behavior to the laboratory was not, however, immediate. Normally, the bats had to be familiarized with the laboratory and then returned to the outdoor cage. In certain instances the cycle had to be repeated several times. Once having initiated catches in

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[1] See Section VI-B.

the laboratory flight space, however, the bats tended to become stable and reliable catchers.

Interest in target detection and pursuit by *Eptesicus fuscus* derived from several sources; for example, (1) rough observations had suggested ranges of detection in the field which appeared to exceed the observed ranges of detection of *Myotis lucifugus*, and perhaps also of *Lasiurus borealis*; (2) *Eptesicus* had appeared to show greater interest in clusters of small flying insects (which raised questions such as the possible greater use of passive listening in the detection or pursuit of small insect targets), and (3) the lower frequency of the emitted signals of *Eptesicus* led to the suspicion that these bats might have reduced capability for the detection or localization of small targets by active echolocation (see e.g. ref 10, p. 154 and ref 25), p. 167). Thus, the wavelengths in the region of maximum radiation energy in *Eptesicus* signals during pursuit is of the order of 10-15 mm--approximately four times the effective diameters of some of the small insects pursued by these bats. With *Lasiurus* the corresponding figure is closer to two times. Although exploration of the capabilities and methods of *Eptesicus* remain as yet incomplete, some relevant observations of interest are reported below.

2. The Detection and Pursuit of Small Targets

In the course of tests on the capacity of *Eptesicus* to discriminate between spheres and mealworms (see Section II-C below), certain relatively small targets were employed. Contrary to the above-mentioned suspicions regarding detection, the Eptesicus used in the tests revealed striking capabilities at detecting spherical targets as small as 3/32" (2.4 mm) in diameter.[2] While we did not establish definitively the range of detection in these instances, the range appeared at least as great, or greater than, that noted with Myotis. Such targets were probably well detected by a distance of a meter or more. At the same time, the capacity of the Eptesicus to make accurate captures of such targets, ballistically projected, appeared definitely inferior to the capacities of Myotis lucifugus and Lasiurus borealis--the latter giving evidence of rapid adaptation for the capture of such objects.

Figure 1a illustrates a near miss of a quarter-inch sphere by Eptesicus. The aim of the bat's head in the first image indicates excellent localization (of the left-hand image of the upper pair), yet the attempted tail-membrane catch failed to touch the target, which can be seen continuing to fall in the final image. Contrary to our findings with Myotis, such errors in the final aim of the catch membrane seemed to involve some miscalculation

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[2] Definitive detection of remarkably small cylinders or projections by other bats are reported in ref 20 and 31.

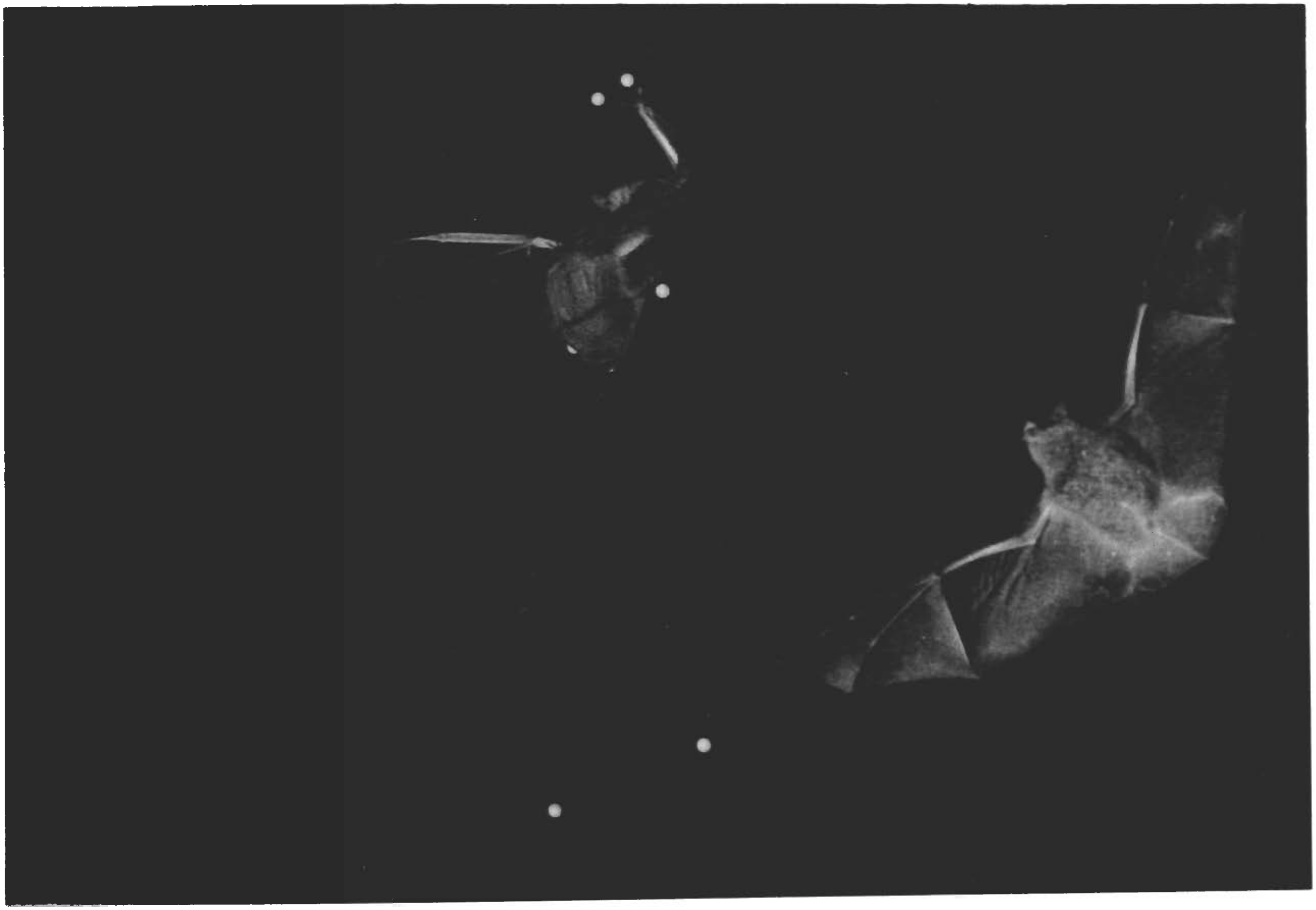

Figure 1a. Near miss of a 1/4 inch nylon sphere by *Eptesicus fuscus*. Central image of the bat shows tail membrane sweeping *forward* for the catch, but the sphere continues to fall untouched. The downward twist of the membrane suggests that the bat was attempting to compensate for its error of trajectory evaluation. (Flash interval here and in subsequent pictures is approximately 1/10 second).

other than the initial failure to appreciate the acceleration of gravity (ref 7), since they appeared less likely to be abolished by practice (as was typically the case with Myotis). Under existing experimental conditions the Eptesicus appeared less able to achieve effective evaluations of the trajectories of small targets than was the case with Myotis, and their techniques proved far less effective than was the case with Lasiurus.

Figure 1b illustrates a rather high-speed backward somersault catch of a 3/32" (2.4 mm) sphere by Lasiurus borealis. While we have previously suspected that this technique may be particularly adapted for the catching of rapidly maneuvering targets (ref 36), the technique may also be useful in compensating for final errors of localization, such as might occur during the high-speed interception of very small targets. In our experience, Eptesicus and Myotis never make use of this technique. A nonsomersault catch of a 1/16" nylon sphere by Lasiurus borealis (accidentally printed inverted) is shown in figure 1 of the previous report (ref 36).

3. The Detection and Pursuit of Multiple Targets

The previous report presented evidence that at least some members of the species Myotis lucifugus and Lasiurus borealis were capable of making accurate selections of one target from a cluster of similar targets that might be

Figure 1b. Backward somersault catch of a 3/32 inch nylon sphere by Lasiurus borealis. Although this technique may be especially adapted for the capture of maneuvering moths, it appears to be effective, also, in the seizure of small targets.

spaced within a few centimeters of each other. Some individual bats would make selections out of clusters as large as 16--though many of the *Myotis* were reluctant to attempt any clusters of targets, often refusing even to pursue one of a pair if the spacing was closer than about half a meter.

In the course of further tests with *Lasiurus borealis* we found that there was essentially no limit to the size of clusters from which certain of these bats would make successful individual target catches. Moreover, we gained further evidence that these bats did not necessarily select the nearest or highest of the targets presented (the location apparently preferred by *Myotis*), but often appeared to select any convenient target that lay close to the anticipated flight path. Figure 2, for example, illustrates the successful catch of one out of 24 mealworms--the bat apparently selecting one located conveniently along its existing flight path.

We were interested to note that *Eptesicus*, like *Lasiurus*, seemed eager to attempt relatively large clusters of targets, and that they were successful in making excellent resolution of a desired target from other nearby targets. Figure 3 shows the capture of the most distant of six mealworms, the mealworm that was most directly in line with the existing flight path of the bat, while figure

Figure 2. Catch of 1 out of 24 mealworms by *Lasiurus borealis*. End of selected mealworm can be seen in the bat's mouth as it comes out of the catch.

Figure 3. Catch of 1 out of 6 mealworms by <u>Eptesicus fuscus</u> Here, the selected target appears to be the <u>one which is</u> located most conveniently along the bat's existing flight path. The mealworm can be seen in the bat's mouth as flight is resumed.

4 shows the selection and capture of one out of 18 mealworms.

4. Techniques of Capture by *Eptesicus fuscus*

Existing photographic evidence, both from multiple flash sequences and from high-speed films, indicates that the techniques of target capture used by *Eptesicus fuscus* are basically the same as those used by *Myotis lucifugus*. With ballistic targets in the laboratory, *Eptesicus* typically attempt tail membrane catches, as previously described for *Myotis* (ref 36,42). Two representative examples are illustrated. Figure 5a illustrates a typical sequence. Immediately prior to seizure (first full image of bat) the bat's head is aimed directly at the target (mealworm), about half a dozen centimeters away and slightly to the left, while the tail membrane is starting its forward sweep in preparation for the catch. Note that the ears are tipped slightly forward and that the tip of the bat's tongue is clearly visible. At the next image the tail membrane has been brought up over the bat's face and the ears are tilted slightly backward. The ensuing image shows the bat still in the process of target seizure. However, in the final image the bat has resumed normal flight with the target in its mouth. Figure 5b shows a rather similar catch, but one which is completed in the course of three 1/10 second intervals instead of

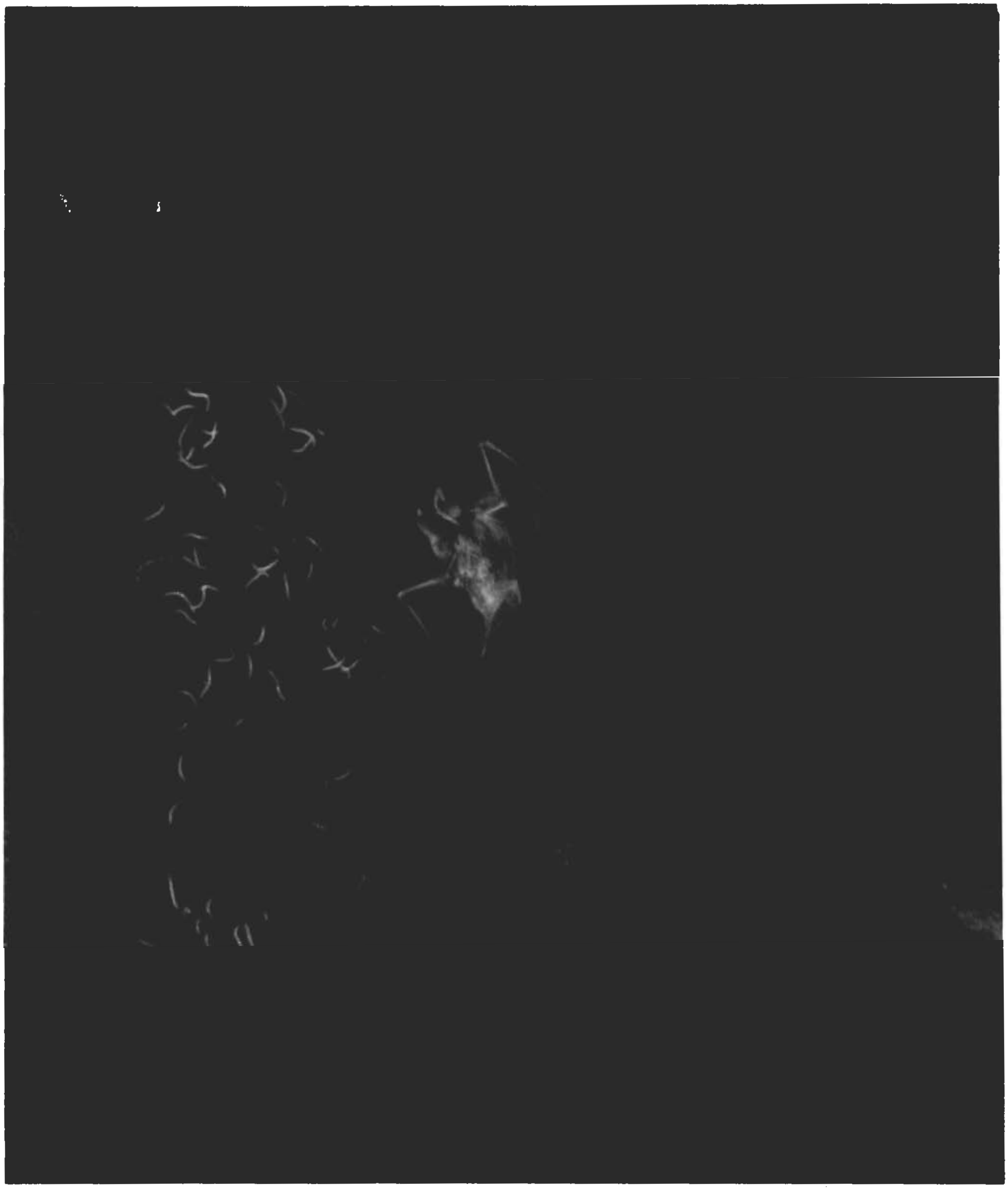

Figure 4. Catch of 1 out of 16 mealworms by *Eptesicus fuscus*.

Figure 5a. Representative tail membrane catch by *Eptesicus fuscus*. Just prior to the catch, the bat's tongue can be seen protruding slightly, with tip bent somewhat upward.

Figure 5b. Tail membrane catch by *Eptesicus fuscus*. Catch is here completed in about 1/5 second.

four. Again the bat's head appears aimed directly toward the target at close range and the ears are tipped slightly forward. Although complete statistics have not been compiled, there is a suggestion that Eptesicus attempt to keep their heads aimed at the target throughout pursuit, while Myotis sometimes relinquish accurate head-following when the target is close at hand. Lasiurus borealis, as previously pointed out (ref 36), may make little or no attempt to follow maneuvering targets at close range with their heads (see figure 5c), yet (with the exception of sudden deflections by fast-moving targets) their captures are typically successful.

Use of the wing membranes in target captures by Eptesicus appears to correspond closely with wing techniques employed by Myotis. Figure 6a shows the seizure of an upward-moving mealworm with the use of the central wing surface. In the middle image the target has been transferred to the tail membrane, which has been brought up over the face. In the next to last image it has been seized with the mouth, while in the last image flight has been resumed with the mealworm held firmly in the teeth. Note that the bat appears to have kept its head directed toward the target up to the point of seizure. Figure 6b shows a rather similar catch in which the target is just beginning to fall. Use of the bent-over wingtip, such as noted in a number of catches by Myotis, is shown in

Figure 5c. Capture of rapidly-falling mealworm by Lasiurus borealis. Target can be seen just striking inner portion of left wing. Note that the bat's head is not directed upward toward the target during the approach.

Figure 6a. Wing-catch of rising mealworm by *Eptesicus fuscus*. (See text)

Figure 6b. Seizure of mealworm with lower wing by *Eptesicus fuscus*. Note bent-over wingtip and curvature of tail membrane toward target.

figure 6c. The target, however, is hidden by the wing membrane and cannot be seen at the time of capture. In the final image, the tail membrane is over the bat's head for seizure with the mouth. A somewhat similar catch is illustrated in figure 6d, but in this instance the target is just visible against the lower wing surface, just above the tip. As was found with both Myotis and Lasiurus, transfer was always made from wing to tail membrane prior to seizure with the mouth.

5. Responses of Eptesicus to Moths

a. Previous observations with moths

Since the interrelations between Myotis lucifugus and sound-emitting moths was not covered in our previous report, a brief review of earlier findings should be given before presentation of the current findings on Eptesicus fuscus (see ref 8,28,29,36,37,39,41). During the summers of 1958 and 1959, Dr. A. E. Treat (who was carrying out tests with bats and moths in the Berkshires) noted that red bats, Lasiurus borealis, tended to veer away from the arctiid moth Halysidota tessallaris when this moth was tossed into their flight paths. By contrast, most nonarctiid moths were actively pursued. Although one of our recordings, made with Treat at the time, revealed trains of pulses we subsequently recognized as similar to those of Halysidota (fig 41 of ref 36), we

Figure 6c. Wingtip catch of falling mealworm by *Eptesicus fuscus*. (See text).

were unable at the time of Treat's tests to establish that the evasions demonstrated by Treat were associated with sound emission on the part of the moths.

The fact that a number of arctiid moths emitted ultrasonic clicks--together with the nature of the click mechanism used by Halysidota--was subsequently clearly demonstrated by Blest, et al. (ref 2). At roughly the same time we noted, during laboratory flight tests, that *Myotis lucifugus* rejected all 14 tosses of actively sound-emitting tiger moths[3] (mostly *Apantesis virgo*), yet they pursued 19 out of 20 nonsound-emitting control moths (capturing 16), the tosses of which were interspersed between the tosses of the tiger moths. During the same tests, the bats caught 4 out of 10 of the *Halysidota* presented. Relatively few of the actively emitting sound-generating moths were available, and hence the samples were inadequate for any final conclusion. The clear-cut results of the available sample of tiger moths, however, strongly suggested that some feature of these moths caused evasion

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[3] The low intensity level of the moth's clicks made an evaluation of click emission impracticable during the actual tests. It was found, however, that when the moths were projected up directly in front of an ultrasonic microphone, they were characteristically emitting clicks--presumably due to the agitation associated with the projection process. Because of the artificial stimulus activating them, the clicks may well have been somewhat different from those normally emitted in free flight.

or cessation of pursuit by Myotis lucifugus--as had the earlier demonstrations by Treat suggested evasion of Halysidota by Lasiurus borealis. Our limited results with Halysidota and Myotis lucifugus were of interest but certainly much less striking than the findings with Apantesis.)

Three chief explanations or hypotheses were proposed to account for the observed avoidances of sound-emitting moths by bats:

(1) that the taste of some sound-emitters was obnoxious to the bats (though the present sound-emitters might only be mimicking those with obnoxious taste),

(2) that some of the sound-emitters had clinging spurs on their legs and might be capable of seriously interfereing with the bat's flight after capture, and

(3) that in the course of the bat's evolution some important predators (perhaps certain birds) have made clicking sounds during their approach.

(Explanations based on masking effects or the production of phantom "echoes" so timed as to deflect the bat from its real target seemed unlikely.)

Although it was not possible to test the hypothesis that the clicks of the available moths might resemble the clicks of offensive-tasting moths, we did find that the bats were often eager to eat either Apantesis or Halysidota when the moths were presented with tweezers. The idea that some of the moths might be capable of serious interference with the flight of the bats gained some substantiation in our observations with certain of the captures of Halysidota. At times the bats appeared to have such trouble disengaging the moths from their flight surfaces that they lost considerable altitude in the process. Some very limited photographic evidence (e.g., fig 8 of ref 36) suggested that, with Halysidota at least, the bats might be making some evaluation of relative orientation--capturing chiefly those with legs pointed away at the time of seizure.

Possibly related to such positional evaluation by the bats was the more conclusive observation that when some bats were placed in a cage with a variety of moths, they characteristically stalked the moths in such a way as to achieve seizure from behind or above the moth's thorax. Since we recorded no pulses during such behavior, the evaluation was presumably made by passive listening. The observations, however, tended to confirm Treat's contention (personal communication) that Myotis lucifugus and Lasiurus borealis typically attempted to seize the thorax of a moth in order to crush the thoracic ganglia and thus paralyze the action of the legs.

b. Present Observations:

At the time of our observations on Myotis lucifugus and sound-emitting moths, no corresponding tests had been carried out with Eptesicus. However, this larger, more aggressive bat might be less concerned with clinging spurs than the smaller Myotis. Unfortunately, no Halysidota were available at the time our Eptesicus were catching in the laboratory. However, we did capture a number of Apantesis and were thus able to carry out tests of the propensity of Eptesicus to pursue these moths.

The procedure used in these tests was the same as that previously employed with Myotis. Immediately prior to their projection into the approach paths of the bats, the Apantesis were tested for their proclivity to emit ultrasonic clicks upon agitation: only those which readily emitted such clicks were employed in the tests. Enough active sound-emitters were available to permit the completion of tests corresponding to those carried out with Myotis.

During the familiarization phase in the laboratory, the response of the Eptesicus tended to be erratic. Gradually, however, the bats came to pursue most moths presented, and the tests were then carried out. As in the previous tests with Myotis, the tosses of Apantesis were interspersed with nonsound-emitting controls and--as with Myotis--most nonsound-emitting moths were vigorously pursued. The response to Apantesis, however, was completely opposite: all 16 tosses of these moths (divided between two Eptesicus) resulting in intensive pursuits, most of which ended in capture. Unfortunately, we had no catching Myotis available at the time of the present tests and were thus unable to interchange Myotis and Eptesicus under fully equivalent experimental conditions. We can only say at this juncture that the pursuit behavior with respect to the sound-emitting Apantesis appears to be different in the two species.

Representative responses of Eptesicus to the moths used in the tests are indicated by a few selected photographs. Figure 7a illustrates what appears to be a failure of proper evaluation of the flight course of a maneuvering moth (nonsound-emitting). At image number 2 the moth is upside down, looping off to the left away from the bat. The bat executes its usual tail membrane scoop maneuver in obvious anticipation of a catch (image number 3), but the moth has escaped and the bat comes out of the maneuver without its target (images number 4 and 5). Figure 7b shows a rather different response to a tiger moth during the familiarization phase. At bat image

Figure 7a. Failure of Eptesicus fuscus to seize a maneuvering moth (non-sound-emitting). The bat carries out a typical catch maneuver and then resumes flight. Note that mouth is partially closed at this point.

Figure 7b. Failure of *Eptesicus fuscus* to pursue tiger moths. After temporarily following the moth with its head, the bat resumes normal flight.

number 2 the Eptesicus appears to be following the moth, but by image number 3 it has clearly relinquished any intent to pursue, as evidenced by the partial closure of the mouth and the cessation of head following. Figure 7c illustrates a direct tail membrane catch of a non-maneuvering silent moth that was projected upward in front of the bat. At image number 4 the bat is coming out of the catch with the thorax of the moth seized in its teeth. An essentially similar catch (of a tiger moth) from a different viewpoint is illustrated in figure 7d. As already pointed out (under section on "techniques" above) the techniques of close-range pursuit and capture in the laboratory appear remarkably similar to those used by Myotis. Under wild conditions in the field, Eptesicus typically employ greater flight velocities and make turns of greater radius during pursuit than do Myotis. Thus we cannot conclude that the techniques with natural targets are fully similar under all conditions. The basic techniques, however, appear to have essential similarities under the conditions of observation.

C. Target Discrimination by Eptesicus fuscus

1. Introductory Comment

Previous target discrimination studies on Myotis lucifugus, reported elsewhere (ref 12,14,36,40,41) demonstrated that these bats were capable of learning to

Figure 7c. Typical capture of silent non-maneuvering moth by *Eptesicus fuscus*.

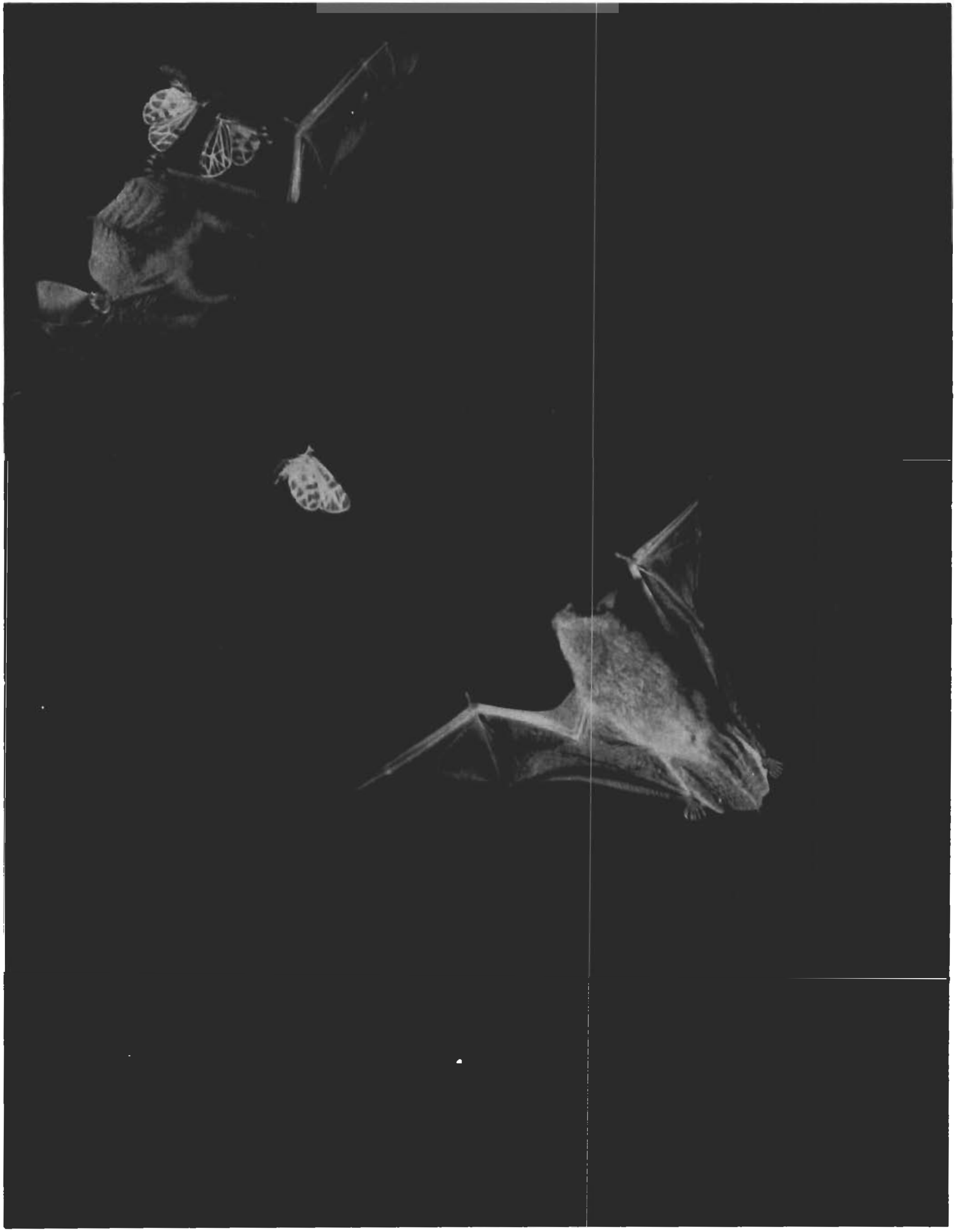

Figure 7d. Typical capture of tiger moth (Apantesis virgo) by Eptesicus fuscus.

differentiate between a standard food target (mealworm) and one or more different classes of inedible objects of roughly the same size (or that returned echoes of roughly the same magnitudes). The investigations of immediate concern are those in which the bats were required to distinguish between mealworms and spheres--the spheres covering a sufficient range of sizes to span the echo magnitudes characteristically returned by mealworms. Experiments corresponding to those carried out on *Myotis lucifugus* have been carried out on *Eptesicus fuscus*, the results being reported below.

2. Experimental Situation

Three groups of tests were carried out on *Eptesicus*. As with the sphere discrimination experiments on *Myotis lucifugus*, these were designated: *sequential single*, *sequential mixed* and *simultaneous paired*. It had been our intent to use a range of sphere sizes that extended from spheres too small to be readily detected to those that were obviously far too large to be confused with mealworms. We did not expect *Eptesicus* to attempt targets as small as the 1/16" spheres occasionally caught by *Myotis*. This was, in part, because of the larger size (and less abrupt maneuverability) of the bat, in part because of the lower frequency of the emitted signal (these spheres having diameters of the order of 1/10 the wave-length of the bat's close-range pursuit signals), and in part because of our suspicion that Eptesicus might be more bothered by wall echoes. For these reasons and because of a limited number of smaller spheres available at the time of the tests, spheres as small as those used in the tests with Myotis were not included.

The procedures used in the three groups of tests were described in the previous report and need not be repeated in detail here. However, the different groups can be summarized as follows: In the sequential single tests, only one target was presented at a time, and during any given test only a single size of sphere was used. Half of the targets presented were spheres and half were mealworms, with a number of different quasi-random orderings being used to guard against possible sequence learning. In the sequential mixed tests, spheres of all sizes under test were presented during each test run, with the orderings again being varied in a quasi-random fashion.

For the sequential tests, the bat normally circled in the flight zone and indicated its readiness for a target presentation by a characteristic pulse-rate increas in the target area. Targets were either tossed by hand or projected by solonoid-driven "gun" into the approach path of the bat. Scoring was specified in three main categories: Contact (C), Attempt (A), or no-attempt (N).

In the simultaneous paired tests, only one size of sphere was used, but two targets were always presented simultaneously by "gun." For these tests the two "guns" were placed about a half a meter apart, and at right angles to the bats' typical path of approach. Although only left-right positions were specifically provided for, enough variations of trajectory occurred so that deviations in range and elevation commonly amounted to a third of a meter (1 ft) or more. Four target categories were used: two mealworms (MM), two like-sized spheres (SS), mealworm-left and sphere-right (MS) and sphere-left and mealworm right (SM).

3. Results

a. First group--sequential presentation, single size of target:

Of the three bats used in this group of tests, adequate data were obtained only on one (RB). Another bat which was tested fairly extensively appeared never to recognize the nature of the experimental situation--continuing to catch spheres of all sizes, even as large as a ping-pong ball of 1-1/4" diameter. (See fig 8a for close approach to a ping-pong ball and fig 8b for a catch and drop of a 3/8" sphere.) Results for the most

Figure 8a. Close approach to ping-pong ball by *Eptesicus fuscus*. Note closure of mouth after decision to avoid.

Figure 8b. Catch and drop of 3/8 inch nylon sphere by *Eptesicus fuscus*.

adequately tested bat are given in figure 9. These tests consisted of 16 presentations of mealworms and 16 of spheres, and the results are plotted in terms of contact-plus-attempts rather than in terms of contacts, as had been done with Myotis. A more meaningful matching of results was possible with the use of this difference, since Eptesicus frequently pursued the smaller targets without reaching them (see fig 1a), whereas the Myotis normally succeeded in making contact with all targets pursued. The use of only five sizes of spheres, instead of ten, was dictated by the need to condense the testing program.

The most striking feature of figure 9 is the 100% error score for spheres of those sizes that returned echoes corresponding in magnitude to the magnitude of echoes most commonly returned by mealworms (i.e., spheres of 1/8", 1/4" and 3/8" diameters). With the two largest spheres--those of 1/2" and 5/8" diameters--there was a sharp decrease in proclivity to pursue. Mealworms were always pursued during these tests. It is of interest to note that the results with this bat correspond reasonably closely to the results with the worst of the Myotis previously tested (ref 40).

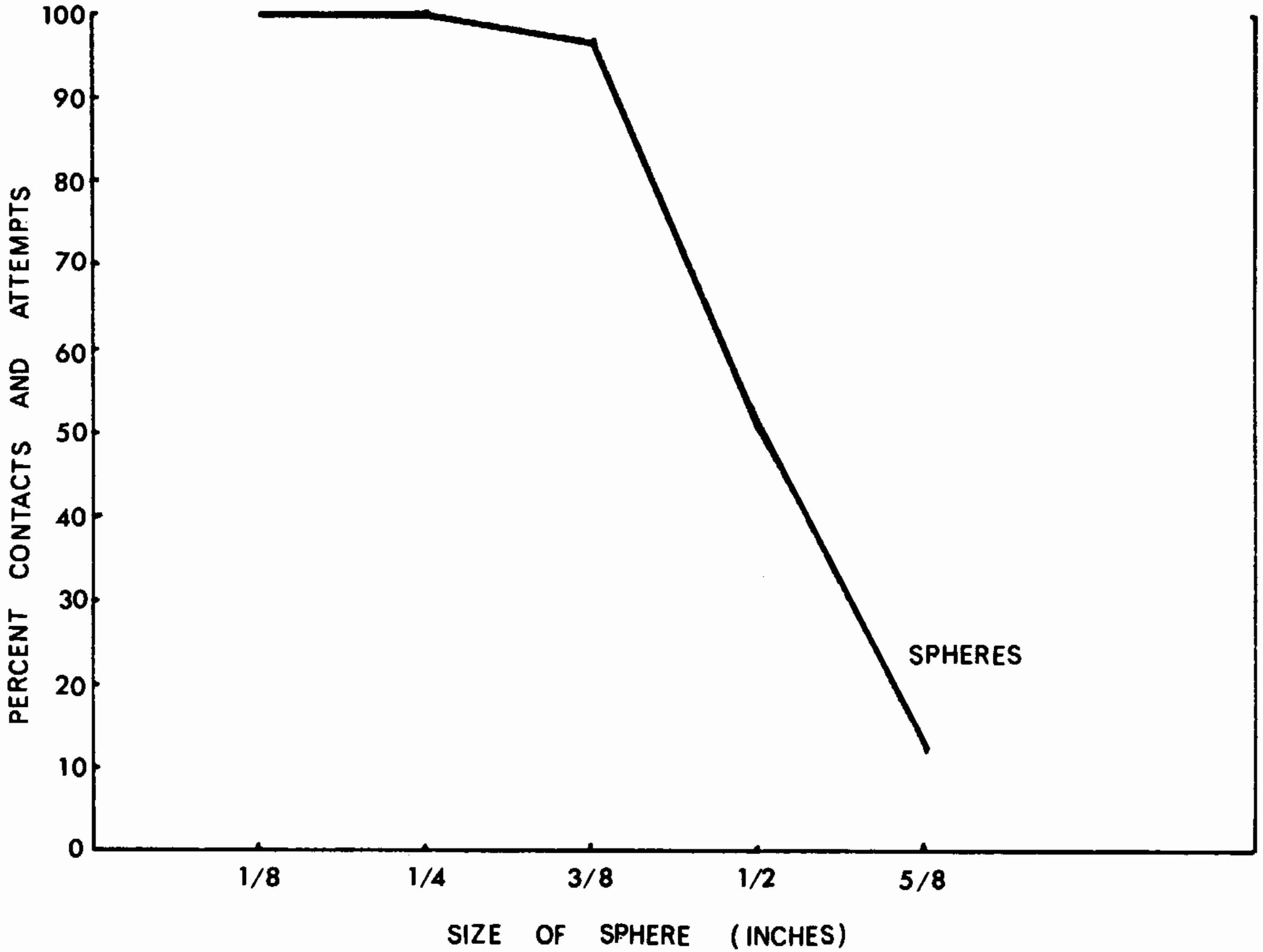

Figure 9. Discrimination performance for one *Eptesicus* during sequential tests using one size of sphere per test. Tests are here somewhat variable in length, averaging about 16 presentations of each class of target per test. Scores are in terms of percent erroneous pursuits (i.e., contacts plus attempts) of spheres. There were no mealworm errors.

b. Second Group--Sequential presentation, mixed sizes of spheres per test

All three Eptesicus trained in the laboratory to catch targets were given tests with mixed sizes of spheres. In addition to the sphere sizes used in the runs with a single size of sphere, additional spheres of 3/32" (2.4 mm), 3/4" (19 mm) and 1-1/4" (32 mm) diameters were included. Plots for the better two bats (RB and MT) are given in figures 10a and 10b. The mixed-size tests for one bat (RB in fig 10a) were interposed between the single-sized tests, while the other bat (MT of fig 10b) was given only tests with mixed sizes of spheres. As previously mentioned, the third bat (results not shown) gave essentially no evidence of discrimination.

The main points of interest in figure 10a are: (1) the continuation of a strong tendency on the part of the bat to catch small sized spheres (including, in two tests, the 3/32" sphere); and (2) the progressive shift, with experience, away from catches of the larger spheres. The small size of the sample and the limitation of score categories to 0%, 50% and 100% preclude the attachment of any significance to the precisely progressive shift that actually occurred.

Results for the second bat of this series (fig 10b) were of the same general form. However, the extent of the

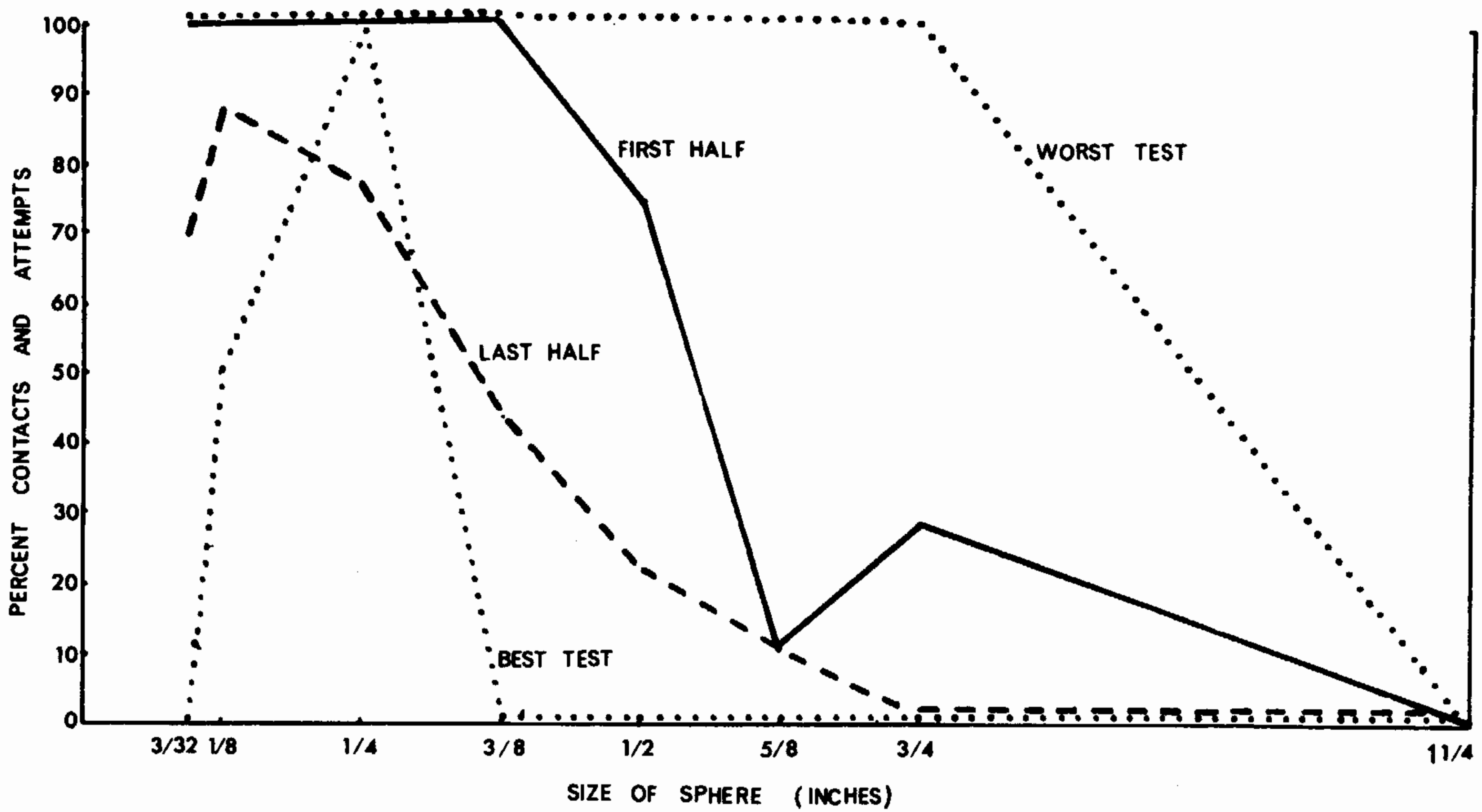

Figure 10a. Discrimination improvement for one Eptesicus during sequential tests using mixed sizes of spheres per test. First and second halves of the tests, showing each half consisting of 5 tests, are compared--also, the test showing the poorest discrimination (first test) and the test showing the best discrimination (ninth test). There were no mealworm errors.

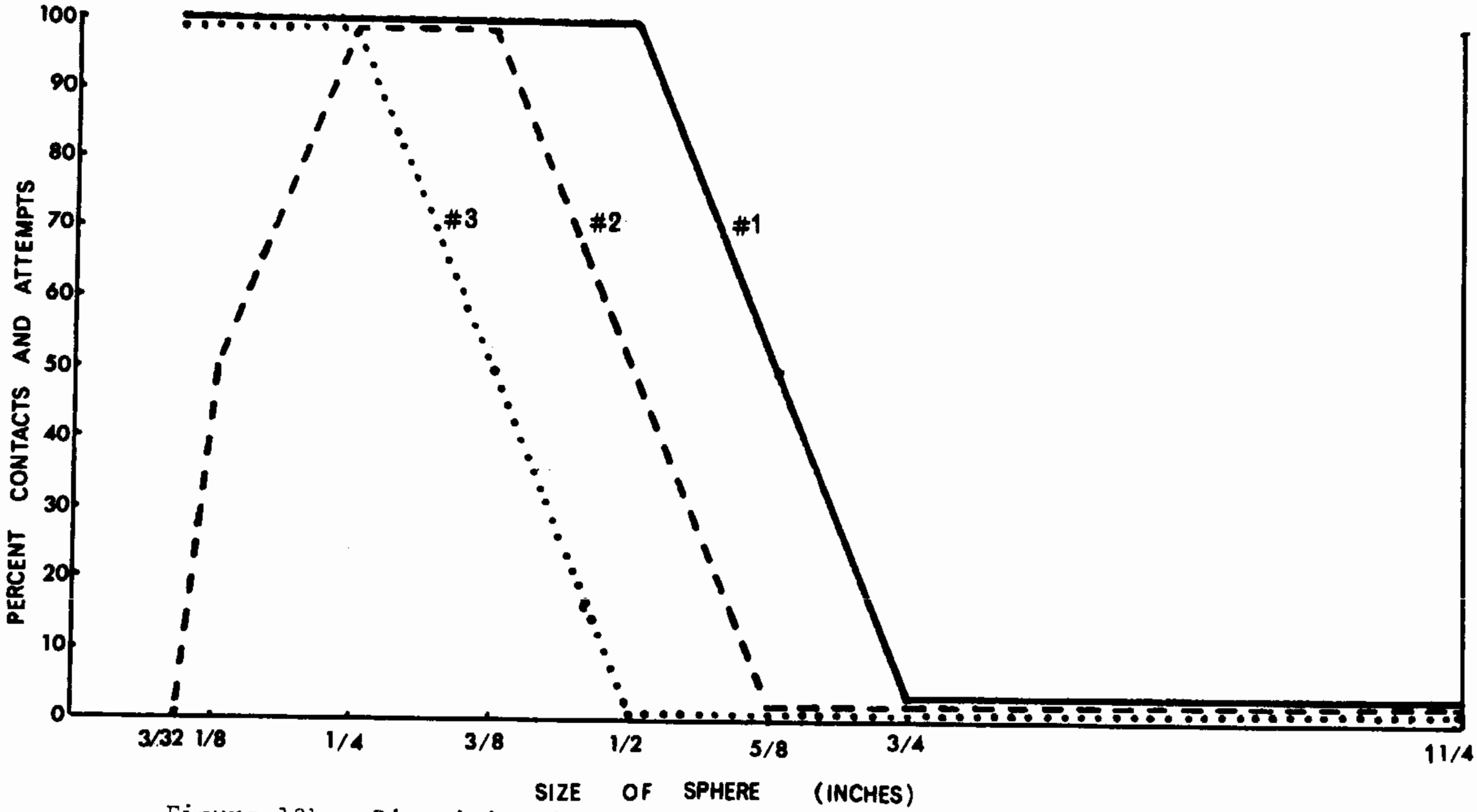

Figure 10b. Discrimination improvement for a second *Eptesicus* during sequential tests using mixed sizes of spheres per test. First, second and third tests are compared, each test consisting of 16 presentations of each class of target. Since only two presentations of each of the 8 sizes of spheres were given per test, the only possible error scores were 0%, 50%, and 100%. There were no mealworm errors.

behavioral shift with learning was greater: the bat showing worse initial discrimination and better final discrimination. As with the previous bat, this bat also showed a strong tendency to pursue small spheres.

In comparing the present sequential results with those obtained during sequential tests with *Myotis lucifugus*, it is clear that both species are capable, in most instances, of acquiring the capacity to distinguish spheres of any size from live mealworms that are projected upward into a standard region of capture. In general, *Myotis* seem able to learn extremely effective discrimination of all sizes of spheres and mealworms, though effective discrimination has tended to evolve more slowly for spheres that were roughly the same size as mealworms, and perhaps also for those that were somewhat smaller. The *Eptesicus* thus far tested have shown greater initial proclivity to pursue both larger and smaller spheres than is typical of *Myotis*. From the small sample available we suspect either (1) that, for *Eptesicus*, the erroneous catching of spheres constitutes a less negative experience than holds for *Myotis*, or (2) that the normal propensity for *Eptesicus* to pursue airborne objects within a certain size range (or zone of echo reflectance) tends to be greater.

c. Third Group--Simultaneous presentation of paired targets, using a single size of sphere per test:

Figure 11a presents the initial and final results with dissimilar targets (MS and SM) for the two bats which showed discrimination capabilities. Although the data are limited, the general form of the results is distinctive. During the first set of tests the bats selected the larger of the two targets presented: choosing mealworms over small spheres and choosing large spheres over mealworms. When the two kinds of targets were of roughly the same size, the bats selected between the two at random. During the final set of tests, the bats correctly chose mealworms over large spheres, but continued to make essentially random selections when the two sets of targets were of roughly the same size.

In comparing the results with those previously obtained on Myotis (figure 11b), two differences stand out: (1) differences in initial response, and (2) differences after training. The Myotis initially tended to make more or less random selections between mealworms and most sizes of spheres, while the Eptesicus initially tended to select the larger of the paired targets. After roughly equivalent experience, the Myotis achieved relatively accurate discrimination between the two classes except that they often continued to make an appreciable number of both mealworm and sphere errors, notably when

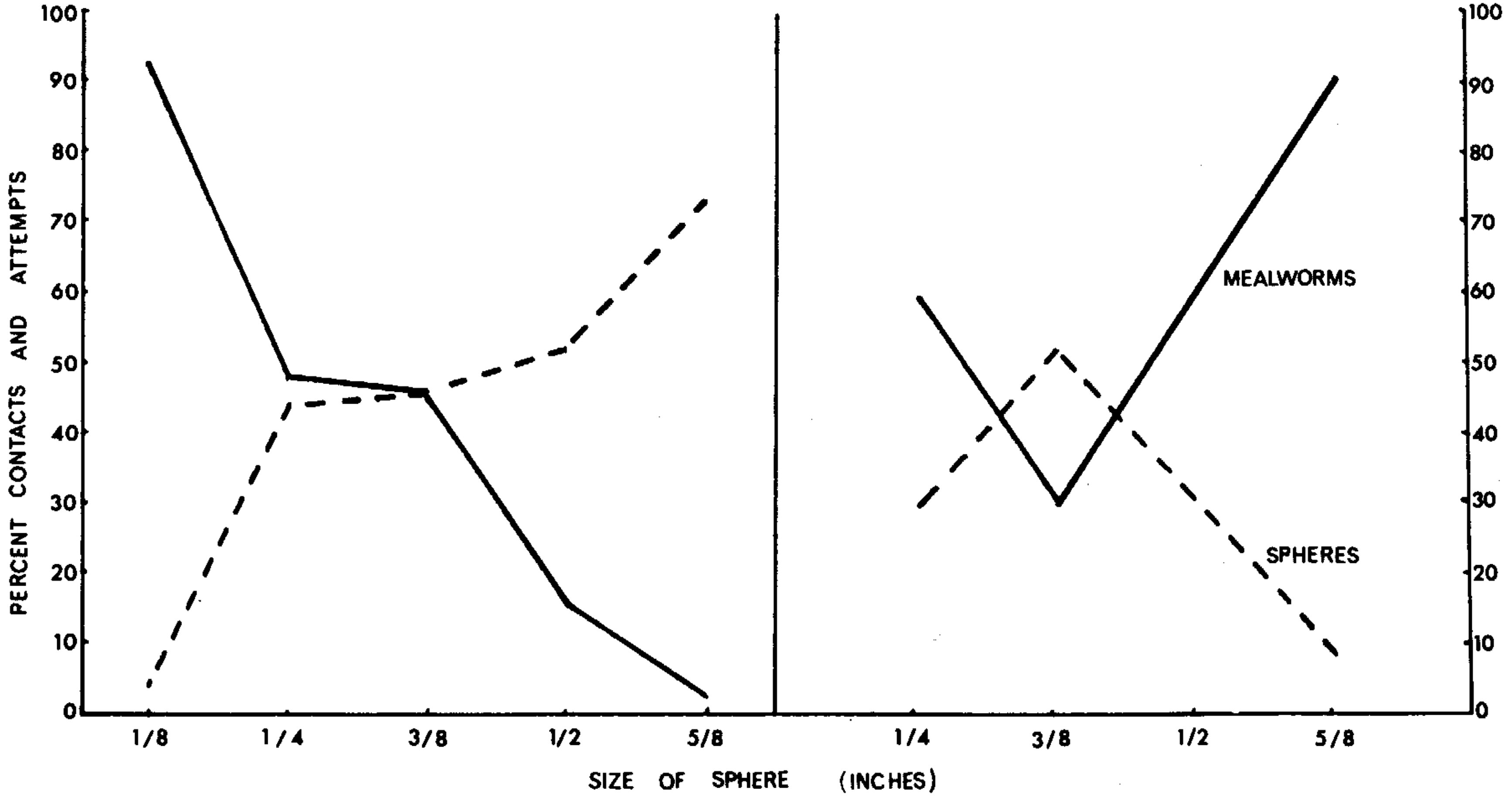

Figure 11a. Discrimination improvement for two Eptesicus during simultaneous presentation of a mealworm and one size of sphere per test. Comparison is here made of the contacts-plus-attempts for spheres and mealworms during the first and last set of tests, each test consisting of about 16 paired presentations of a mealworm and a given size of sphere. For results with similar pairs (two mealworms or two spheres) see text.

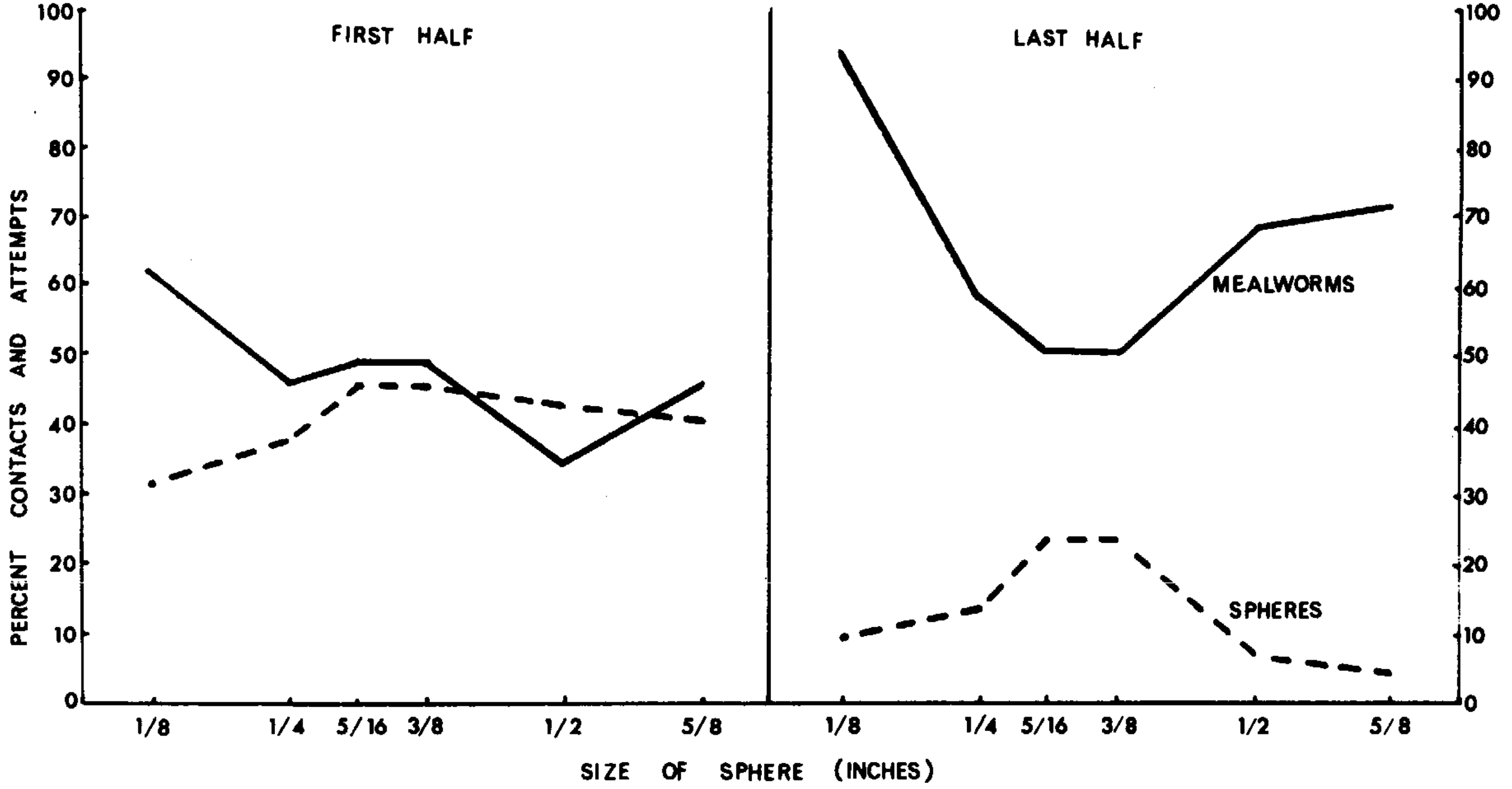

Figure 11b. Discrimination improvement for three *Myotis* during simultaneous presentations of a mealworm and one size of sphere *per test*. (This is figure 14 of the previous report, reproduced here for comparison with the present findings with *Eptesicus*.)

spheres within the size-range of 1/4" to 3/8" diameters were paired with the mealworms). The Eptesicus only learned to discriminate more extreme size differences. Although strongly suggestive of better discrimination between dissimilar pairs by Myotis, as compared with Eptesicus, the present sample is not comprehensive enough to draw final conclusions about the differential responses on the part of the two species.

When like pairs of targets were presented, the behavior of different individual bats tended to vary widely. Although all 155 presentations of two mealworms to Eptesicus resulted in pursuits, the proclivity to pursue one of a pair of simultaneously presented spheres varied from bat to bat, ranging from about 50% to about 90%, with some apparent preference for the pursuit of smaller spheres.

d. Summary of Differences

Perhaps the most significant findings suggested by the present results are the following:

(1) the striking capacity of Eptesicus to detect, and their strong proclivity to pursue, small-sized targets; for example, spheres of 3/32" (2.4 mm) diameter);

(2) the more persistent apparent confusion between

the two classes of targets (spheres and mealworms) when the two were of roughly the same size--most particularly when a mealworm and similar-sized sphere were presented simultaneously.

SECTION III

SOME SPECIES DIFFERENCES IN EMITTED SIGNALS

A. Introduction

Among investigators of animal echolocation, much speculation has arisen as to the significance of the widely differing properties of the emitted signals (ref 3,4,10,11,35,37). At the same time, however, certain basic similarities have been evident (ref 26). Among the echolocating bats, for example, wide differences exist from species to species with respect to: pulse carrier frequency, pulse duration, duty cycle, harmonic content, rates of frequency sweep, average intensity, intensity variation pattern; also with respect to associated actions of the transmit-receive mechanisms (e.g., nose shape in nostril emitters and ear action--especially in the CF bats) (ref 13,36,37). Yet all echolocating bats--in fact most echolocating animals--make use of certain common mechanisms of variation (ref 6,11,18,21,22,23,24, 25,30,33). Thus, they generate longer, more widely spaced pulses when their chief concern is with distant objects or configurations, and they generate shorter, more closely spaced pulses when their chief concern is with objects at close range. Moreover, the pulse patterns tend to have characteristic features in the two instances. The longer pulses tend to exhibit irregular spacing or are emitted in small groups (often in pairs or triples), while the shorter, high-repetition-rate pulses normally exhibit regularized spacing (or regularized shifts of spacing); though sudden shifts of interval spacing, or intermittently-dropped pulses, may occur. Furthermore, in the transitional phase from low rates to high rates echolocators which use frequency sweep normally make use of increased rates of frequency sweep. In addition to the low and high repetition rate modes, certain special and intermediate modes appear to characterize particular activities--sometimes particular phases of these activities. The fact that a human listener can often judge the specific activity being carried out by different bats, sometimes even the context in which the activity occurs (simply by listening to the rectified pulses) suggests that these activities must have definable properties which can be extracted independently of the species. It is also true that a listener can often judge the species by listening to a sample of the bat's activities.

These observations have suggested that it might be possible to design devices for two important needs of investigators of bat behavior and performance: the need to recognize different species of bats in the field by the pulses they emit and the need to activate equipment (for example, cameras) at the onset of some specified phase of activity. From a technical point of view, either of two approaches has been considered feasible: the use of real time analysis with a small, high-speed computer and the use of special analytical equipment constructed to comply with pre-analyzed aspects of the signal configuration. The present section is chiefly concerned with systematic comparisons of the pursuit signals of three species of bats, as a possible basis for species identification. A subsequent section deals briefly with a specific analytic device designed to activate equipment at specified phases of a bat's target pursuit.

B. Comparative Pursuit Signals of Myotis lucifugus, Eptesicus fuscus and Lasiurus borealis

1. Introductory Comment

The pulse patterns of vespertilionid bats are characterized by several features which may lead to a succesful basis for species recognition and identification. Tape recordings provide data on three distinct aspects of the bats' approach signals: (1) pulse repetition rate and pattern, (2) pulse duration, and (3) pulse frequency structure.

(1) Pulse repetition pattern: When a trained and motivated bat circles within the laboratory flight room, passing through the target presentation zone on each circuit, it tends to emit one of two easily recognized types of signal patterns, depending on whether or not a target is presented. When no target is presented, the bat circles the major portion of its circuit without the use of closely spaced pulses. Although the rate varies widely, bats of different species commonly use a rate of the order of 10 pulses per second, though sometimes using temporary rates of from 5 to 30 pulses per second. Upon entering a region a few feet short of the expected point of target presentation (when a standardized point of presentation is used) the pulse rate commonly increases in anticipation, and may have doubled by the time the bat is very close to the point where the target usually appears. If, in fact, no target is detected the pulse rate reverts to its previous range. Usually there is not a sudden decrease but, rather, a gradual shift.

When a target is presented, the rate tends to increase gradually, as it does in the no-target case, as the zone of target presentation is approached. Normally, however, there follows a rather sudden acceleration of the pulse rate which leads into a "terminal buzz." The buzz is a rapid sequence of brief pulses, which may show some variation in the rate at the start, but which tends to reach a very stable rate as the buzz progresses. The durations of the buzzes of trained bats in the laboratory usually range from about 25 msec. (roughly 5 pulses) to occasionally over 200 msec. (roughly 40 pulses). At the end of the buzzes, or within a brief interval thereafter, target seizure is carried out. Following seizure of the target, there is commonly a pause in the pulse pattern, after which the normal cruising rate of pulse emission is resumed.

(2) Pulse duration: Previous observations (ref 5,6,14,22-24,35,36) have shown that the duration of the pulses used by the bat during the successful capture of a target tend to follow the trend of the pulse repetition rate. That is, as the pulse interval decreases preceding the buzz, so does the pulse duration. This is true chiefly in a statistical sense, rather than in a strict 1:1 correspondence. The relation also does not hold for all portions of the observed pursuit sequences or in all situations. In the terminal buzz, for example, the pulse rate

often remains constant while the pulse durations continue to shorten.

(3) Frequency structure: The signals of vespertilionid bats are characterized by a downward sweep, typically of about an octave. As viewed on a graphical display with linear scales of time and frequency, the longer pulses show a marked decrease in the rate of downward frequency sweep as the pulse progresses (ref 26). The rate of frequency sweep typically increases as the pulses shorten, and the signals of some bats show a pronounced lowering of average frequency as the pursuit signals progress into the terminal buzz.

2. Procedure

The bats were first trained to catch mealworms tossed into their flight paths from a relatively fixed region in the outdoor cage. After their approach paths had become reasonably stabilized, they were brought to the laboratory and familiarized with the smaller flight space. The *Myotis* and *Lasiurus* adapted readily to the reduced dimensions, while the *Eptesicus* were at first reluctant to fly at all. The three *Eptesicus* which made successful adaptation to pursuits in the laboratory were among the first bats of this species to be successfully trained. One of these was chiefly used in the present study.

For the tests the bat flew a counter clockwise pattern within the laboratory flight space, and approached the target firing zone through an inverted V-shaped opening in a plastic curtain which tended to increase the uniformity of their approach paths. In all tests, tape recordings of the sound patterns were made at a tape speed of 60 inches per second. Initially, single mealworms were tossed by hand as the bats approached, and no cameras were operated during the actual tests so that camera and strobe-light noise would not interfere with the recordings. In later tests multiple flash photographs were made to record the precise moment of the catch and the position of the bat during the catch maneuver, for each. Randomly interspersed, during the tests, were blank passes in which all details remained the same as with the target presentation flights except that no target was actually used. Notes were also kept on the nature of the bat's approach and whether or not it resulted in a catch. In the hope that major shifts of condition or motivation would be avoided, all tests were made in a relatively short period of time.

Approximately 12 "typical" catches with good recordings were selected for each species of bat. The tapes were then replayed at a speed of 1-7/8 inches per second for photographic recording from a Tektronix 502 dual beam oscilloscope with a Dumont 321 camera. The upper beam showed the recorded pulses in slowed down time, while the lower beam presented the simultaneous output of a zero-crossing meter, and thus gave an indication of the frequency structure of these pulses.

3. Methods of Data Analysis

The pulse repetition patterns were plotted in the form adopted by Griffin (ref 12,16) where inter-pulse interval is plotted vertically and time is plotted horizontally. The ratio of the two scales is 5:1 in the present plots. When several such plots are to be compared, but the precise point of target seizure has not been photographically determined, some common reference point has to be arbitrarily selected. Since target seizure normally occurs either at the termination of the buzz, or within a time interval seldom exceeding 25 msec. in the laboratory, the termination of the buzz has commonly been selected. However, the variable lengths of the terminal segments often result in a wide spread of the final pulse acceleration phases, and this variability tends to obscure the points of similarity in the approach phases.

4. Results

a. Pulse Repetition Patterns for Target Pursuits: Figure 12 shows the overall envelope pattern for all the flights of each bat. The plots were made by tracing the

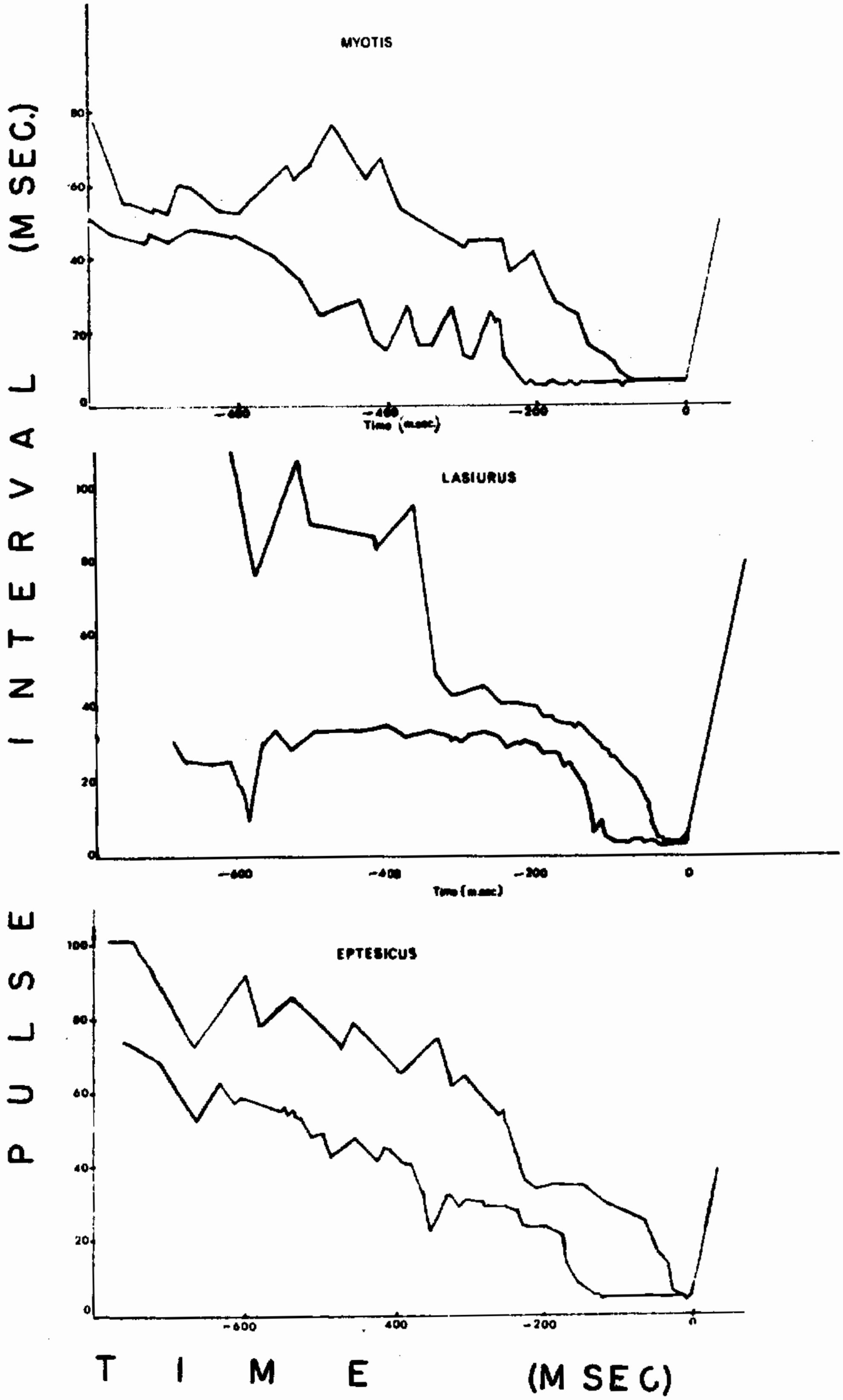

Figure 12. Overall envelope patterns for pulse repetition rates for all pursuits by each species of bat, with buzz termination selected as the common point of reference.

outside lines where all the pulse patterns of a particular bat were superimposed, with buzz termination selected as the common point of reference. In spite of the above mentioned obscuring factors, certain typical features are evident.

First, the pulse intervals during the early approach phase show irregularities with most of the deviations scattering within ± 20% of the average interval, and seldom decreasing to much less than 30 msec. for any of the bats. Second, the phase of pulse acceleration tends to be characterized by a rather definite point of transition into the terminal buzz, although this point is not as marked for Eptesicus as it is for the other species. Third, the buzz is established when the pulse interval decreases to approximately 6 msec. The final pulse spacings of the Lasiurus buzz are somewhat shorter than for the other two species, usually shortening to 4 msec. (a pulse rate of 240 sec.). The Eptesicus show the most strikingly uniform buzz patterns, with a pulse interval approximating 5-1/2 msec. (a pulse rate of 180 per sec.) which is longer than for the other bats. Fourth, there is a distinctive pause at the end of the buzz, which in these tests typically exceeded 50 msec., sometimes reaching 250.

When the scattering due to individual flights is removed by averaging the pulse intervals, as a function of time until catch, certain of the differences between the patterns of different bats can be seen more clearly (figure 13). For example, the pulse acceleration zone for the Myotis occurs at about double the time from the point of catch as it does for Lasiurus. Since, however, the approach flight speed of the Myotis is roughly half the approach speed of the Lasiurus, the distance to target for the different pulse accelerations is about the same.

For the Eptesicus the start of the pulse acceleration occurs at just about the same time from the catch as for the Lasiurus, but the slower flight speed of this bat implies that the distance to target at this point must be appreciably less. The terminal buzzes of this bat are considerably briefer than for the other two bats, varying from a minimum of three buzz pulses to a maximum of twenty-five. The Myotis tends to use the longest buzzes, with 16 pulses as a minimum and 44 as a maximum.

b. Pulse Repetition Patterns for Blank Passes

The single Myotis used in these tests showed little of the anticipatory speedup of pulse rate typical of most bats as they approached the target zone. This bat also exhibited more variability of approach path than did some of the test bats. For these reasons the establishment

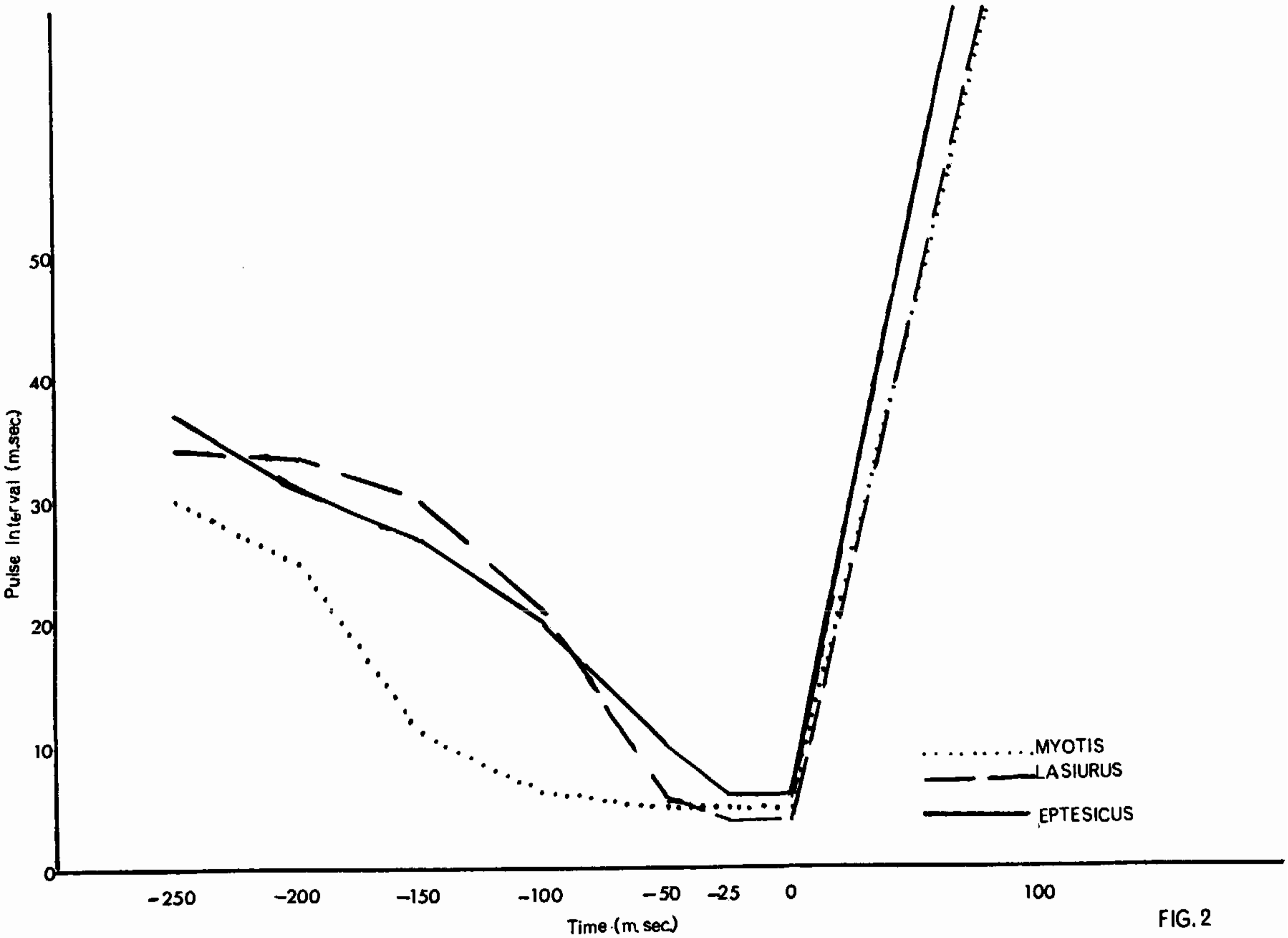

FIG. 2

Figure 13. Pulse pattern averages for the flights of Figure 12.

of a zero reference point was more difficult and more subject to error than was true with the other bats. The envelope tracing (figure 14) is thus the result of a number of rough approximations and cannot be taken as an exact representation. In one or two instances the bat appeared to make a sudden last instant intensification of its search as it passed through the center of the target zone; hence, the distinctive dip in interval seen in the envelope tracing. When compared with composite target presentation patterns, a definite speedup of pulse rate is evident--obviously associated with target detection--at least 300 milliseconds from the point of catch. The target is presumably detected at five or six feet, perhaps when it has risen only a foot or two above the propelling gun.

In contrast with the blank passes for the Myotis, the blank passes for the Lasiurus, when compared with the pulse records for catches, show no significant deviation of pattern until about 200 milliseconds prior to the expected point of catch. Even at a flight speed of fifteen or sixteen feet per second, this represents a distance of only about two feet--a distance also, at which the target was more or less in front of the bat instead of rising from some distance below. Moreover, there was no evidence in the photographs (except for

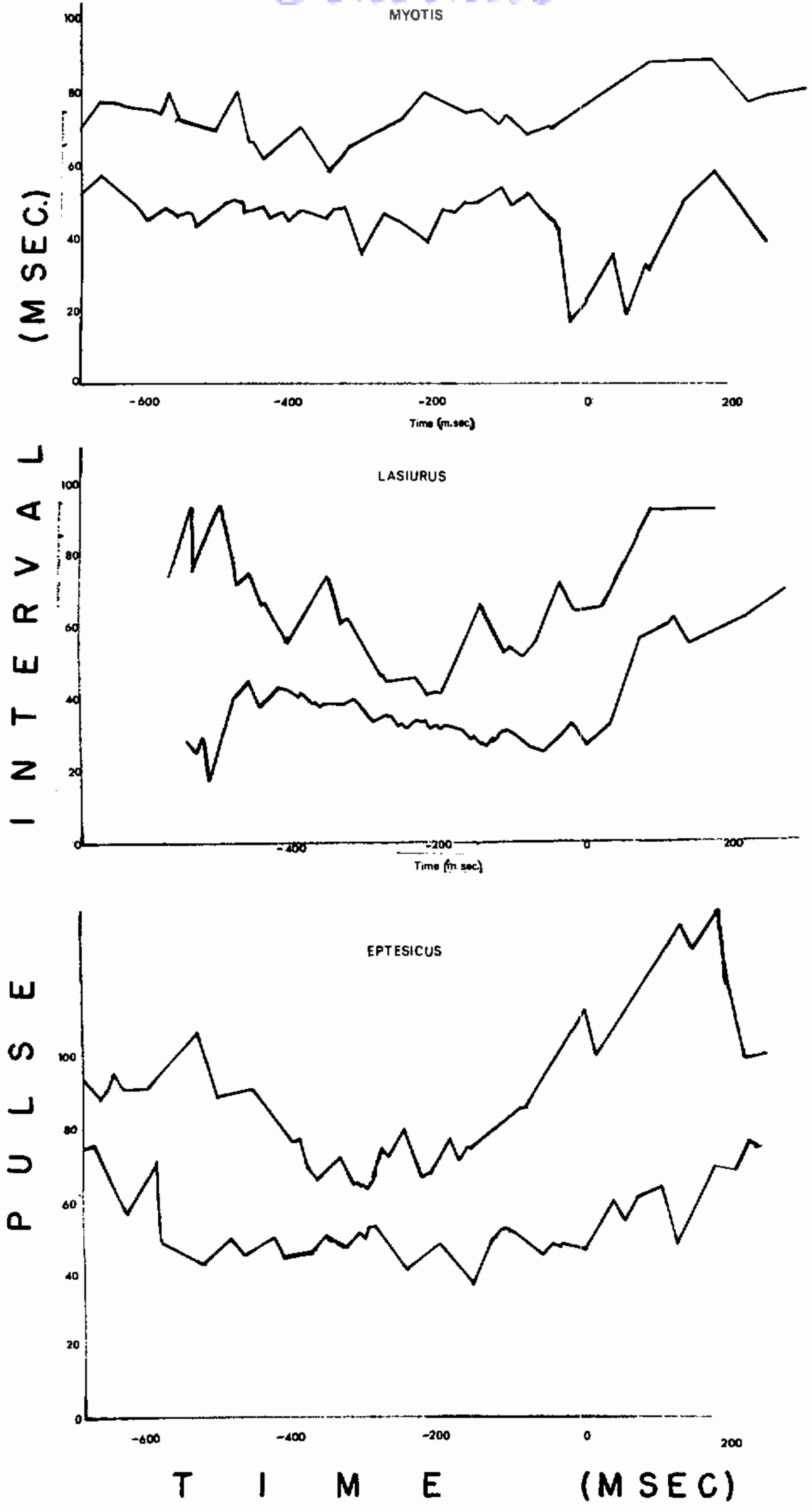

Figure 14. Overall envelope patterns for pulse repetition rates for the blank passes during the tests of Figure 12.

one turnaway at about 3-1/2 feet) of any behavioral differences between the target and no-target passes until about two feet from the expected region of capture. On the basis of present evidence, in other words, it cannot be said that the sudden reduction of interval scatter about 350 milliseconds short of the point of capture is necessarily associated with target detection. Further behavioral tests would be required to provide evidence on the problem.

With the *Eptesicus* the deviation of pulse pattern (between target and no-target passes) occurs at roughly 400 milliseconds--corresponding, approximately, to a target distance of 5 feet.

c. Pulse Durations

Figure 15 shows that the pulse durations for all the bats tend--on the average--to shorten progressively from the region of detection to the point of buzz termination. The pulses of *Lasiurus* show a later shortening, with a more rapid fall-off, than those of the *Myotis*. The *Eptesicus*, on the other hand, appears to rely less on an extended terminal buzz and maintains longer pulses--more nearly matching the trend noted with the *Lasiurus*. The overall shortening ratios, as illustrated in the present plots, are roughly the same for the different bats.

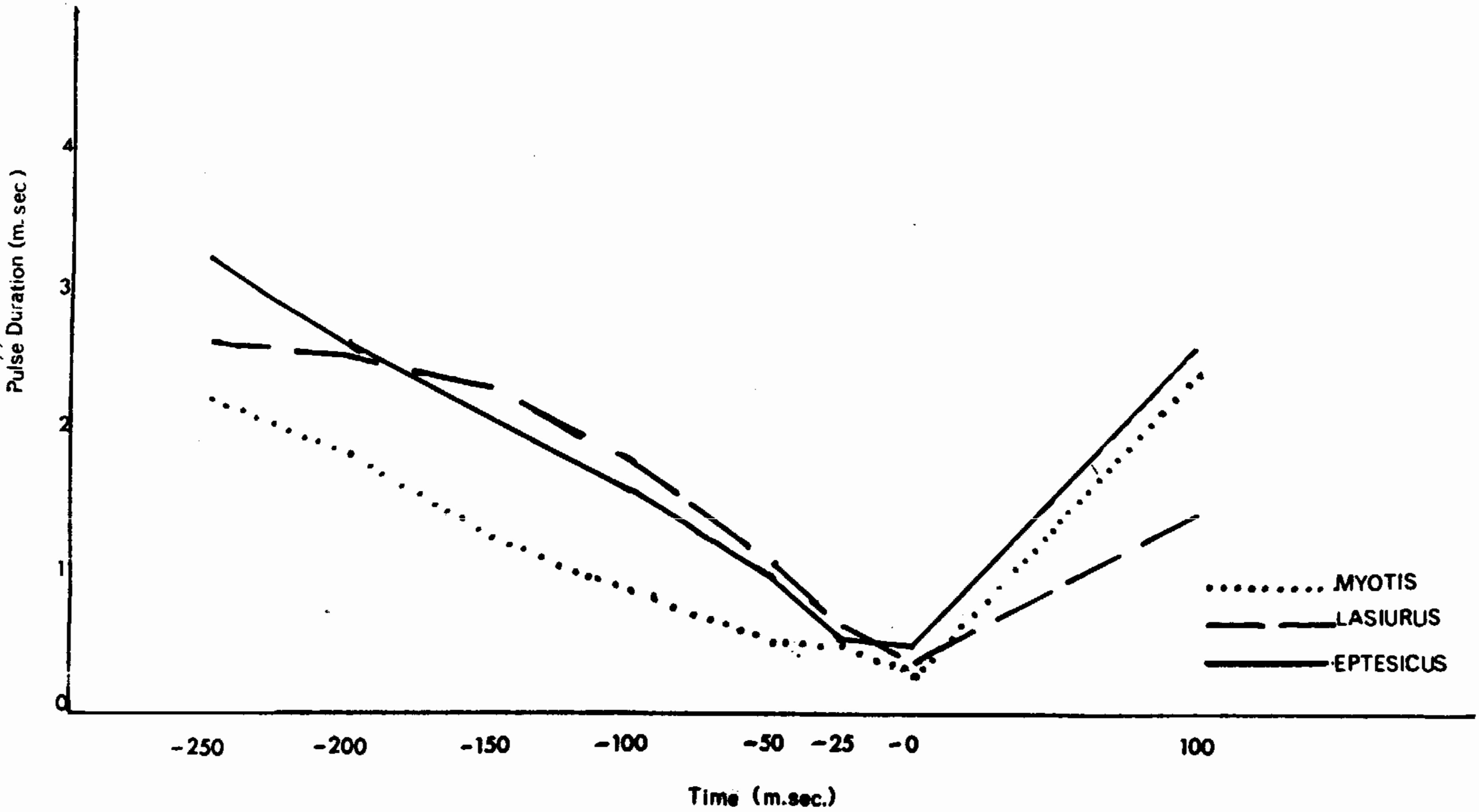

Figure 15. Pulse durations for the tests of Figures 12, 13, and 14.

In round figures, the durations start about 3 milliseconds and fall to roughly 0.3 milliseconds. However, the shortening pattern is not always parallel; that is, there may be regions of abrupt shortening of interval that are not accompanied by corresponding shortenings of duration, and vice versa.

d. Duty Cycles

An associated measure of interest is the duty cycle (fig. 16), which is the percentage of the pulse interval that is occupied by pulse emission. Since pulse durations tend to shorten progressively throughout pursuit, while pulse intervals tend to show an accelerated shortening and then a relatively uniform plateau, the corresponding duty cycles will increase in the region of buzz initiation and fall off again toward buzz termination. Such a trend is clearly shown by the present curves. It is of interest, however, that both the *Lasiurus* and the *Eptesicus* show a later peak than the *Myotis*. Prior to the region of pulse-rate acceleration, the duty cycles lie in the vicinity of 7% for *Myotis* and *Lasiurus* and in the vicinity of 9% for the *Eptesicus*. Maximum values of 13% are reached by the *Lasiurus* during the pulse acceleration phase; while after the catch the values tend to fall to a very much lower level--only 2 or 3%.

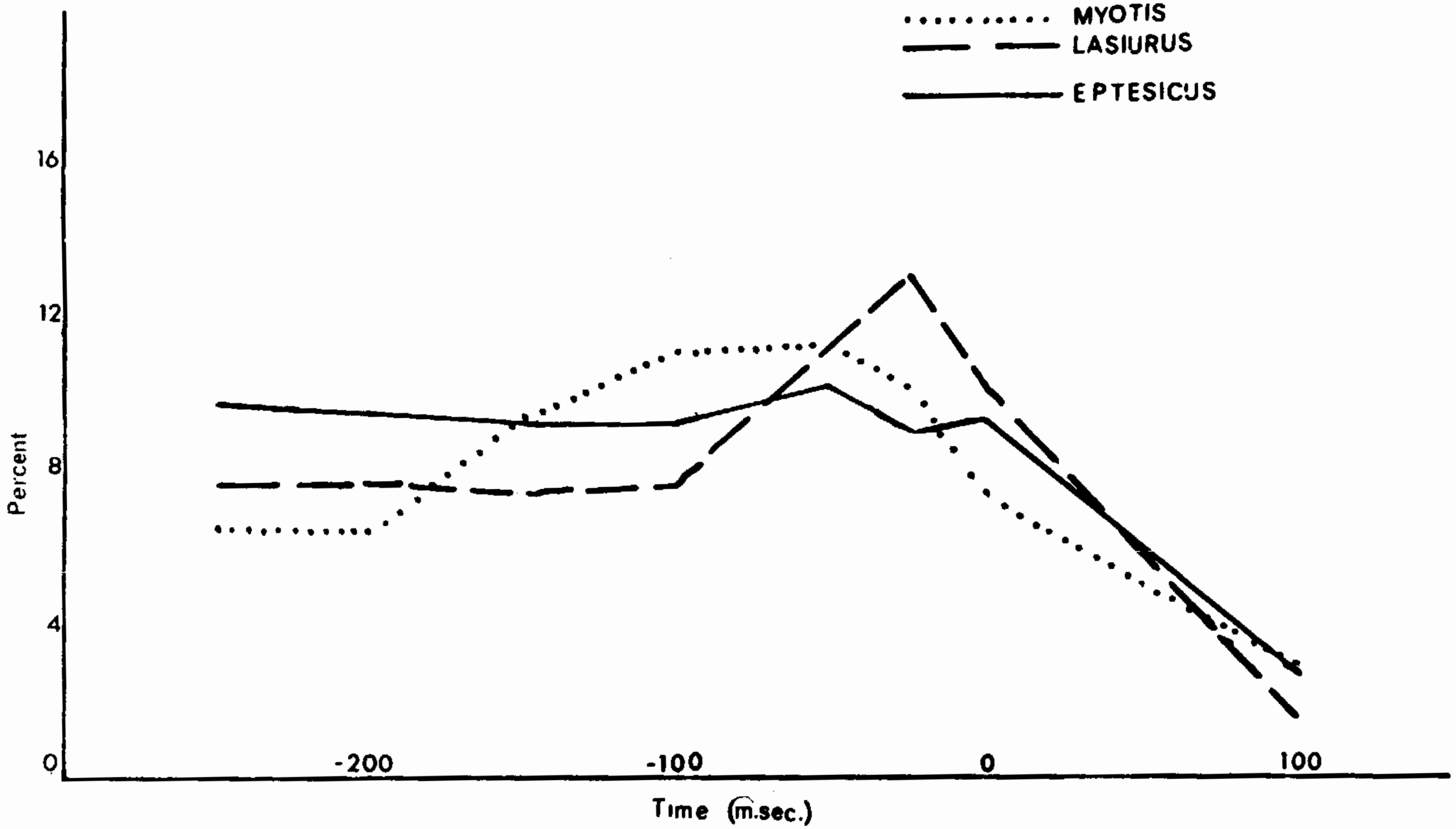

Figure 16. Duty cycles for the tests of Figures 12, 13, and 14.

It is important to note that both pulse durations and pulse intervals in the laboratory commonly differ very markedly from values observed out of doors and that the differences are not parallel for the different bats. Thus, in the present records maximum pulse durations generally reach about 4 milliseconds, or sometimes slightly more, for the three species of bats. Such durations also represent a common outdoor maximum for Myotis lucifugus. However, the outdoor cruising pulses of both Eptesicus fuscus and Lasiurus borealis may reach 15 milliseconds. Cruising duty cycles may fall to 3% in the wild because of the wider pulse spacings sometimes used.

e. Pulse Frequency Structure

The frequency structure of representative pulses are summarized in table I. The pulses selected for analysis were chosen to represent four distinctive stages of the pursuit pattern:

(1) A pulse emitted by the bat beyond the zone where shifts associated with target detections are normally evident. In the present records 5 to 6 feet was used. For approximate equation of the distances for the different bats, multiflash pictures of the bats' approaches along measured paths were made outside the routine tests.

Flight velocities for the different bats averaged: for Myotis, 8 ft/sec; for Eptesicus, 11 ft/sec; and for Lasiurus, 18 ft/sec, without very appreciable deviations.

(2) The first pulse occurring after a pulse interval of 30 milliseconds.

(3) The first pulse occurring after an interval of 7 milliseconds or less, where ensuing intervals remained below 7 milliseconds.

(4) The last measurable buzz pulse.

As represented in frequency durations plots (figure 17a), bats clearly exhibit different frequency-duration sequences while target pursuit is in progress. The sequences of Myotis show an early reduction of pulse length and then a distinctive fall-off of both initial and terminal frequencies. The early phases of the Lasiurus sequences do not differ greatly from those of Myotis. Although slightly lower in average frequency, many of the individual records overlap. In the terminal phases of pursuit, however, the Lasiurus pulses show almost none of the drop in average frequency which is so characteristic of the pursuit signals of both Myotis and Eptesicus. At all phases, the signals of Eptesicus

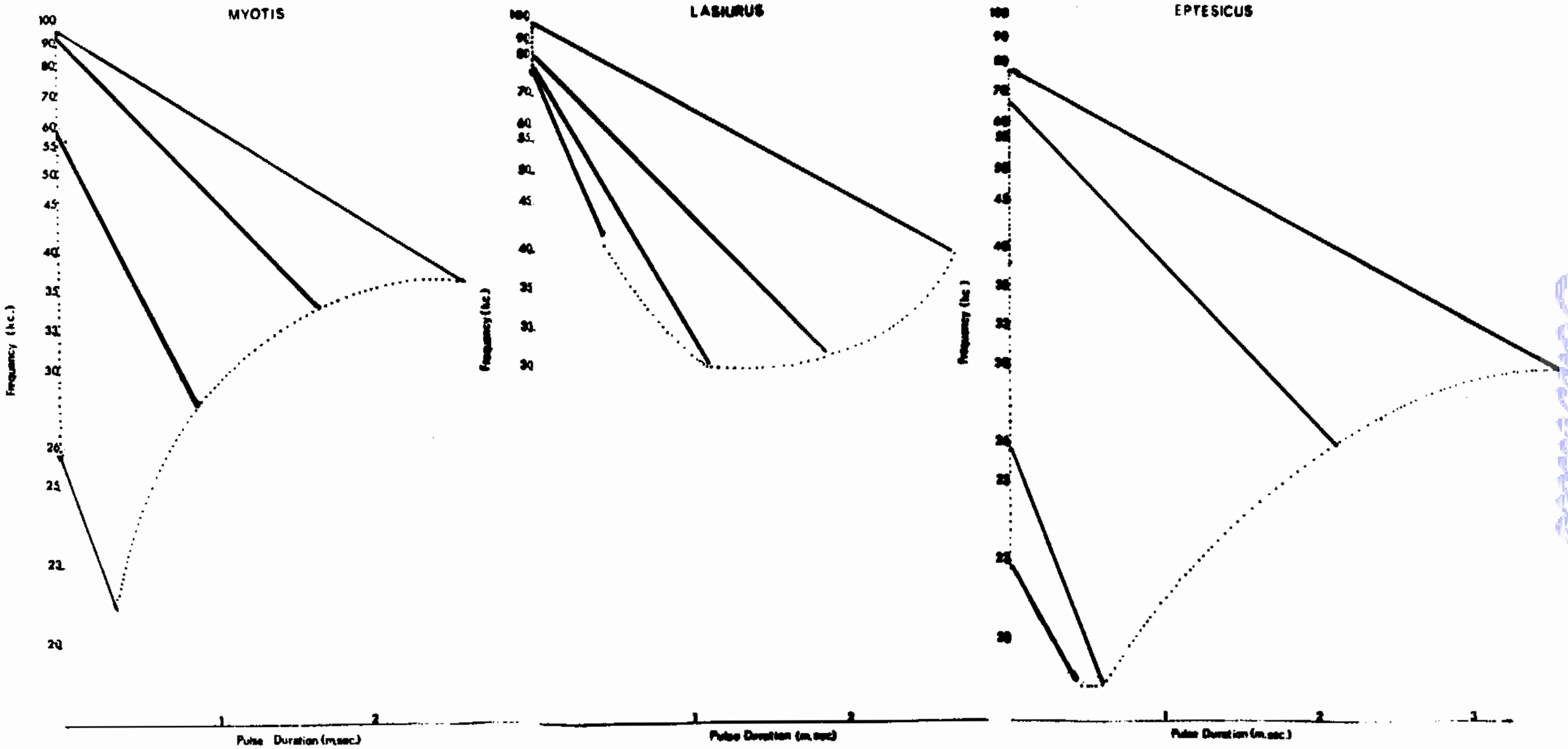

Figure 17a. Frequency-duration plots for the three species of bats during pursuits: average values for four criterion points discussed in the text.

occupy a lower frequency range than do the signals of Myotis or Lasiurus. Durations also tend to remain longer in the region of pulse acceleration and buzz transition.

For the blank passes, pulses representative of three distinct stages in the approach pattern were chosen:

(1) A pulse which corresponded spatially to pulse (1) of the target pursuit sequences,

(2) the pulse which occurred at the end of the shortest recorded pulse interval, and

(3) the pulse which occurred closest to the estimated point where the catch would have been made, had a target been present.

In figure 17b the dotted line shows the pulse after the shortest interval (during the bat's approach) and hence should reflect shifts associated with the bat's decision that no target was present in the usual location. It is immediately clear that no significant deviations of pulse structure appear at this point either with Lasiurus or Eptesicus. Moreover, the drop in terminal pulse frequency of the pulses of Myotis is too small with the available sample to be regarded as definitely significant. The uniformity of these frequency duration plots suggests that all significant changes in pulse structure occur, in the event of target

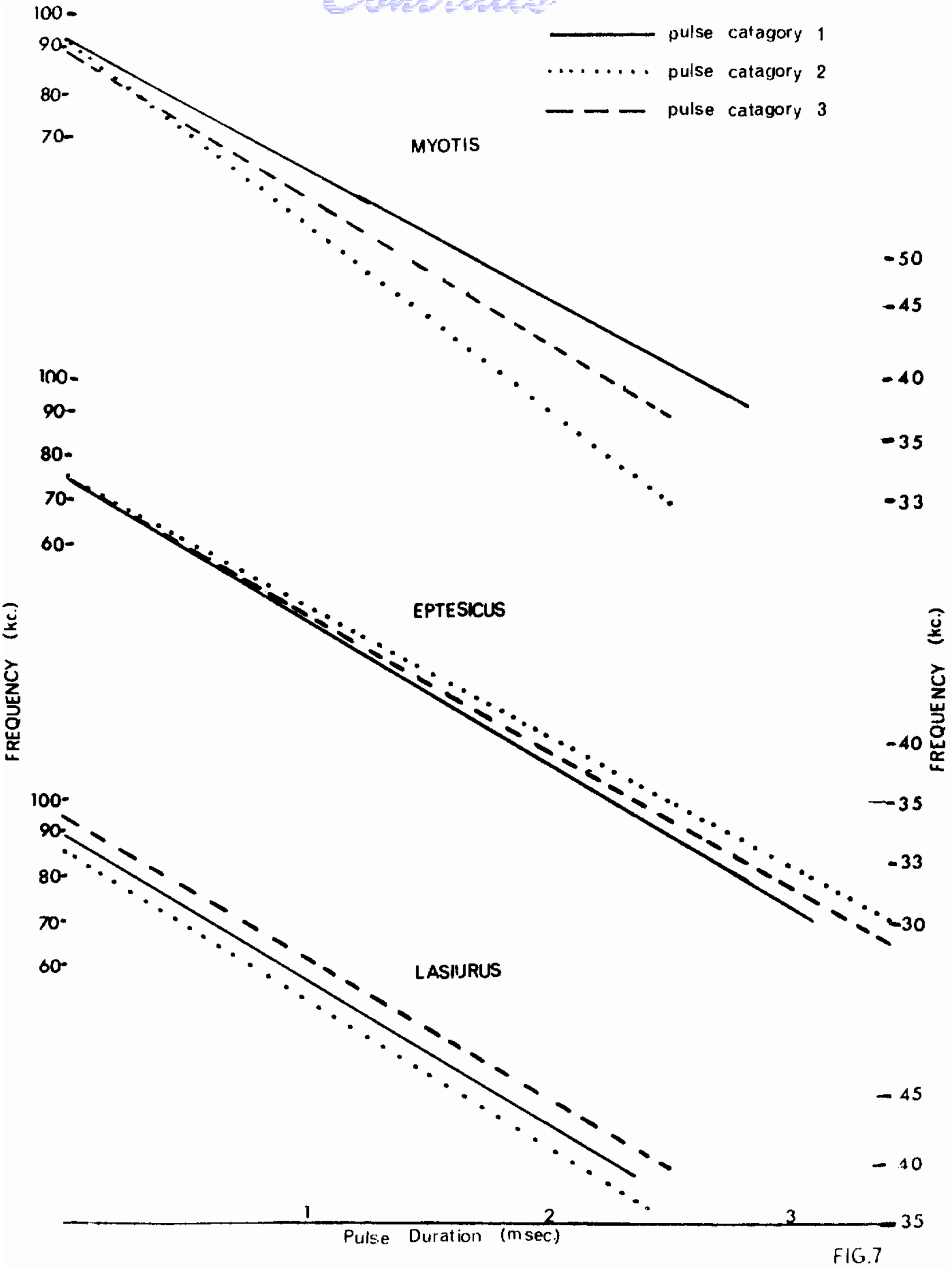

FIG.7

Figure 17b. Comparative frequency-duration plots for blank passes.

detections, after the pulse interval has dropped below 30 milliseconds.

f. Flight Speeds During Target Pursuit and No-Target Passes

Flight speeds with target: Partly because of the bat's flight pattern and partly because of its greater flight speed, the Lasiurus was less adequately photographed during the early phases of pursuit. By the point of catch the bat's average flight speed was 14 or 15 feet per second but was falling off rapidly (since the bat often climbed sharply or performed some other speed-reducing maneuver). The Eptesicus approached less rapidly, and normally did not slow down as markedly as did the Lasiurus. The Myotis exhibited the slowest approach (8 or 9 feet per second) and also the least drop in average flight speed at the time of catch.

Flight speeds without target: Initial flight speeds for Lasiurus and Eptesicus were essentially the same whether or not a target was present. Although the sequences for Lasiurus were too brief for adequate measurement, it seems likely that the speed dropped by a few feet per second as the bat climbed through the target zone. The flight speeds of the Eptesicus remained for the most part in the 10-12 foot-per-second range, but showed some drop as the bat turned away. With the

Myotis, the speed was relatively constant. Apparent differences in the initial speeds (as compared with the target pursuit sequences) may have been due in part to measurement errors associated with the different flight paths followed; but there was also a suggestion that target detection sometimes produced an early spurt of speed, both with Myotis and Lasiurus.

g. Discussion

The present analysis of the comparative pursuit signals of three species of bats, when taken in the light of earlier observations, reveal certain points of interest. First, definable differences do appear to exist between the pursuit signals of the three species of the bats tested: Myotis lucifugus, Lasiurus borealis and Eptesicus fuscus. These have been most distinctly brought out, in the present measurements, by frequency-duration plots made at certain criterion points. Important differences, however, may exist not only between individuals of the same species (while executing a given pursuit task), but in the same individual when presented with different pursuit tasks or when required to perform under varied surrounding conditions. This variability among indivuduals of the same species could make it very difficult to provide an absolute basis for reliable species identification.[4] Second, analysis of the signals emitted when a target is presented in a given location, as compared with the signals when no target is presented, may give rise to misleading conclusions. For example, some bats give no clear evidence of detection or nondetection until they are relatively close to a target, while collateral evidence (such as early turnaways) sometimes suggests that the bats have evaluated the situation far in advance of the evidence revealed by the emitted signals. Third, the relatively stable configuration of approach signals seen under laboratory conditions does not reflect the great variability of conditions encountered under natural or quasi-natural conditions.

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4. In this connection, limited tests on a different Eptesicus than the one reported in this paper showed this bat to be using a pulse pattern rather similar to Myotis, and also a similar trend in pulse duration. This Eptesicus showed other differences, such as an earlier peak in the duty cycle (about 100 msec prior to buzz termination). At the time of these tests this bat became increasingly sluggish in behavior, and since its motivation did not seem to be on a par with the other bats, the observations on its flights were not included in the report.

TABLE I: TARGET PURSUIT
SUMMARY OF PULSE DATA AT FOUR CRITERION POINTS

Myotis lucifugus

CRITERION CATEGORY	(1)	(2)	(3)	(4)
Flights analyzed (total number)	9	9	9	9
Average pulse duration (msec)	2.6	1.7	0.9	0.38
Range of pulse duration	2.1-3.2	1.0-2.0	0.6-1.0	0.25-0.5
Average frequency-sweep (kc/msec)	98-36	94-34	60-28	26-22
Range of initial pulse frequency	105-90	105-80	80-44	30-23
Range of terminal pulse frequency	40-35	38-31	38-19	25-19
Av number & range of pulses in buzz--	27 16 - 44			

Lasiurus borealis

CRITERION CATEGORY	(1)	(2)	(3)	(4)
Flights analyzed	19	19	19	19
Average pulse duration	2.7	1.9	1.1	0.45
Range of pulse duration	2.4-3.0	1.5-2.3	0.7-1.4	0.3-0.5
Average frequency sweep	97-40	85-31	82-31	81-42
Range of initial pulse frequency	100-85	100-80	95-65	90-65
Range of terminal pulse frequency	45-35	40-27	35-27	50-30
Av number & range of pulses in buzz--	14 9 - 22			

Eptesicus fuscus (Bat RB)

CRITERION CATEGORY	(1)	(2)	(3)	(4)
Flights analyzed	12	12	12	12
Average pulse duration	3.5	2.1	0.6	0.43
Range of pulse duration	3.0-4.2	1.5-2.5	0.4-1.1	0.25-0.6
Average frequency sweep	77-30	67-26	26-19	23-19
Range of initial pulse frequency	80-72	75-58	32-21	26-20
Range of terminal pulse frequency	31-27	30-24	20-19	20-19
Av number & range of pulses in buzz--	10 3 - 25			

TABLE II: BLANK PASSES
SUMMARY OF PULSE DATA AT THREE SELECTED POINTS

PULSE CATEGORY	(1)	(2)	(3)
	Myotis lucifugus		
Flights analyzed	9	9	9
Average pulse duration	2.8	2.5	2.5
Range of pulse duration	2.4-3.0	2.1-2.9	2.0-2.9
Average frequency-sweep	92-37	92-33	90-36
Range of initial pulse frequency	100-85	100-80	100-80
Range of terminal pulse frequency	40-35	37-30	40-33
	Lasiurus borealis		
Flights analyzed	13	13	13
Average pulse duration	2.6	2.4	2.5
Range of pulse duration	2.2-3.2	1.2-3.1	1.8-3.0
Average frequency-sweep	90-39	85-36	95-40
Range of initial pulse frequency	100-80	100-70	100-90
Range of terminal pulse frequency	42-36	38-33	50-35
	Eptesicus fuscus (Bat RB)		
Flights analyzed	12	12	12
Average pulse duration	3.1	3.4	3.4
Range of pulse duration	2.1-4.0	2.8-4.2	2.5-3.8
Average frequency-sweep	74-30	75-30	74-29
Range of initial pulse frequency	80-65	80-70	80-65
Range of terminal pulse frequency	31-26	32-27	33-26

SECTION IV

ECHO STUDIES

A. Human Listening

1. Introductory Comment

Experimental evidence has established that echolocating bats can discriminate between like-sized targets of different shapes (ref 12,14,31,36,40,41) and attention has focused on the possibility that human listeners could make similar evaluations. Obviously, if objects of the size discriminated by bats were to be discriminated by human beings, the echoes from ultrasonic pulses with which the objects were radiated would have to be transformed into the human auditory range. Furthermore, since human auditory sensitivity relative to that of bats tends to be severely masked immediately following an intense outgoing pulse (ref 17,18), it would be necessary to attenuate the outgoing pulse greatly if subtle features of the returning echoes were to be detected.

In the confined space of the laboratory, the alternative approach--that of using lower frequency signals and correspondingly larger targets--was not practical.[5] In any event, since both equipment and space dictated the use of signals in the ultrasonic range of bats, we recorded the echoes of various objects and configurations with the use of pulses within the typical frequency range of bats. These were then listened to at slowed-down playback rates such that both the frequency and duration of the echoes were theoretically compatible with effective human listening.

Two previous sets of observations gave clues of possible relevance. The first was an investigation, conducted in part at this laboratory, by J.A. Rupf.[6] This study was concerned with the capacity of human listeners to identify relatively large objects with the use of constant frequency ultrasonic pulses, the echoes

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[5] It must be recalled, also, that at 100 kHz sound is attenuated at about 3-1/2 dB per meter. For a target a meter away, the respective attenuations would thus be roughly 7 dB and 4 dB. If we scaled size and distance upward by a factor of 10, and frequency downward by a like factor (to put it in the audible range), the corresponding attenuations would be roughly 4 dB and 2 dB respectively. This shift could modify the evaluations made with the use of an octave-swept signal or other types of signals with equivalent bandwidth.

[6] John A. Rupf, "Time expansion of ultrasonic echoes as a display method in echolocation." A thesis submitted in partial fulfillment of the requirements for the degree of Electrical Engineer, MIT, September 1954.

from which were slowed down for human listening. Pulses of 1 millisecond duration, and a frequency of 40 kHz, were directed at a rate of 20 pulses per second at the test objects. The objects were: a stool, a wastebasket, a bush and a person--placed at several different relative orientations. For human listening, the outgoing pulses were removed from the tape, and the tape then played back at slow-down ratios of 8, 16, 32 and 64. Listeners were asked to identify the objects and the differences in orientation. Chief findings of interest relative to the present studies were: (1) that at the maximum slow-down rate (X 64), the objects were, after familiarization, almost always identified correctly (and the different orientations ordinarily recognized), but (2) that the correct identifications fell off strikingly as the slow-down factor was decreased--only about 1/3 correct identifications occurring when the slow-down factor was reduced to 8.

The second set of observations came from a very preliminary attempt[7] to find out whether or not a U-curved mealworm returned echoes (from a representative bat pulse) that a human listener could distinguish--when sufficiently slowed down--from echoes returned by

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[7] Cahlander and Webster, unpublished.

a smooth sphere of corresponding average reflectance. Pulses of 1-millisecond duration, sweeping from about 85 to 35 kHz, were directed toward a 5/16" sphere and toward the U-shaped mealworm, which was suspended from the two ends by 1-mil wires and then rotated to different relative orientations. Recordings were made at a tape speed of 60 inches per second, with the outgoing pulses gated out. The echoes were then listened to at a playback rate of 1-7/8 inches per second (a slow-down ratio of 32X). Using earphones, three listeners made about a dozen attempts each to judge between the two kinds of targets, with essentially negative results. Modifications of the ear coupling (e.g., partial withdrawal of the phone) produced variations in tonality and occasionally appeared to bring out a marginal difference between the sphere and the mealworm, notably when the mealworm was oriented so as to produce maximum interference patterns. However, the 1/30-second duration of the slowed down pulse seemed insufficient for any reliable discrimination, even under obvious conditions.

2. Plan of the Present Experiments

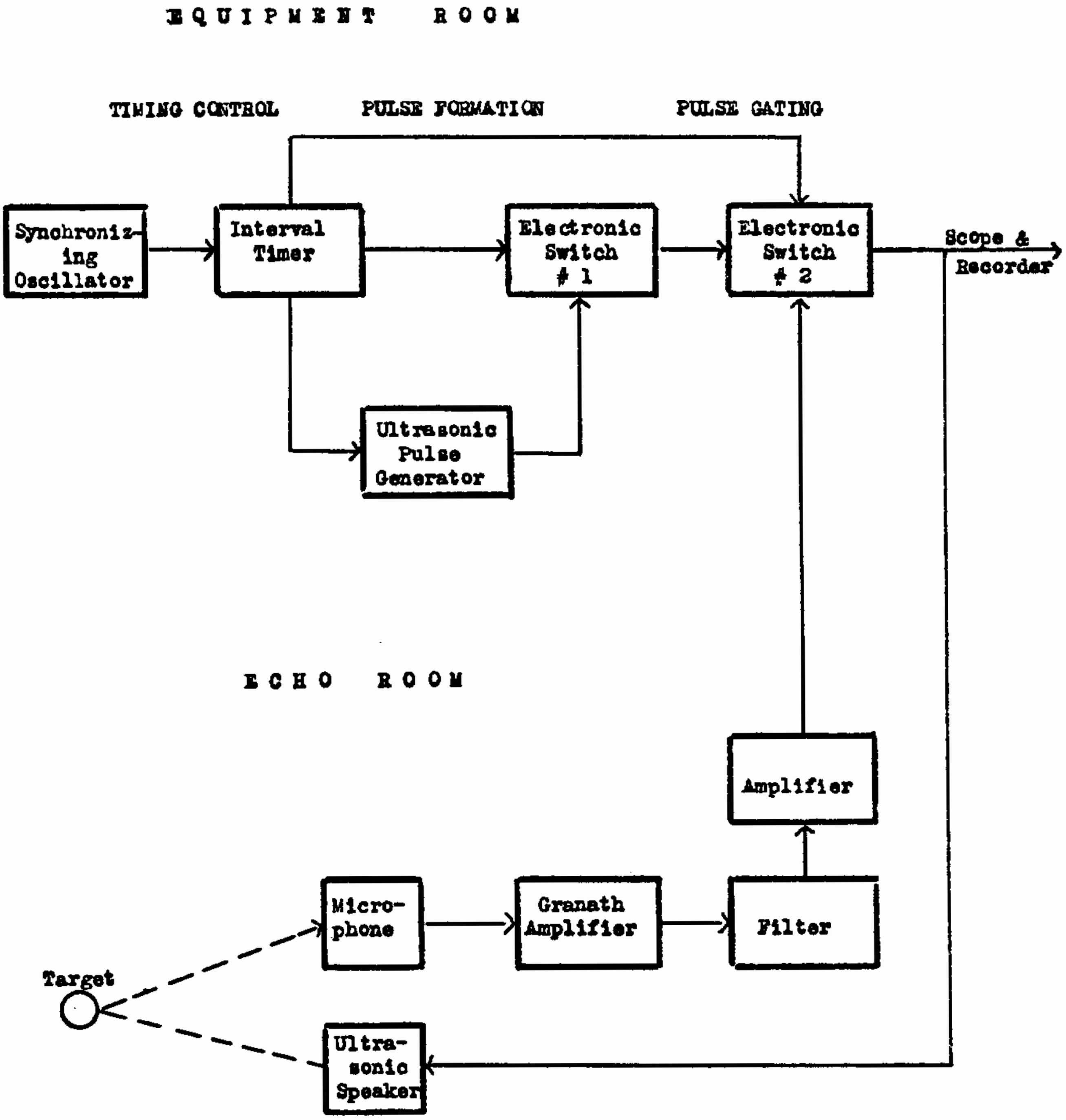
The plan of the present tests was dictated in part by the observations mentioned above and in part by other considerations. First, the echoes returned by various test objects should be slowed for human listening by a factor of at least 64, preferably 128--though lesser slow-down factors might also be evaluated. Second, the outgoing pulses should be gated out to prevent obnoxious masking effects. Third, the test objects should include not only the items of initial interest--namely, spheres and mealworms--but larger or more complex objects which might give more distinctive clues for human listeners. Fourth, besides using a frequency-swept pulse approximating that of a representative vespertilionid bat, other types of pulses should be used for comparative purposes. And fifth, additional problems, besides discrimination between a pair of different shaped objects, should be sampled: for example, the problem of detecting a small, compact object against a massive but diffuse clutter background.

3. Procedure

Since we were interested in comparisons of several kinds of pulses, four categories of pulse structure were originally selected: octave swept (downward), constant frequency, random noise and bursts of brief pulses. Of the many kinds of recognition problems dealt with by bats, we selected three for preliminary test: (1) recognition of the echo differences between two objects of different shapes (but without exploration of varied relative orientations), (2) recognition of two discrete objects, as against one, and (3) detection of a small, compact object close to a clutter background of different physical structure. Little effort was made to test evaluations of texture, distance, motion or shifting relative orientation.

A block diagram of the layout used for generating, gating and transmitting the ultrasonic pulses, along with the general arrangements for receiving the echoes and recording them, is presented in figure 18. Test objects were suspended--within a cubical space lined with 6-inch fiberglass insulation--by wire or thread (mostly of 2 or 3 mil diameter), too fine to return detectable echoes. Ultrasonic pulses were directed at the objects from a flat two-inch speaker (of the design of Kuhl, et al., ref 19): the outgoing pules being gated out of the system prior to recording. Recordings were made at a tape speed of 60 inches per second, then slowed to 1-7/8 inches per second for transfer to a portable recorder operating at a tape speed of 7-1/2 inches per second. For listening at a slow-down factor of 128, these recordings were played back at 1-7/8 inches per second.

To study the discrimination capacities of human listeners, the general method of Rupf's experiments was adopted. Targets or configurations were evaluated in



EQUIPMENT ARRANGEMENT FOR INITIAL OBSERVATIONS OF ULTRASONIC ECHOES

Figure 18. Block diagram of electronic equipment used in echo tests.

groups of four--this being as many as a listener seemed readily able to keep in mind at once. At the beginning of each tape of tests, samples of the slowed-down echoes were identified by voice with the associated object or configuration. Half a dozen or so samples of each of the echoes were played through twice during the familiarization phase. This portion of the tape was normally followed by 10 or more echo presentations, unidentified except by sequential number. The listener attempted to categorize this quasi-random sequence of the different target echoes into the four categories presented initially. Each of these sequences was listened to three times by each of two listeners. In addition, two or three other observers listened to samples and attempted to specify the criteria they were using to achieve identifications. The data in this sampling are not, however, included in the tabulations.

4. Results

Results for two observers are given in table III. Because of the diversity of the findings with respect to different (and often evanescent) features of the echoes, or momentary aspects of the test situation, the observations are not compatible with any succinct summary. The most useful provisional interpretation can perhaps be made with reference to the following aspects; (a) pulse type, (b) inter-test and inter-observer variabili-

TABLE III

ECHO LISTENING RESULTS (AT 128X SLOW-DOWN)
(For two observers: A & B)*

Tape No.	Test Objects	Number of test echoes	Pulse category	Run #1		Run #2		Run #3		Total Correct
				Obs. A	Obs. B	A	B	A	B	
2	2-1/2TB,1-1/4SS, 3/4SS,3/8SS.	8	90-45	75	25	75	38	75	50	57
(5)	MLC, MSC 2-1/2SS,1-1/4SS	19	90-45	47	26	37	42	37 (26)	74	44
(6)	Same	19	45-22½	63	21	74	37	58 (31)	63	53
7	5/16SS,MW(90°), MW(45°),MW(0°).	10	90-45	90	60	90	80	80	80	80
	Same	10	45-22½	80	60	70	70	60	70	68
	Same	10	40	40	90	70	90	80	100	75
8	3/8SS,APC1, APC1(st),APC1(s3)	12	90-45	83	42	92	100	92	50	77
	Same	12	45-22½	67	67	92	92	67	92	80
	Same	12	40	58	42	75	33	75	75	60
9	3"SH,MLC Coil,1"R	13	90-45	62	46	100	70	100	85	72
	Same	13	45-22½	31	54	54	62	23	62	45
	Same	13	40	15	38	38	31	38	46	35
10	3/8SS,MW, 3/8 + 5/16, S-P	13	90-45	69	92	77	69	69	46	71
	Same	13	40	69	23	62	46	85	62	58
11	5/16SS,5/16 + 3/8 2-1/2ss, MLC	13	90-45	77	54	62	46	77	77	66
12	Same	13	Noise	46	31	46	23	54	38	40

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* See Legend for Table III on pages 88 and 89.

LEGEND FOR TABLE III

TEST OBJECTS

Spheres

2-1/2 TB:	Fuzzy tennis ball roughly 2-1/2" in diameter.
2-1/2 SS:	Smooth rubber ball of roughly the same diameter.
1-1/4 SS:	Smooth ping-pong ball of 1-1/4" diameter.
3/4 SS:	Smooth nylon ball of 3/4" diameter.
3/8 SS:	Smooth nylon ball of 3/8" diameter.
5/16 SS:	Smooth nylon ball of 5/16" diameter.
5/16 + 3/8:	Two nylon spheres of these diameters almost along the axis of sound propagation.
S-P:	Same as above, but one sphere swinging along axis.

Cylinders (placed perpendicular to the speaker-microphone system)

MLC:	Medium large cylinder: 4-3/4" X 3/8"
MSC:	Medium small cylinder: 2" X 1/4"

S-Hook

3" SH:	S-hook: 3" X 1-3/4" X 1/4" (thick)

Ring

1" R:	Plastic ring, about 1" in diameter and 1/8" thick.

Coil

Coil:	Coil slightly over 1" in length and diameter of 1/8" solder wound into 4-5 turns.

Mealworm

MW:	Mealworm, roughly 3/4" X 1/8" X 3/32", bent into a half circle, orientation unspecified.
MW(90°):	Same, perpendicular to the speaker-microphone system.
MW(45°):	Same, about 45° out of the perpendicular plane.
MW(0°):	Same, roughly in-line with the speaker-microphone.

Legend for table (continued)

Clutter

APC1:	Artificial pine clutter--plastic artificial needles (several dozen in a roughly 3" X 3" X 4" array), mostly directed more or less toward the speaker.
APC1(st)	Same, but with 5/16" sphere touching just inside nearest needle tips.
APC1(s3)	Same, but with sphere 3" closer to speaker.

TESTS WITH INCOMPLETE RESPONSES

Tests (5) and (6) are parenthesized to indicate that in most instances no effort was made to distinguish between the two cylinders and the two spheres. Chance scores here would have been about 50%. In two instances (indicated in parentheses), one observer attempted complete evaluations.

(Test length variations and noneven figures were due chiefly to intermittent failure of the recording switch.)

ties, (c) familiarization and clues for learning, (c) prominent physical features and (e) subtler variations.

(a) Pulse type: Four categories of pulse were used, all of 2-millisecond duration: (1) Frequency-swept, 90-45 kHz, (2) Frequency-swept, 45-22.5 kHz, (3) Constant frequency, 40 kHz, and (4) Random noise, filtered into a band from 25 to 100 kHz. Pulse bursts were inadequately sampled to be included. Although unequal numbers of tests with the different pulses were completed, due to transient malfunction of equipment, there seems justification for the estimate that the decline in discrimination success, from best to worst, was in the order just listed.

When comparisons were made of corresponding groups of tests completed with the higher-range frequency-swept pulses as against the other types, the results were as follows: The 90-45 kHz pulses gave 71-72% correct responses, while corresponding tests for the 45-22.5 kHz pulses gave 64% correct responses and the 40 kHz constant frequency pulses gave 56% correct responses. The one test completed with random noise pulses yielded only 40% correct responses, as against 66% on the same test for the 90-45 kHz pules. Few tests, even with the 90-45 kHz pulses, yielded 100% correct scores. The test objects yielding the best differentiation were: (1) a smooth cylinder suspended crosswise to the axis of sound propagation, (2) an S-hook suspended almost crosswise, (3) a coil made of 4 or 5 turns of solder spaced about 1/4" apart (producing definite interference patterns), and (4) a ring (also suspended so as to produce interference patterns). Although amplitude clues played a role in some of the tests, such clues were avoided in most instances either by the use of echoes of approximately equal amplitudes, or by manipulation of the amplification factor.

Learnable differences in quality appeared to account for the fact that the test just cited produced echo differences that were clearly discriminable by one of the listeners. Curiously enough, the same test objects produced chance results (approximately 25%) with the 45-22.5 kHz pulse and poor results (38% correct) with the constant frequency pulse in the same listener. The results were thus remarkably sensitive to pulse modifications which might seem unlikely to produce such differences. All observers agreed that the random noise pulses gave rise to no echo structure that would permit fine discriminations to be made.[8] Some sense of pitch

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8. Evidence that noise pulses may provide important clues (by way of interference patterns that set up frequency or beat structures) for evaluating spatial relations of larger configurations has been presented by Wilson (ref 43).

variation between different objects or configurations was, however, sometimes discernable. The constant frequency pulses--though generally producing relatively poor discrimination results--occasionally (as in tests #7 and #10) produced better discriminations than the 90-45 kHz pulses. The observers ascribed this result to the fact that certain of the temporal and "quality" structures stood out more clearly due to better matching with human auditory sensitivities--despite the far lower actual information content of such echoes.[9]

(b) Inter-test and inter-observer variabilities: Table III shows that there was no consistent pattern of improvement when a given observer listened successively to the same set of echoes. In fact, striking variations or reversals were sometimes noted. In test number 8, for example, successive scores for observer B were: 5, 12 and 8 (out of a possible 12). Moreover, differences between observers were also striking in some instances. Thus, in test number 10, the scores for observer A were 9, 8 and 11 (out of a possible 13) while the corresponding scores for observer B were: 3, 6 and 8. Much seemed to depend on subtle clues which might or might not be noted at a given time.

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[9] Some more general aspects of the matching problem have been discussed by Batteau (ref 1).

(c) Familiarization and clues for learning: Observers noted two chief difficulties in their attempts to distinguish between echoes: (a) inability to hear any clearly distinguishing feature (even though visual inspection of the corresponding oscilloscope displays often indicated that radically different amplitude patterns existed), and (b) inability to form or hold adequate mental standards for distinctive acoustical images) for comparing the different echoes. Basically, the problem might be said to resemble the problem of learning the vocabulary of a language that was badly mismatched to human auditory sensitivity.

(d) Prominent physical features: In the present tests and in some previous sampling tests, two categories of stimulus configuration were noted in which human auditory sensitivities to slowed-down echoes provided significant clues. The first was when two discrete objects were placed more or less along the axis of sound propagation and the distance between them varied. For example, with a 90-45 kHz pulse, inter-object distances of 3, 6, 9 and 12 cm were recognizable from the beat rates in the interference patterns. In some instances this held true even when the objects were of radically different size or shape (e.g., two mealworms, a mealworm and a sphere, or two different-sized spheres). Moreover, since sounds of the wavelengths in question bend around the spheres used (ref 9), the separation of a small sphere invisible behind a large sphere, could often be well judged. The second physical situation which sometimes provided significant clues was that in which the echo of a compact object was imbedded in the echo of a diffuse configuration: for example, when a sphere was placed within the echo region of a pine branch.

(e) Subtler variations of echo structure: In certain instances, where a good match between human auditory sensitivities, where a good match between human auditory sensitivites and the echo structure existed, rather subtle shifts in the physical situation sometimes produced readily detectable shifts in the echo. This applied, for example, in some instances where small temporal shifts in details of the echoes with the 40 kHz pulse were readily detectable. One gains the impression that the bat's auditory system has evolved an extensive language of echoes; but that if a like language was to be evolved for human listening, a variety of transformations would have to be made in order to achieve effective matching.[10] One must not forget either that the bat is using many other information input channels and that a diversity of information feedback loops (ref 38) characteristically exist in the bat's situation.

B. Echoes from Mealworms and Spheres

1. Introductory Comment

Previous behavioral studies on the capacity of Myotis lucifugus to discriminate mealworms from spheres had raised certain questions regarding the comparative echoes returned by the two classes of targets and the clues that the bats might be using. Investigations on discrimination performances had demonstrated the following relations:

(a) In the course of sequential target presentations, several bats proved capable of achieving essentially perfect selections (in excess of 99%) of mealworms over spheres of a variety of sizes. They were also capable of avoiding all but about 5% of the spheres; however, the true discrimination scores may have been somewhat better, since the

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[10] Certain observed or hypothesized specializations of the auditory system of bats are discussed in ref 5,15,17,18,30,36,37,38. (A correction to the speculated function of the medial superior olive, mentioned under figure 46 of ref 36, is given on page 657 of ref 38.)

bats hit some spheres even though they appeared to have identified them prior to contact (see, for example, Appendix II of the previous report).

(b) When the instantaneous discrimination problem was made more difficult by the use of paired presentations of dissimilar targets (i.e., a mealworm and a sphere simultaneously), significant errors both for the selection of mealworms and for the rejection of spheres tended to persist--most notably when spheres of 5/16" and 3/8" diameter were presented at the same time as the mealworms (roughly 3/4" X 1/8" X 3/32" in size).

(c) During initial sequential tests, the bats commonly exhibited two error peaks: one with spheres of 1/8" diameter, the other with spheres of 5/16" or 3/8" diameter. (See figures 8-11 of previous report and the additional recent data of figure 19 in this report.) However, with continued experience the apparent "zone of confusion" (occurring with spheres ranging mostly from diameters of 1/8" to 3/8") tended to disappear, or nearly so--in which case a small error zone centered approximately at the 1/4" sphere was likely to persist.

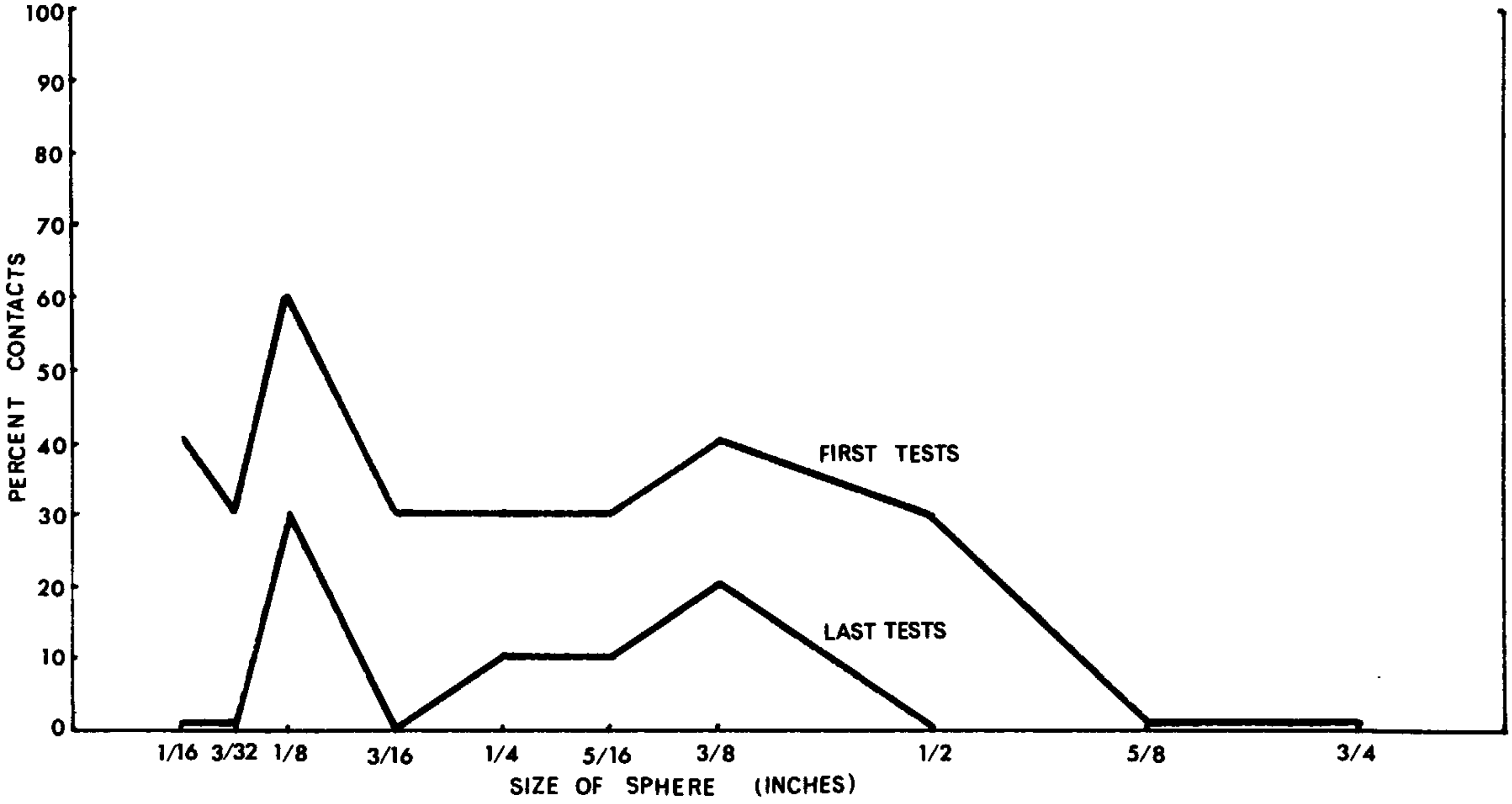

Figure 19. Comparison of first and last set of sequential discrimination tests on one Myotis lucifugus. One size of sphere was used per test, with each test consisting of 10 presentations of mealworms and 10 of spheres. In the first set of tests there were 2 mealworm errors; in the second set there were none.

These findings with respect to final discrimination capabilities, difficult discrimination configurations, and discrimination learning trends posed two general questions regarding the discrimination problem:

(a) Do there exist clearly definable echo correlates (in the echoes from mealworms) that match the form of the behavioral discrimination curves?

(b) Do sufficient numbers of mealworm echoes exhibit enough fluctuation (over a representative interval of evaluation) to account for the discrimination scores achieved, or do the findings suggest that other discrimination clues are involved?

2. Methods and Procedure

The echo tests were divided into two main portions: (1) statistical measures of selected differences between the echoes from mealworms and those from spheres, and (2) observations of properties of selected individual samples of echoes.

A block diagram of the electronic equipment used in the echo tests is given in figure 18. Pulses of 2-millisecond duration, sweeping linearly from 95 to 45 kHz, were used. They were directed toward a target zone, about 2-1/2 feet (3/4 meter) away, at repetition rates of mostly 100 or 50 pulses per second. Targets were either suspended in the approximate center of the sound field or else projected, from about 2-1/2 feet (3/4 meter) below, through the approximate center. Judgment of the suitability of each target projection was made either visually or by camera with reference to a cross-hair on a fine thread passing through the center of the field. The outgoing pulses were gated out and the echoes photographed directly on moving film by use of a Dumont 321 oscilloscope camera.

To evaluate the relation of the echoes to the specific position and orientation of the target, either one camera or two cameras at right angles were used in conjunction with two EG & G 501 stroboscopic units. Multiple flash pictures synchronized with the pulses were thus obtained.

3. Results

a. Previous Observations

Three sets of previous observations had given partial information with respect to the questions posed. First, a preliminary attempt had been made to equate the average reflectance of a suspended U-shaped mealworm with several sizes of spheres. The most probable echo magnitude had been judged variously as most closely matched to the 5/16" or the 3/8" sphere. Second, a far more extensive study of suspended targets (ref 14) using both curved mealworms and those which were relatively straight, revealed that the straighter mealworms were characterized by very great differences in echo intensity: the echoes vanishing into the equipment noise level (25 dB below maximum echo level) for most orientations greater than 30° out of the plane perpendicular to the sound axis. Neither of these sets of observations, however, gave any indication of the actual echo distributions encountered by a bat as it approached a series of mealworms projected into its approach path. They also gave no indication of whether or not significant echo-variations occurred in a sufficient proportion of instances (e.g., greater than 97%) so that overall echo fluctuation per se could be assumed as the sole required basis for discriminating mealworms from spheres. However, a third, very preliminary, set of observations had suggested that when mealworms were projected upward in front of an ultrasonic transmit-receive system there was a significant proportion of instances, possibly of the order of 10%, in which rather minor fluctuations in overall magnitude occurred during the interval (perhaps 1/5 second) during which the bats appeared able to make their discriminations.

b. Present Observations

As indicated under Methods and Procedures above, the present tests were divided into two main categories: (1) Statistical measures, and (2) Individual echo samples. The observations are discussed below under these two headings:

(1) Statistical measures

(a) Instantaneous echo maxima

The central question here was: When the echoes from projected mealworms are compared with the echoes from various sized spheres, what size of sphere returns echoes corresponding in magnitude to the most probable maximum instantaneous amplitude returned by a mealworm? To establish a reference line for making the comparisons, different-sized spheres were suspended approximately at the center of the sound field, and were also projected upward into it. Recorded echo amplitudes were then plotted on an arbitrary scale (see figure 20).

Approximately 100 mealworm tosses through the sound field were made, but only about half of these were judged suitable for measurement. Those which went too far to one side or which failed to reach a suitable elevation were rejected. The

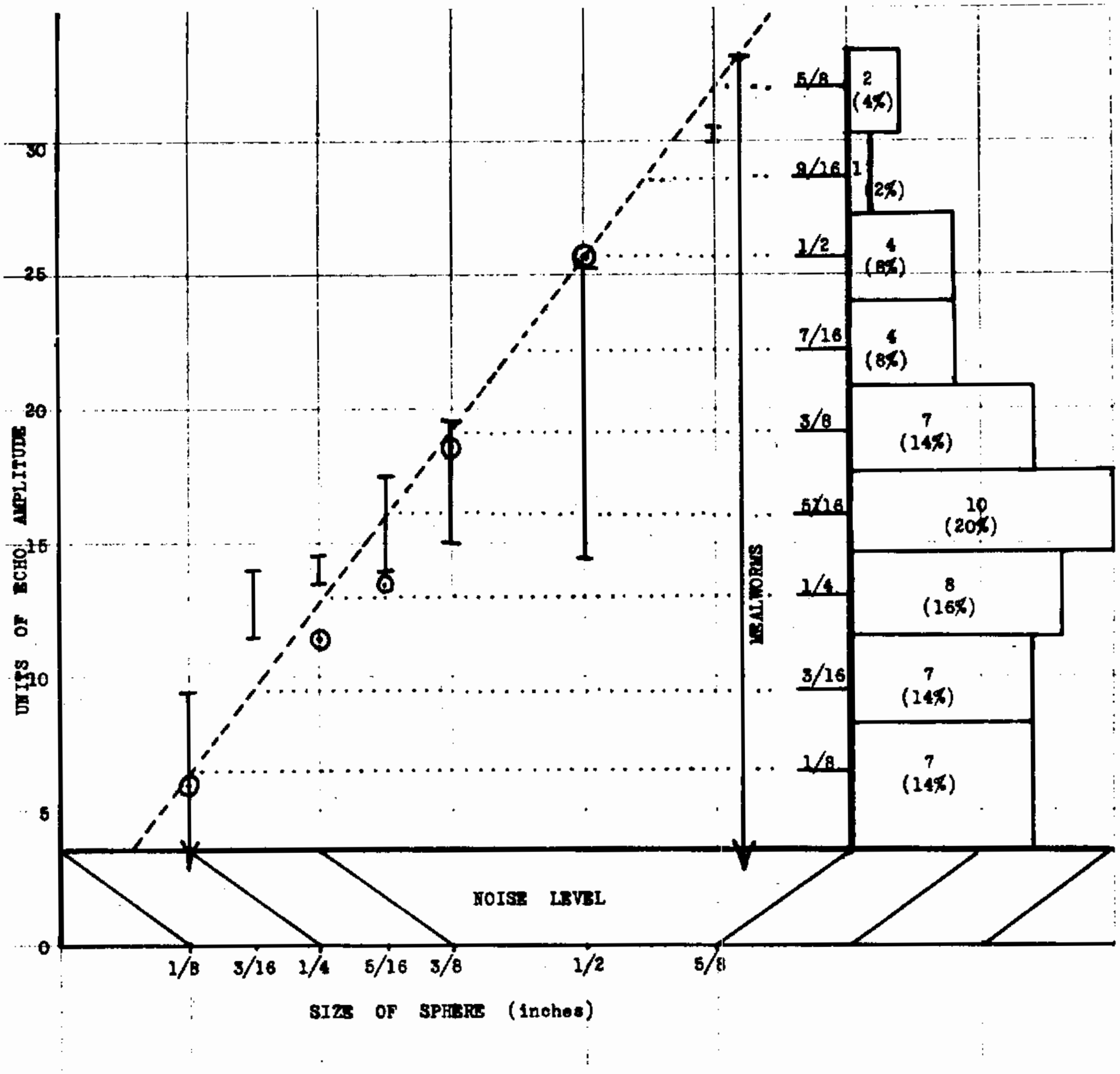

Figure 20. Instantaneous echo maxima for spheres and mealworms. Diagonal broken line indicates relative echo amplitudes for spheres suspended at the approximate center of the sound field. Vertical line segments show echo-range for maximum levels obtained when the spheres were projected up into the sound field from below. The reason why spheres of 3/16 inch and 1/4 inch diameters tended to return such large echo maxima is not clear. The long vertical line at the right side shows the range of echo amplitudes obtained when mealworms were projected upward into the sound field in the same manner as the spheres. For discussion of the distribution of instantaneous echo amplitudes returned by mealworms, see text. (Note that the lowest values of the distribution are grouped into a single category. This is because echoes from spheres smaller than 1/8 inch were not accurately measurable.)

results for the acceptable tosses are shown in figure 20, with reference to the sphere line discussed above. The unparenthesized figures at the right side give the number of tosses in which the maximum instantaneous echo (over the 1/5 second interval used for analysis) reached the amplitude of the echo returned by a given sized sphere that was suspended in the center of the sound field. For example, in 10 tosses (out of a total of 50), the maximum instantaneous amplitude corresponded in magnitude to that of a 5/16" sphere suspended at the center of the sound field.[11]

It is important to note that the tosses of mealworms scattered out from the center of the field and that it was necessary to make some estimate of the average effect of this scatter. This was done in various ways, including the corresponding projection of the various sized spheres through the sound field. To a first approximation, the effect of this scatter was estimated as corresponding to a shift of 1/16" of sphere diameter. According to

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[11] It will be noted in figure 20 that the echo amplitudes from some of the projected spheres deviated from the amplitudes of the corresponding suspended spheres. The reason for such deviation has not yet been clarified.

this estimate the echo-values for mealworms, given in figure 20, should be shifted upward one size unit in order to provide a suitable correspondence with sphere echoes. This would indicate that, in actual practice, the <u>3/8" sphere</u> returned an echo which most closely corresponded in magnitude to the most probable maximum instantaneous echo returned by a 100 mg mealworm over a 1/5 second interval (when radiated with 2-millisecond pulses, sweeping 90 to 45 kHz, at a repetition rate of 50 pulses per second).

It is of interest to note that the curve is skewed markedly downward into the noise level, indicating that in many cases the maximum instantaneous echoes reached levels corresponding only to very small spheres. Although instantaneous echoes reaching the magnitude of those returned by a 3/4" sphere did occur, echoes greater than those returned by a 3/8" or 1/2" sphere were comparatively rare.

(b) Integrated echo values

The corresponding question as the above, but with respect to integrated values, is: What size of sphere returns echoes corresponding in magnitude to the most probable average or integrated value of a representative sample of mealworm echoes? To obtain the integrated values of mealworm echoes relative to sphere echoes, a reference line for integrated echo-amplitudes from spheres had first to be obtained. An attempt was made to derive a reference line corresponding roughly to the reference line (for suspended spheres) of figure 20. To derive the values, several "ideal" sphere tosses for different sized spheres, were selected (i.e., those that went through the sound center and reached the prescribed height). Plots for the 1/5-second interval were then made and traced onto heavy uniform paper, after which the tracings were cut out and weighed (see sphere line of figure 21). The values for mealworms were obtained in a similar manner, except that all acceptable tosses were used. The distribution obtained is shown at the right-hand side of figure 21. A correction for the effects of scatter, amounting to about one size unit (as in figure 20), is thus approximately applicable in this instance also. It will be noted that relatively few of the mealworm tosses produced integrated echo values exceeding the integrated values of echoes from a 1/4" sphere (with scattering correction included). Integrated

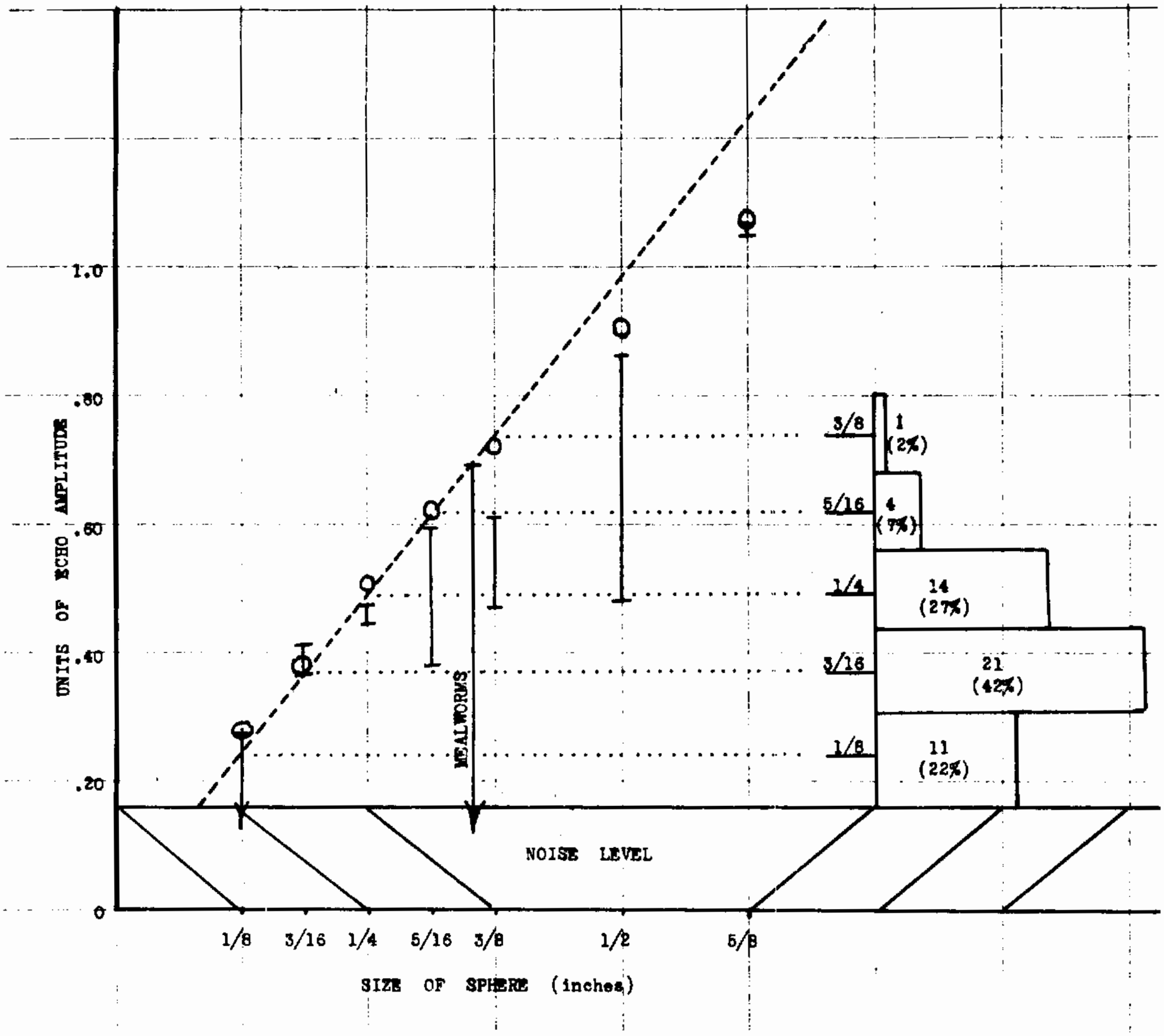

Figure 21. Integrated echo amplitudes for projected spheres and mealworms. Diagonal broken line indicates idealized values for integrated echo amplitudes with spheres (i.e., it represents the values for a sphere that passes through the sound center and reaches the prescribed height). Elimination of values outside the 1/5 second analytical interval produces some spurious decrease of magnitudes for the largest spheres relative to the smaller spheres. Vertical line segments show range of integrated values for actual sphere tosses (which tended to deviate somewhat from sound center). Long vertical line near center shows echo range for mealworms (measured in similar fashion). Right-hand distribution shows the correspondence of integrated mealworm echoes with idealized sphere values. For discussion, see text.

values exceeding those from a 3/8" sphere were very rare.

(c) Discussion of maximum instantaneous and integrated echo measures

If we assume that a bat, during the early phases of discrimination tests, makes use of both instantaneous echo maxima and average echo levels, we would expect an initial discrimination curve characterized by many erroneous catches of spheres of approximately 3/8" diameter, together with a significant number of errors for smaller spheres, extending all the way down to spheres small enough to produce echoes approximating the noise level of the equipment (i.e., 3/32" diameter). Relatively few errors, however, would be expected for spheres larger than the 3/8" sphere. Thus, if one assumes the premise that early discrimination clues are based, in considerable measure, on echo magnitudes, the general form of the behavioral discrimination curves is in basic conformity with the findings relating to maximum echo values and average echo values for projected mealworms.

The specific peaking of many of the early error curves at spheres of 1/8" diameter (see e.g. figure 19) is not explained by the present findings. Previous hypotheses included: (1) that the 1/8" sphere might correspond, in reflectance magnitude, to preferred natural targets, (2) that this sphere, though large enough to be readily detectable, is detected at such close range that there is inadequate time for evaluation of detailed properties, and (3) that natural targets of these sizes, though readily detectable, are not likely to be obnoxious and thus do not call for discriminative evaluation.

(d) Rates of amplitude shift

Among the discrimination clues, other than instantaneous or average echo magnitudes, the following were considered potentially applicable: echo fluctuation, echo structure and effects due to object shape and spatial extent (presumably involving binaural effects). One specific question raised above was: Does a representative sample of mealworm echoes exhibit a sufficient incidence of significant fluctuations in overall magnitude to account for the discrimination scores achieved with spheres and mealworms? Preliminary evidence had suggested that possibly as many as 10% of the tosses of mealworms were characterized by such minor fluctuations of overall amplitude that the bats seemed likely to call on other clues to achieve the observed discrimination scores.

In order to obtain more systematic data on this question, the present acceptable tosses of mealworms were measured for maximum amplitude shifts during 10-millisecond and 20-millisecond intervals, and the results compared with amplitude shifts occurring with tosses of spheres. Figure 22a is a direct plot of the data on maximum amplitude shifts: the left-hand plot representing 20-millisecond pulse spacings. Figure 22b is plotted in terms of the ratio of maximum shift to integrated echo amplitude (X 100). The ratio measure is presented chiefly to permit a convenient visualization of the distortions due to noise. In other words, since noise produces relatively large amplitude shifts at low echo amplitudes, some clarification of the noise contribution is essential to proper evaluation of the true shifts.

In the direct plots for spheres, there is a progressive rise in the rate of increase of echo-shift as the size of the spheres is increased: but there is some scatter about the line of increase. Such scatter derives from several sources, chiefly

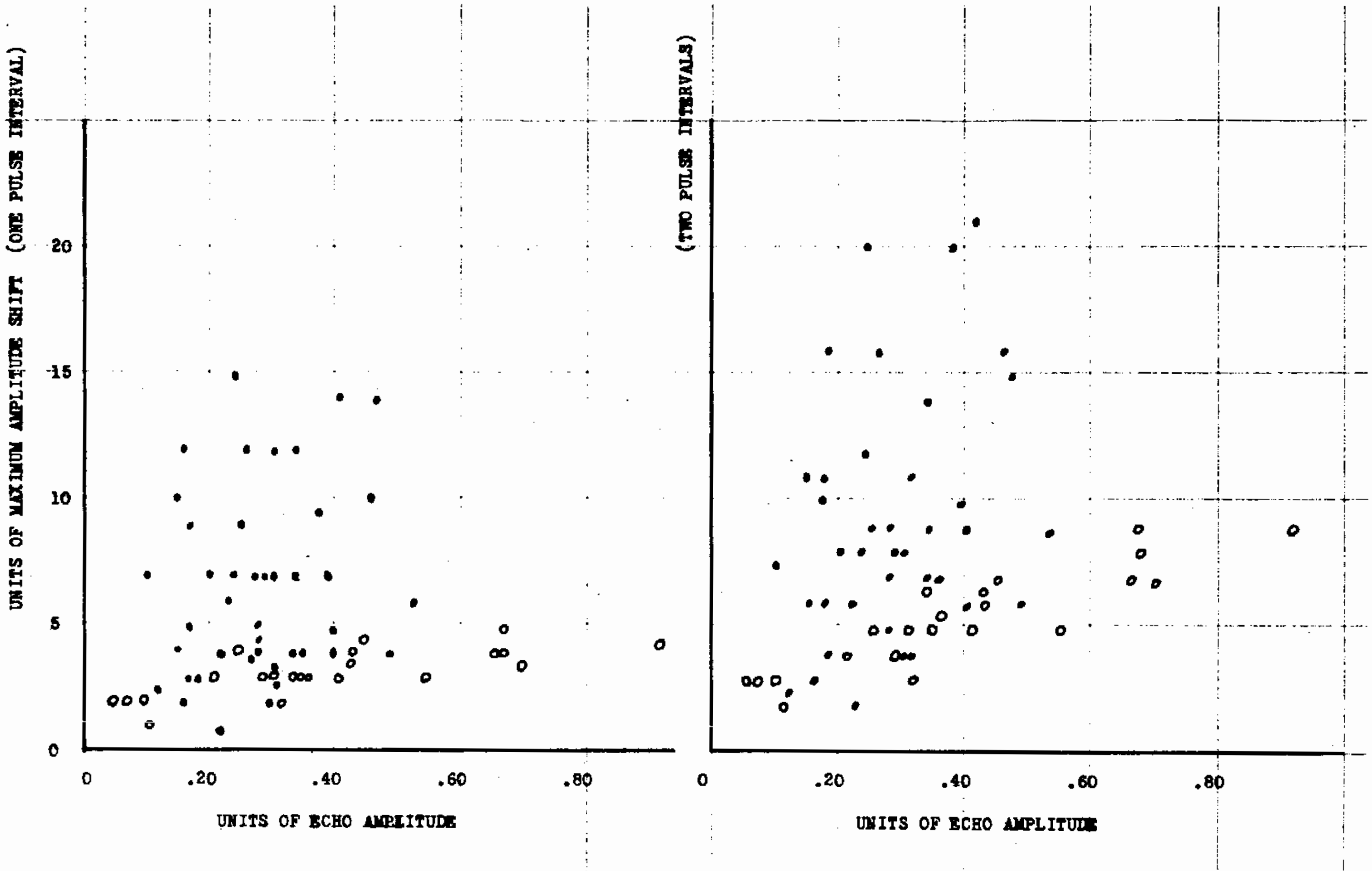

Figure 22a. Echo amplitude shifts relative to total echo amplitude. Left-hand plot represents amplitude shifts over single pulse intervals of 10 milliseconds each, while right-hand plot represents amplitude shifts over double pulse intervals (20 milliseconds). Sphere values are indicated by circles, those for mealworms, by points. The slope trend of the sphere echoes is due to the increase in the magnitude of shifts for larger spheres as the spheres pass into, or out of, the sound field. It is thus roughly doubled for the two-pulse intervals as against the one-pulse intervals. Amplitude shifts for mealworm echoes are scattered more or less at random. Moreover, a significant proportion of mealworm echo-shifts are of the same order as the echo-shifts for spheres. (For discussion, see text.)

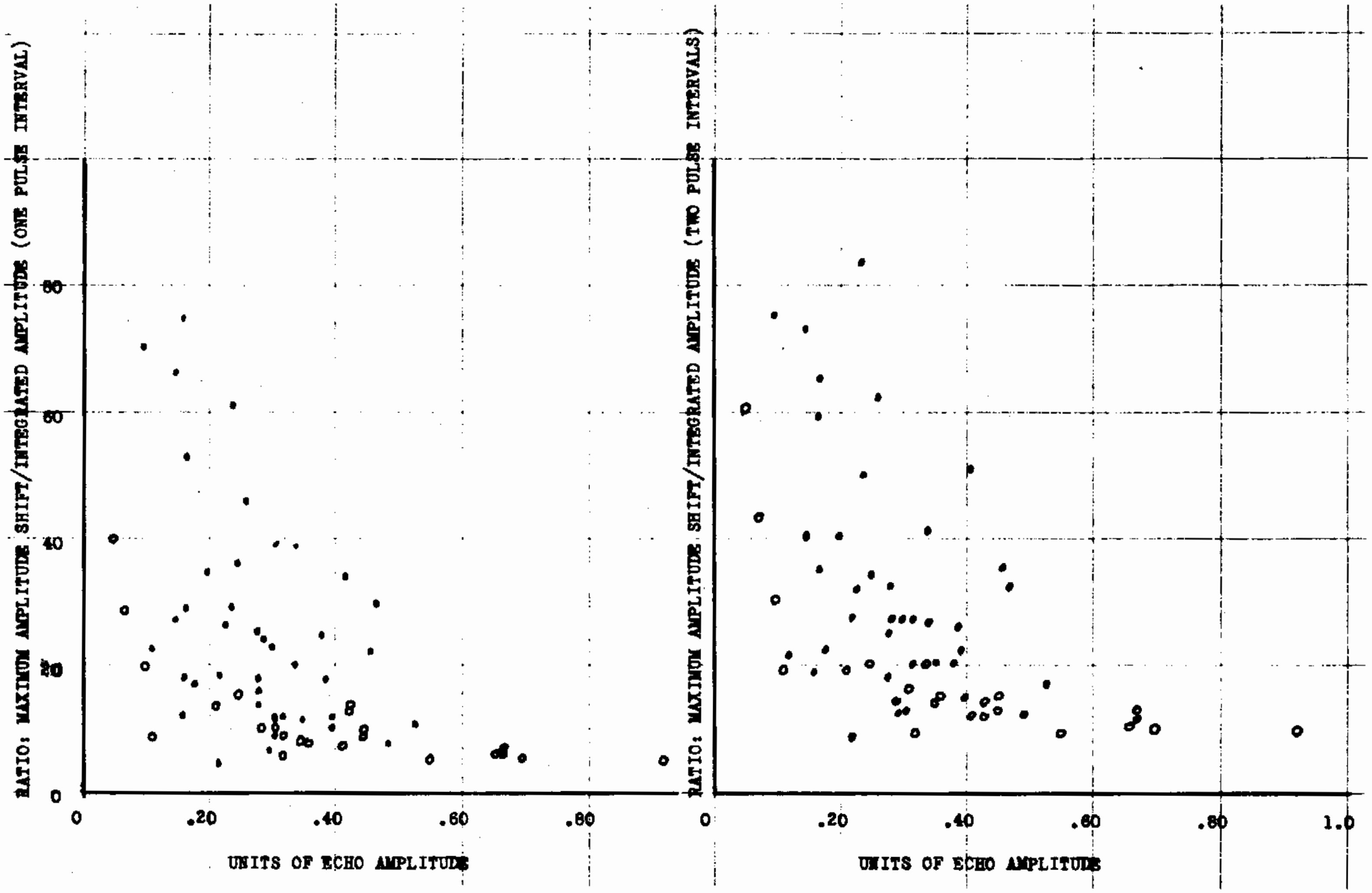

Figure 22b. Echo amplitude shifts relative to integrated values. These plots represent the same data as the left and right portions of the previous figure, with the exception that the amplitude shifts have been divided by the integrated echo amplitudes in order to permit visualization of the large relative contribution of noise disturbances with the smaller-amplitude echoes. (Note rapid rise in relative echo-shift magnitudes toward the small-sized spheres--a situation which applies likewise to the smaller echoes returned by mealworms) For discussion, see text.

equipment noise and variations in the rate of passage of the targets through the sound field. As might be expected, the slope of the amplitude-shift line for spheres is almost doubled in the plot for two-pulse (20 msec) spacings, as against that for one-pulse spacings (10 msec), due to the greater echo-shift with respect to the center of the field.

In the ratio plots for spheres, it is clear that as the integrated area decreases, the relative magnitude of the amplitude shifts increases. Since the echo from a smooth sphere is theoretically uniform, regardless of orientation, the magnitude of the interpulse shifts, for a given size of sphere, should depend almost entirely on the rate of passage through the sound field and the proximity to the center. The large dispersion of relative amplitude-shifts for small spheres is due to the relatively large contribution of noise disturbances, and gives an indication of the extent of the noise contribution to amplitude shifts seen with small echoes in general.

In the direct plots of amplitude-shifts obtained with mealworm echoes (figure 22a) there is little change in the magnitude of echo-shift with shifts of the integrated echo area. Relative orientation, in other words, provides the main source of amplitude shift. At the same time--and most significant for present purposes--there is a very significant proportion of instances, possibly 20%, in which the measured magnitude of shift is no greater than the measured magnitude of shift for spheres. Examples of echo sequences from spheres and mealworms in this overlap region are given in figure 24.* Although the system noise contribution prevents precise specifications, present data strongly suggest that at least 10% of the mealworm tosses are characterized by such small shifts in overall amplitude (over the assumed 200-millisecond interval of evaluation) that discrimination on this basis alone seems unlikely.

These findings with respect to overall shifts of echo amplitude do not, of course, exclude the use of subtler variations in echo form. As will be seen in the observations on individual echoes reported below--even though echo structure has not been evaluated in detail--there are indications that various kinds of echo shifts may occur with

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* Figure 24a appears on p.119; figure 24b appears on p.121.

very minor changes in the shape or relative orientation of mealworms.

(2) Observations on individual echoes

The purpose of these observations was to obtain samples of the echo shifts which occurred as the relative orientation of individual mealworms shifted. Unlike the systematic study already reported (ref 14), present observations were chiefly concerned with projected mealworms, rather than with tethered mealworms, although one set of measurements was also made on the relation of echo magnitude to angle of tilt for a straight mealworm suspended in the sound field. Since this latter set of measures provides useful orienting information, it will be presented first.

(a) Mealworm echoes as a function of rotation and tilt

Mealworms have often been considered as having roughly the form of a bent cylinder. According to this assumption, a mealworm which was only slightly bent would produce an echo which was relatively independent of rotation about the longitudinal axis. Since photographs revealed that many mealworms were essentially straight, it seemed relevant to discover how much echo variation was derived from rotational orientation as such. Additional observations on the echo fall-off with increasing angle out from the plane perpendicular to the axis of sound propagation also seemed essential to any systematic interpretation of the echo distributions of projected mealworms.

Figure 23 presents echo data for a single suspended mealworm that was pierced lengthwise with a fine needle to hold it straight. The left-hand portion of figure 23 shows a segment of amplitude-shift recorded as the mealworm was rotated approximately in the plane perpendicular to the axis of sound propagation. The right-hand portion of the figure compares these results with several different tilts out of the perpendicular.

To carry out the measures, a 25 mm mealworm was pierced lengthwise with a 30 mm needle--the eye of the needle being imbedded in the head of the mealworm. A length of 0.025 mm (1 mil) wire was threaded through the eye and the mealworm suspended in the center of the sound field. For the rotational measures in the perpendicular plane, the wire suspension was wound up and then allowed to unwind while the ultrasonic pulses were directed at the

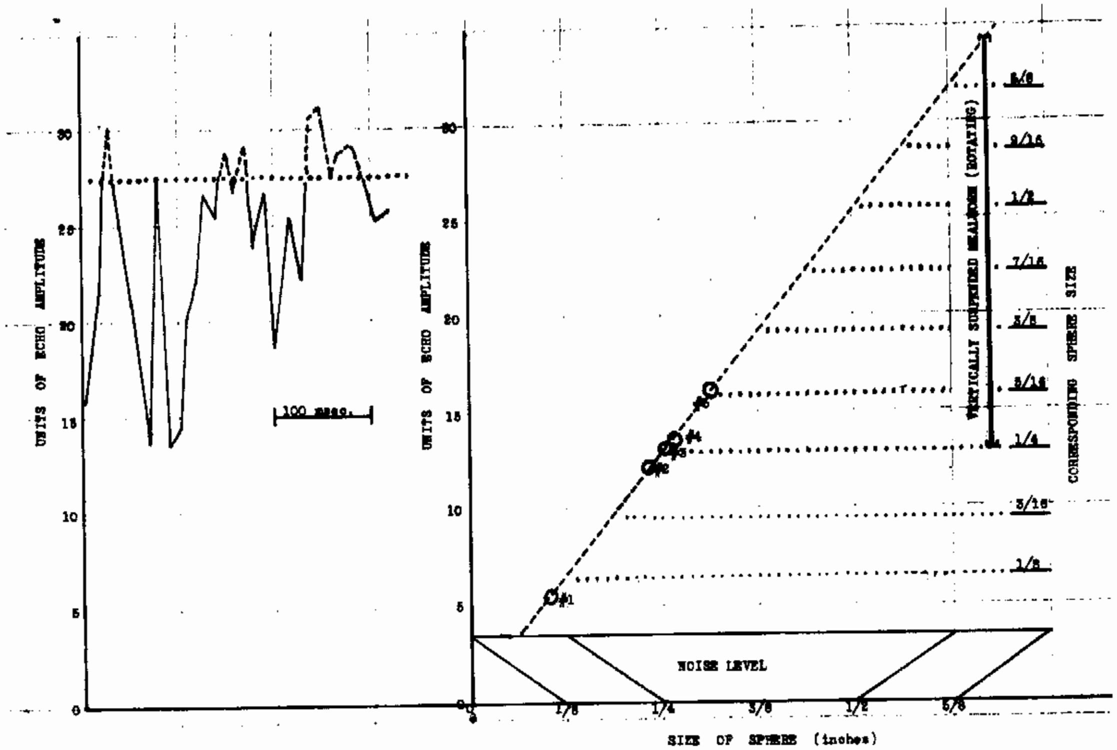

Figure 23. Mealworm echoes as a function of rotation and tilt. The left-hand portion of the figure shows the sequence of echo amplitude shifts that occurred over a 1/30 second interval while 2-millisecond ultrasonic pulses were directed at a mealworm rotating approximately in the plane perpendicular to the axis of sound propagation. Levels indicated in broken lines are above the clipping level of the equipment and are therefore only approximations. The right-hand portion of the figure illustrates relative echo magnitudes of echoes returned while the mealworm was held stationary at different tilts from the perpendicular plane. Points numbers 5, 3 and 1 were obtained when the rounded side of the mealworm was directed toward the speaker, and illustrate the echo levels for tilts away from the perpendicular of 8°, 13°, and 33° respectively. Point number 4 was obtained with the flat side of mealworm toward the speaker at a tilt of 51°; and point number 2 was obtained with the mealworm end-on in line with the axis of sound propagation. Note that the end-on value is larger than the value for a 33° tilt. The range of values obtained with the rotating mealworm is indicated by the vertical line at the right.

rotating mealworm. For the tilt measures, the lower end of the protruding needle was allowed to rest on the fine cross-wire (used for judging the suitability of tosses) while the upper end was lowered to produce several different angles of tilt.

The results of the rotational test (left portion of figure 23 show some very rapid doublings and halvings (6dB shifts) of amplitude, apparently with relatively small changes in rotational orientation. Unfortunately, concurrent photographs were not made, so that the relations of amplitude to orientation were not established. It is clear, however, that a mealworm has divergencies from a cylinder sufficient to produce marked variations in the magnitude of returned echoes.

Echo shifts with different tilts from the perpendicular plane are given in the right-hand portion of figure 23. The points for echo amplitude are plotted along the line which represents the magnitude of echoes from suspended spheres (of diameters indicated along the abscissa). Points numbers 5, 3 and 1 illustrate the decrease in echo amplitude occurring as the mealworm, with rounded side toward the speaker, was tilted successively out of the perpendicular plane by 8°, 13° and 33° respectively. Point #4, although representing a still greater tilt (51°), produced a larger echo than #3--presumably because in this instance the mealworm was flat side toward the speaker. Of some interest is the unexpectedly large value of #2, obtained when the mealworm was along the axis of sound propagation, and hence seen end on from the position of the speaker. Comparison of the echoes from the tilted mealworm with the range of the rotated mealworm can be made with reference to the range line for the tethered mealworm at the right-hand side of the plot.

Even though the present measures are made with reference to an obviously idealized case, they could provide some useful indications regarding echo contributions of certain important parameters in the total echo picture.

Figure 24a illustrates selected sequences of amplitude shifts for spheres and mealworms that were projected upward into the sound field. The profiles were made by plotting the (maximum) amplitudes, above basic equipment noise level, of 20

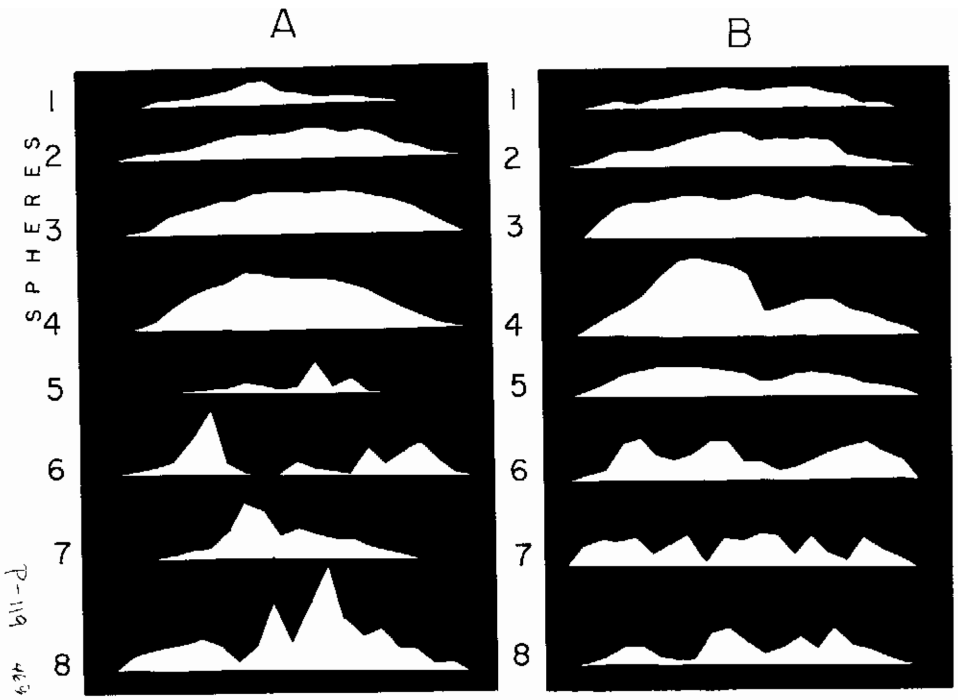

Figure 24a. Some amplitude shift patterns in the echoes from spheres and mealworms. In these plots, 20 successive pulse echoes at 10-millisecond intervals are represented in terms of the individual echo amplitudes. Normally, the target was projected nearly through the center of the sound field to a point slightly above center.

Sequences A-1 through A-4 show echoes obtained with spheres of 1/8", 3/16" 5/16" and 3/8" diameters respectively.

Sequences B-1, B-2 and B-3 show echo sequences from mealworms which have echo variabilities of the same order as those noted with spheres as a result of noise disturbances or trajectory variations.

Sequences A-5, A-6, and to some extent A-7 and A-8, illustrate instances in which relatively high instantaneous peak values occurred, while the total integrated value of the echo remained at a much lower level.

Sequences B-5, B-6, B-7 and B-8 suggest cyclical shifts of different rates--pissibly associated with spinning of the mealworms. (These plots represent rectivied portions of echo sequences, above noise level.)

successive echoes obtained as the target passed upward close to the center of the sound field, going slightly above, then fell back through it. Due to various minor echo-shifts and disturbances the profiles for the sphere echoes (A-1,2,3 & 4) are not uniformly smooth; also, due to lateral deviations from the sound center, the up-going and down-going portions are not always symmetrical. Note that three of the mealworm sequences (B-1,2 & 3) do not differ greatly in variability or in magnitude from the first three sphere sequences (representing echoes from spheres of 1/8", 3/16" and 5/16" diameters respectively).

Sequences A5,6,7 & 8 illustrate instances in which relatively large instantaneous amplitudes were associated with relatively much smaller integrated echo values. Profiles suggestive of cyclical shifts are seen in sequences B-6,7 & 8. A traced portion of the oscilloscope record from which sequence A-6 was obtained is shown in figure 24b.

(b) Synchronized photographs and echo measurements of projected targets

To obtain stroboscopic photographs synchronized with the echoes, two EG & G 501 stroboscopic units were triggered so as to produce a flash as the

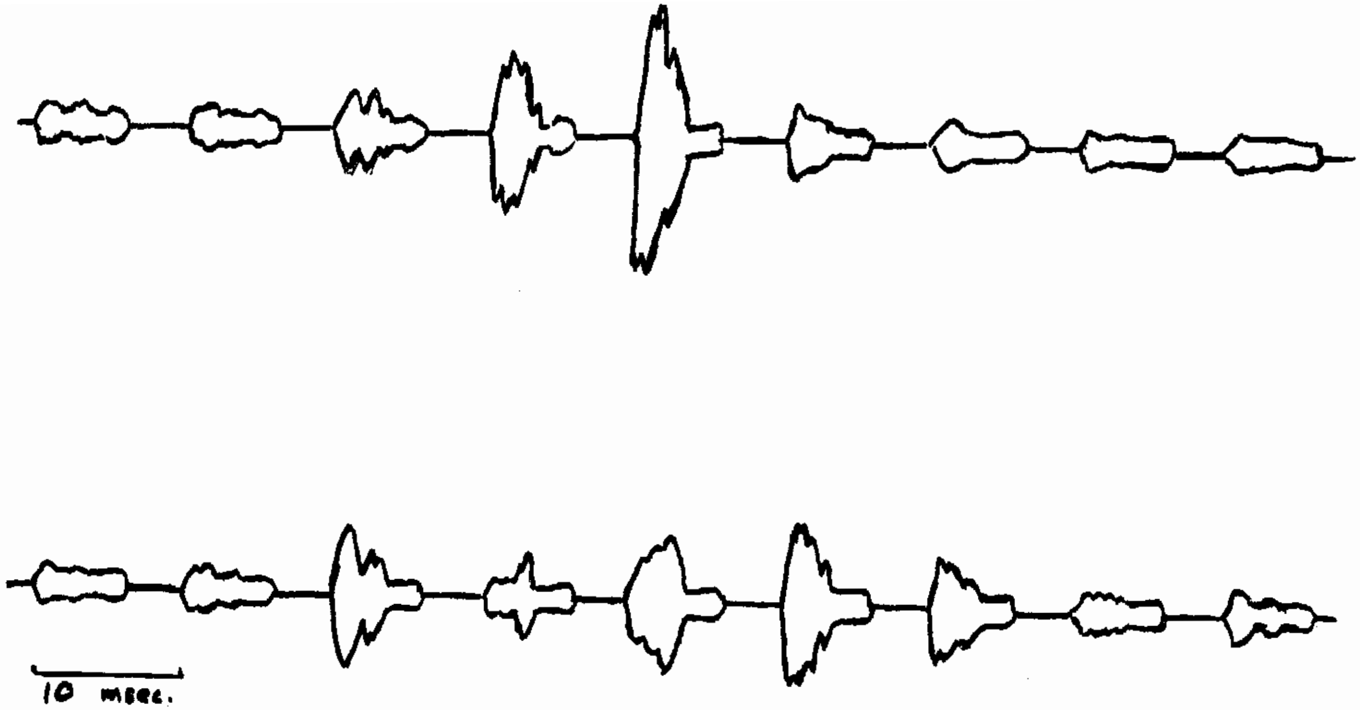

Figure 24b. Echo sequences traced from the oscilloscope photographs used for Profile A-6. Upper tracing shows the echoes for the first main peak (of fig. 24a, sequence A-6), while the lower tracing shows the echoes for the final pair of peaks. In this instance the first peak corresponded in amplitude to the echo returned by a sphere of 7/16 or 1/2 inch diameter, yet the total integrated echo magnitude corresponded only to the integrated echo magnitude of a 1/8 or 3/16 inch sphere. Line segments between pulses represent the region where outgoing pulses were switched out of the receiving system. The segments 4-5 mm thick following the echoes represent the system noise level. Since the frequency response was not entirely flat, the measured point of maximum amplitude did not necessarily represent the true maximum. Such distortion may have accounted for certain measurement discrepancies. Differences in the form of the amplitude curve also occurred for the case of a target entering the sound field as against the case where it was leaving the sound field. Echo notchings, such as those seen here, are normally the result of interference patterns produced by reflections from different portions of a bent mealworm.

terminal portion of each pulse was being returned by the target. In selected instances, paired flashes were employed--one occurring as the pulse front reached the target and the other as the terminal portion reached it. However, the 2-millisecond separation (i.e., the pulse duration) was too brief to be characterized by significant echo shifts. A primary camera was placed just above the transmit-receive elements, while a secondary camera was placed at right angles at one side of the projected targets. Pulse rates were mostly at 50 pulses per second, and matching of the echo pictures with the stroboscopic pictures was achieved with the use of an auxiliary flash unit which produced an intense image in the picture sequence and a mark along the photographed pulse train.

Figure 25 illustrates a representative projection of a sphere (3/8" diameter) and provides a useful calibration function. The line running across the center of the field represents the nylon filament used as a positon reference: the cross-mark indicating the center of the sound field. As can be seen from the echo indications (placed below the sphere images, with corresponding numbers) the half-amplitude points are roughly 1-1/2 inches above

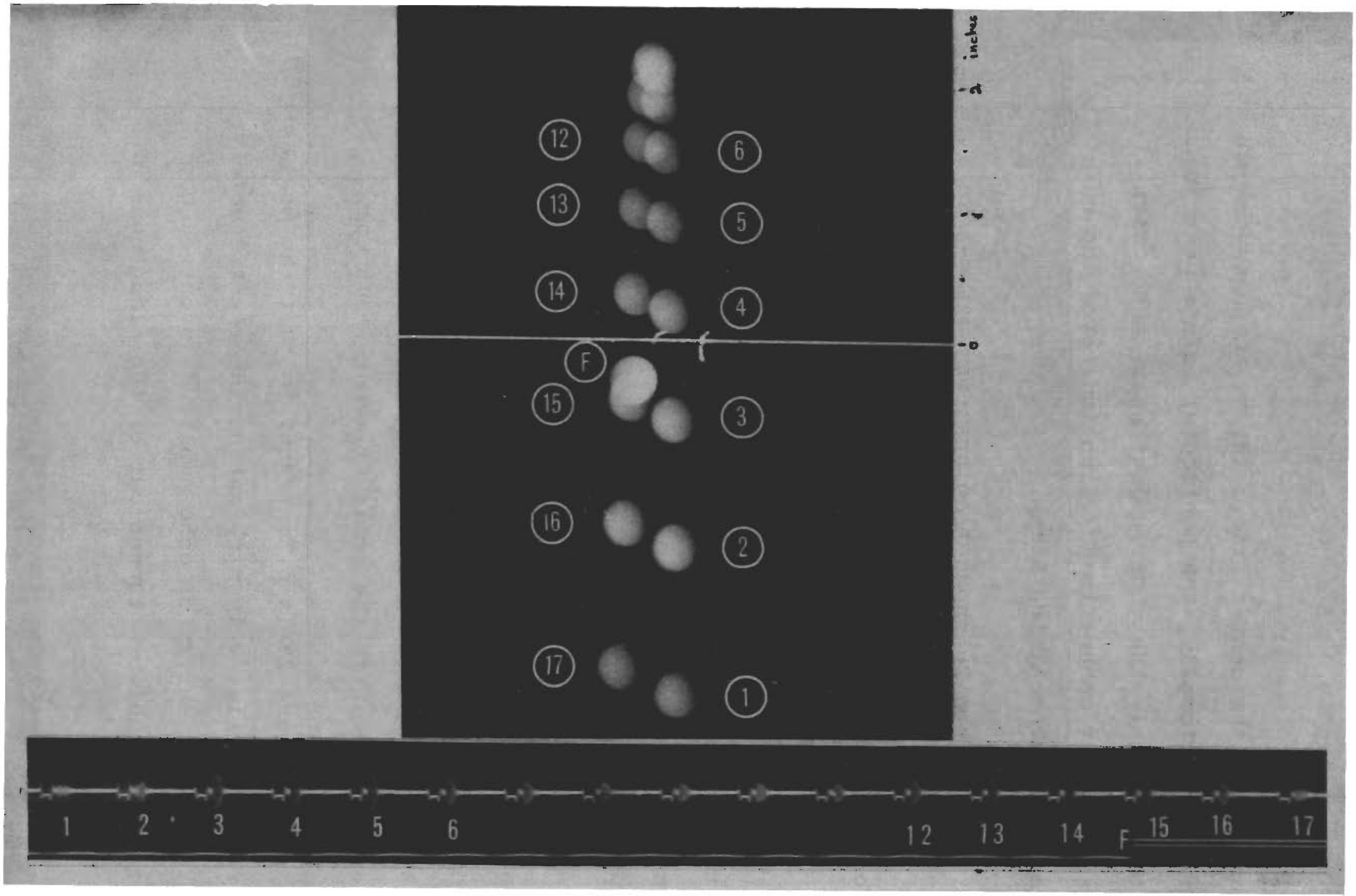

Figure 25. Echoes and positions (with respect to sound center) for 3/8 inch nylon sphere projected into sound field. Center of field is marked by larger cross-hair on horizontal filament. Echo indications are marked below with corresponding numbers. The half-amplitude points are roughly 1-1/2 inches above and below the center line. Lateral and horizontal half-amplitude points were at about the same distance. Just below the center line is an extra image, indicating the point of the synchronizing flash.

and below the center line. (By swinging suspended spheres laterally, the horizontal points were found to be roughly the same.) Just below the center line is a bright sphere image which indicates the point of the synchronizing flash.

Figure 26 shows tracings from a two-camera record of a projected mealworm that struck the cross-line on the way down. Images from the right-angle camera have been placed alongside the respective front-view images, outside the echo tracings. The left-hand echoes suggest that considerable variations in echo magnitude occur with rather small shifts of orientation or shape. The right-hand echoes from the falling mealworm show a number of interference patterns due to the curvature of the mealworm in the plane more or less parallel to the sound axis. These become particularly pronounced after the cross-filament is struck.

Figure 27 is of interest in that the mealworm remained relatively straight during the trajectory. Very large shifts of echo amplitude occurred each time the mealworm turned out of the plane more or

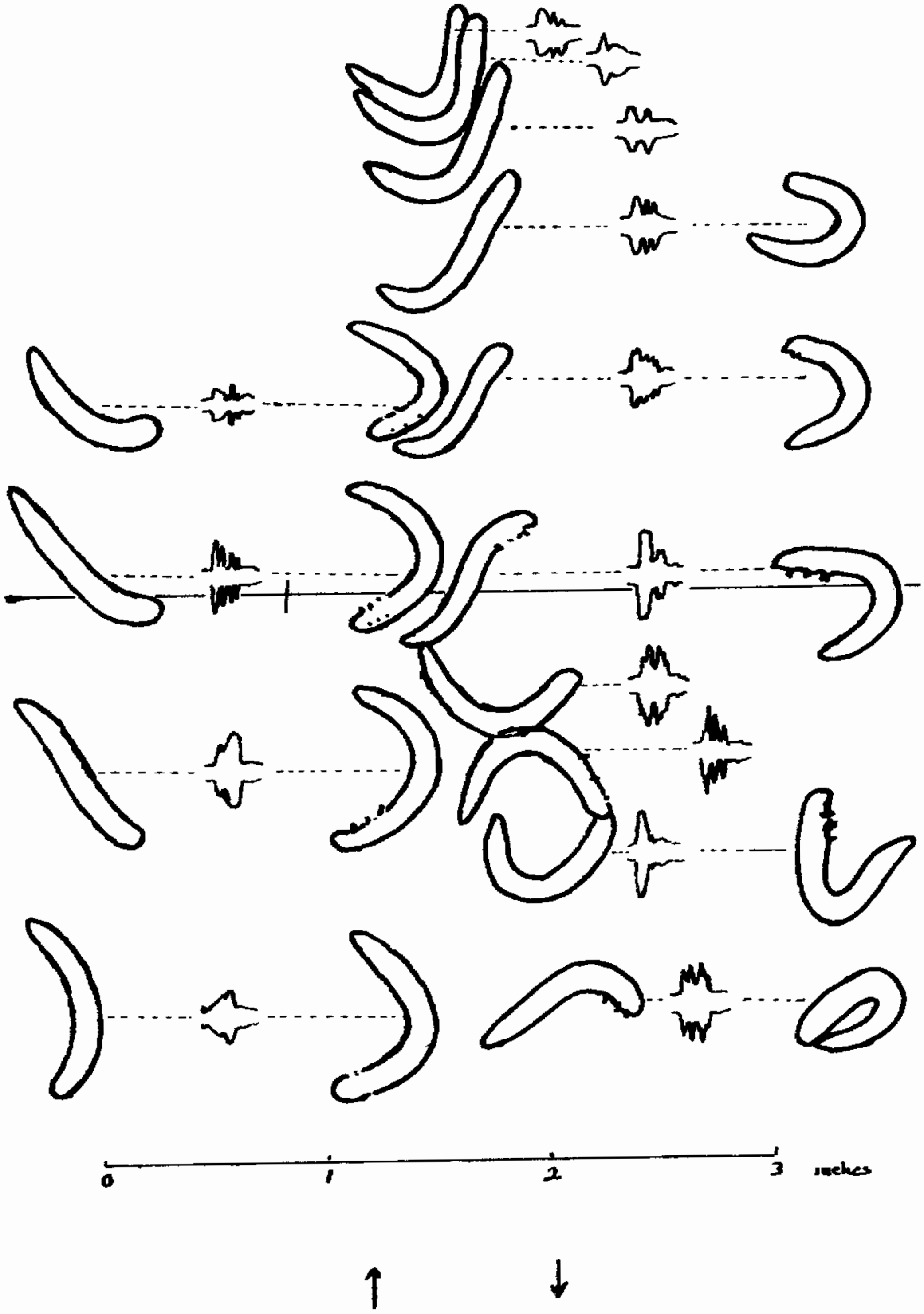

Figure 26. Selected tracings of two-camera record of a projected mealworm. Mealworm images from the right-angle camera have been placed alongside the respective front-view images, outside the echo tracings. The left-hand echoes (while mealworm was rising) suggest that considerable variations in the echoes occur with relatively small shifts of orientation or shape. The right-hand echoes from the falling mealworm show a number of interference patterns, particularly after the mealworm struck cross-filament.

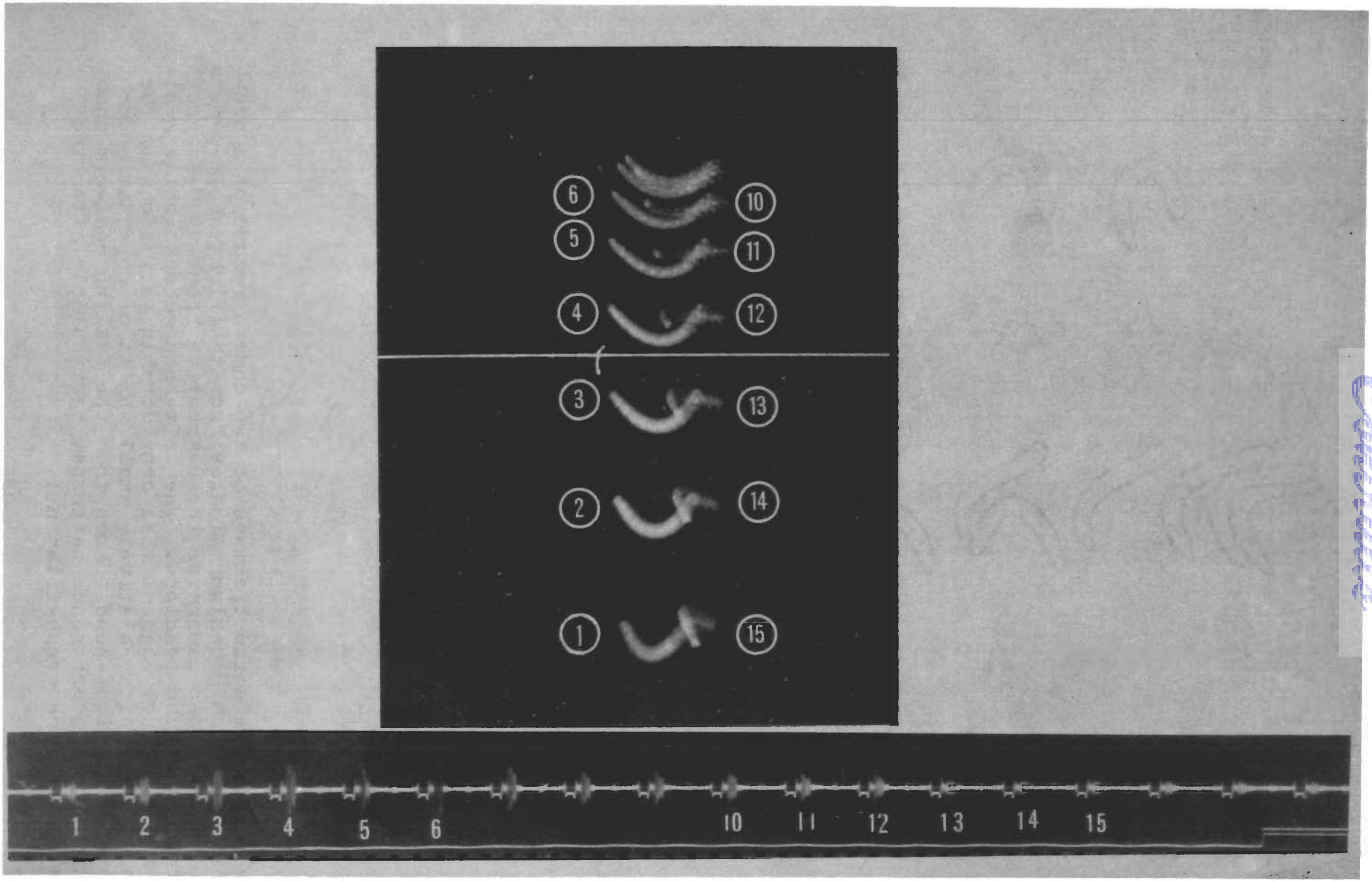

Figure 27. Projected mealworm that remained relatively straight. Large increases of echo-amplitude are seen as mealworm turns approximately into the perpendicular plane (#6).

less perpendicular to the axis of sound propagation.

Figure 28 illustrates one of the largest amplitude echoes obtained during the tests (well over double the amplitude produced by the 3/8" sphere of figure 25, when corrected for displacement from the center of the sound field). Marked shifts in echo form are evident as the mealworm turns into the plane perpendicular to the axis of propagation and then turns out of it again.

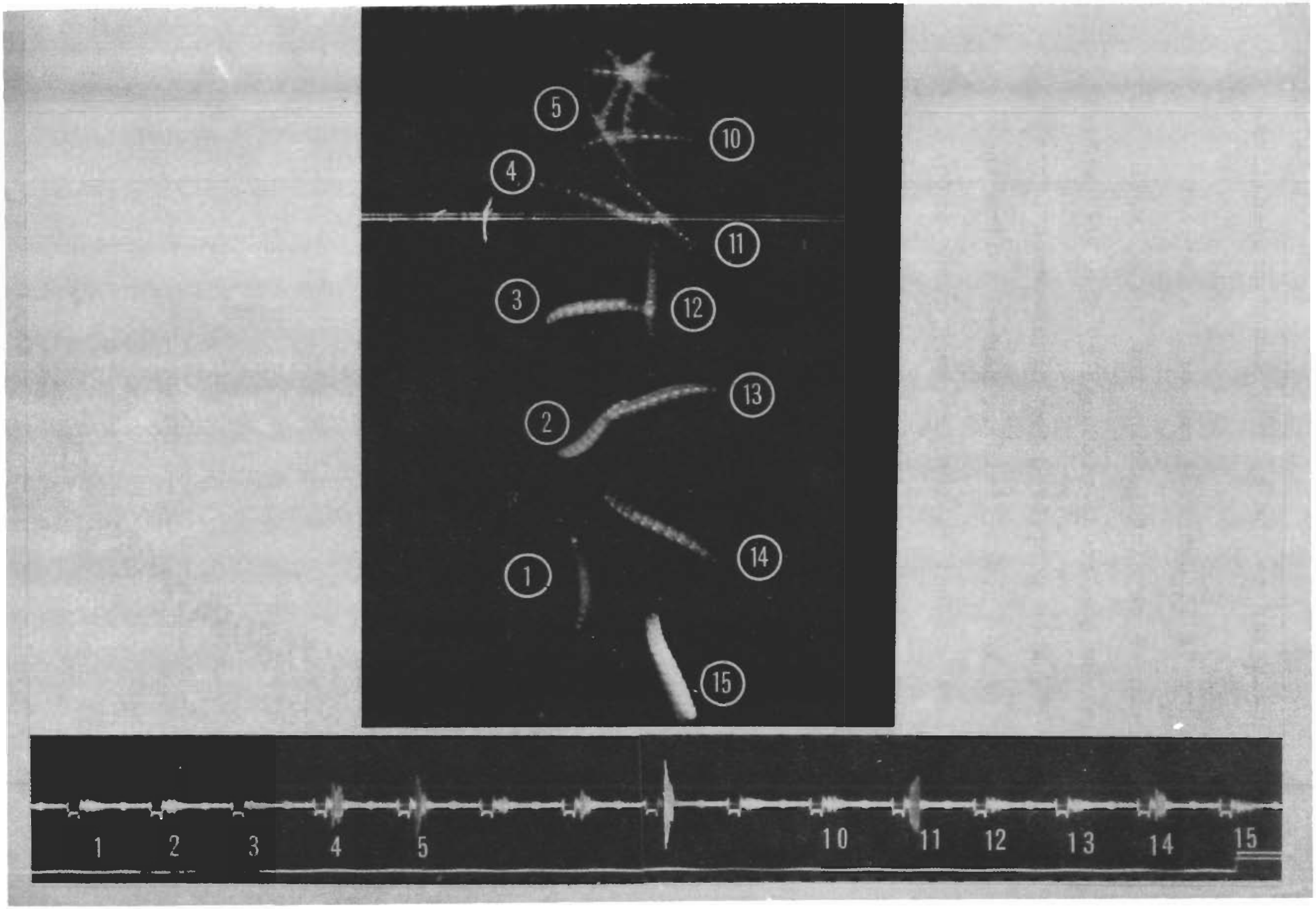

Figure 28. Extreme shifts of echo amplitude. Here, mealworm rotates into, and then out of, the perpendicular plane. Echo corresponding to upper mealworm image (accentuated in echo sequence) would have been approximately double the existing amplitude if the target had been at the center of the sound field.

SECTION V

OUTDOOR CAGES AND FIELD OBSERVATIONS

A. Introduction

Within the artificial and confined space of the laboratory, observations on the performance characteristics and signals of bats suffer from a number of limitations and distortions. For example: (1) Many bats adapt with extreme difficulty, or are totally unable to adapt to the conditions imposed by the laboratory flight space. (2) Gross modifications of behavior and emitted signals occur in many instances: flight-speeds are often greatly reduced, cruising pulses markedly shortened and pulse patterns radically changed. (3) Many experiments cannot be carried out; neither can the variety of natural hunting be duplicated. (4) Flight behavior tends to become stereotyped and motivation greatly reduced. (5) Many situations characteristic of a bat's natural mode of existence are completely absent.

With these and other limitations in mind, two partial solutions have been attempted: large outdoor cages have been constructed and certain observations have been made of bats in their natural habitats.

The outdoor cages posses a number of advantages over the laboratory flight space. For example, they are large enough so as not to crowd the bats' freedom of flight to nearly the extent that occurs in the laboratory space; moreover, the enclosing mesh gives little reflection from the bats' signals, while the walls of the laboratory must often send back reverberating echoes. In addition, ultraviolet lights within the cages attract a variety of natural targets and thus provide hunting conditions much closer to natural conditions. At the same time, the outdoor cages possess some of the advantages of the laboratory in that they permit fairly extensive instrumentation and they make possible much of the experimental control characteristic of laboratory conditions.

The cages do not, however, permit observations under natural conditions. Even in the cages, flight speeds are often greatly reduced and the bats' hunting maneuvers modified. Moreover, many tests and observations cannot be carried out at all. For example, the space is far too small to measure maximum ranges of target detection. In addition, many aspects of a bat's natural mode of existence are obviously totally removed. A good example is seen in the possibly rather complex interrelations of the natural roosting and hunting situations of the fishing bat Pizonyx, discussed below. Effective field instrumentation will have to be developed and integrated before adequate natural observations can be made; and suitable locations for the study of natural hunting will have to be undertaken before many of the crucial questions related to the pursuit activities of different bats can be properly answered.

B. Outdoor Cages

1. Location, Construction and Arrangements

Two outdoor flight cages have been built, each using a common plan of construction, but different detailed materials. The cages were designed by Geometrics, Inc., of Cambridge, Massachusetts, and are based on a plan which permits a maximum of internal space with a minimum of construction material and associated costs. The design consists of 50 interconnected triangles, each roughly 9-1/3' X 20' in size. Approximate overall dimensions of the frame are: 55' long by 36-1/2' wide by 30' high (roughly 17 X 11 X 9 meters) with side walls slightly under 20' in height. One of the cages was constructed during the spring and summer of 1965 on the grounds of the Massachusetts Audubon Society at Drumlin Farm in

Lincoln, Massachusetts. The other cage was constructed in the summer of 1966 at Sensory Systems Laboratory in Tucson, Arizona.

The Drumlin Farm cage was fabricated with the use of 6-inch steel I-Beams of sufficient strength to permit construction of a solid roof, if desired. A major portion of the cage bottom is covered with a concrete floor which permits the use of a "rolling tower" which can reach almost any portion of the interior. A drinking trough runs along one side of the concrete base while an earth strip outside the trough provides an area of natural grass and foliage. The lower portion of the vertical walls are lined with hardware cloth with mesh openings of about 1/4" diameter, the mesh being dug into the ground as a guard against burrowing rodents. To the upper portion of the hardware cloth is stitched a light 3/16" X 1/4" dacron mesh. The mesh size is such that the breaking of any single strand does not leave an opening large enough for a bat to escape, and to date no bats are known to have escaped, even though minor breaks have sometimes occurred. The mesh is held up with the use of ropes and pulleys in such a way that the material can be partially lowered to reduce the height of the flight space, when desired. During the winter months the dacron mesh is removed.

Insects are drawn to the cage with the use of ultraviolet lights in the interior: large numbers of small insects normally being attracted at dusk, together with a few medium sized moths. Moths with tympanic organs seldom fly within the cage while bats are present--though they sometimes rest on the surface of the netting, where they may be attacked by bats. To roost, the bats generally locate folds in the mesh, or crawl into the cracks between the mesh and the ridgepole tube which holds up the central portion of the netting. Certain bats habitually seek the shelter of wooden boxes placed high in the central region, protected from rain by an overhead wooden platform.

The cage at Tucson is of far lighter construction--being made of 1-1/2" steel tubing of 1/16" thickness. The enclosing material is wire with roughly 3/8" hexagonal openings. This enclosing mesh is stretched over the exterior of the frame and provides additional rigidity, needed with the light tubular construction. A pond of about 25-feet diameter is located on one end to permit experiments with fishing bats. The larger mesh of the Tucson cage permits larger insects to enter, though we suspect it may have the disadvantage that occasionally bats tend to injure their wings in attempts to escape.

2. Use and Observations

In constructing the outdoor cages, four main functions were considered:

(a) Improved adaptation of bats to captive conditions,

(b) more effective training for pursuit in the laboratory,

(c) observations of pursuits closer to natural conditions,

(d) increased longevity of captive bats.

(a) Improved adaptation to captive conditions:

When brought into the laboratory, many bats give evidence of decreased motivation and lessened intensity of pursuit. This decline of pursuit propensity and vigor tends to result in changes in pursuit tactics and the associated signals (see number 3 below). Also, a number of the bats become untrainable and some continue to lose weight.

Our observations in the Drumlin Farm cage suggest that, in many of the bats, adverse changes are postponed, and--when sufficient natural targets are present--may scarcely occur at all. Moreover, after the bats have shown a decline under laboratory conditions they tend to regain some of their natural propensities if they are returned to the outdoor cage. However, species and individual differences in adaptation exist: Eptesicus fuscus appearing to gain the greatest advantage of the several species tested. Thus far, no bats have fully maintained themselves in the cage, though many have caught large numbers of naturally-flying insects and shown weight gains over limited periods. This has been particularly true in the case of Eptesicus fuscus. To maintain their weights, the bats are intermittently caught and returned to auxilliary cages where they are given supplementary feedings with mealworms.

(b) Preliminary training for pursuits in the laboratory

Intensive effort--sometimes as much as an hour per day per bat, for a week, is required either to train a bat for catching in the laboratory, or to decide that a bat is basically unsuitable for laboratory tests. Moreover, prior to the construction of the Drumlin Farm cage, no Eptesicus fuscus had ever caught a target in the laboratory, despite repeated efforts over the preceding half dozen years.

To train Eptesicus to catch in the laboratory with the use of the outside cage, the following procedure has proved effective. The bats were first released in the outdoor cage at a time when a number of natural targets were present. Almost invariably, the bats began catching spontaneously within the first hour. As suggested above, likely reasons for the willingness of the bats to catch in the outdoor cage, as against the laboratory flight space (where natural targets have also been introduced) are: greater maneuvering space, greatly reduced wall echoes (since relatively nonecho-producing mesh replaces the solid walls of the laboratory) and the larger number and variety of natural targets. After natural catching is well initiated, regions commonly used by the bats for catching are noted, and mealworms are tossed into these areas. Normally, the bats soon pursue the mealworms and after a few catches begin to take cognizance of the locality where the mealworms are being tossed. Generally speaking, after an evening or two of familiarity with these tosses they adopt consistent flight patterns and are then ready for initial trial in the laboratory flight space.

The shift to the laboratory usually results in reduced flight activity or extensive exploratory behavior. After a bat has gained sufficient familiarity with the flight space, it is returned to the outdoor cage for additional training with targets. Normally, two or three exchanges between the two locations is sufficient to induce catching in the laboratory. Once they have started catching, the Eptesicus thus far trained, have tended to become stable and reliable catchers.

Several different species of bats (e.g., Myotis, Pippistrels, Lasiurus) have also been released in the outdoor cage, with almost immediate initiation of spontaneous catching. Although training the bats to a stable flight pattern sometimes proves difficult in the cage, the transition to catching in the laboratory is relatively simple for these species.

(c) Observations of pursuit closer to natural conditions

Three factors appear to favor the occurrence or persistence of pursuits closer to those under natural conditions than to the pursuits noted under laboratory conditions. First, the greater space permits longer pursuits and greater freedom of maneuver. Second, the existence of large numbers of natural targets prevents complete stabilization in the approach paths usually prescribed in the laboratory; and third, the bats are often left to hunt on their own schedule rather than being immediately recaptured and returned to small cages, as is usually done in the laboratory. The outdoor cage thus forms an important link in efforts to bridge the gap between the rather artificial pursuits of laboratory conditions and the completely unrestricted conditions of out-of-doors. As an example of a prolonged pursuit recorded in the outdoor cage, see figure 1b(I) of ref 37, which illustrates the pulse repetition pattern of *Lasiurus borealis* during a prolonged pursuit. The sequence of 105 rapidly-repeated pulses is broken into several bursts--the final burst consisting of 52 pulses that occupy about a quarter of a second at a rate approaching 250 pps.

Although *Myotis lucifugus* tend to stay out of the swarms of insects that collect around the lights of the cage, *Eptesicus fuscus* commonly make a series of rapid passes to and fro through the swarms. To discover the significance of this behavior further observations will be required.

(d) Increased longevity

No systematic effort has yet been made to evaluate the effect of the outdoor cage on longevity. Any such efforts would involve many more aspects of a bat's activities (e.g., hibernation conditions) than have thus far been attempted. Intermittent use of the outdoor cage does, however, appear to keep the bats in better general shape than those that are kept in small cages. More comprehensive studies should eventually be carried out.

C. Field Observations

1. Introductory Comment

The present field observations of chief interest are those relating to the fishing bat Pizonyx vivesi. This bat, a vespertilionid related to the Myotis (ref 34), lives on islands and along the shores of the Gulf of California and--like the other investigated fishing species Noctillio leporinus-- possess strikingly developed claws on its hind feet for the capture of small marine creatures (ref 10). Two important sets of observations on this bat are: (1) that by Reeder and Norris (ref 27), and (2) by Suthers (ref 32). Few details are known about the feeding habits of the bat because of its remote location and its failure, thus far, to capture prey under captive conditions. However, specimens have been observed fishing in the vicinity of shrimp boats, where small marine creatures were at the surface. The remains of small fish (about 3 cm in length) have been found at some roosts by H. Baldwin and others. The following excerpts from Reeder and Norris (Ref 27) cite certain of the few observations that have been made on the feeding of this bat.

> p. 85: "As they circled in flight, the bats periodically curled their long tails downward and forward and momentarily dipped them into the water, not rhythmically, but at irregular intervals of several seconds. One bat flew over the water holding a shining little fish in its hind feet. The stomachs of the two bats that were killed were filled with small crustacea. There was no noticeable concentration of such invertebrates in the water on this night, though a light suspended in the water attracted considerable numbers of small atherinid fishes (Atherinops affinis) and small anchovies (Engraulis mordax). George A. Bartholomew examined the stomachs of three bats captured at Puerto Refugio, Angel de la Guarda Island. Two were empty and the third contained many fragments of insects."
>
> p. 86: "....The irregularity of fishing movements suggests that these bats received some sensory cue from their prey and that capture is not the result of random dipping. It is interesting that these bats also catch insects, in view of the probability that methods used are different from those employed to catch fishes and crustacea."

By and large, so little is known about the details of Pizonyx hunting that systematic attempts to get proper instrumentation to the feeding sites is in order.

The study of Pizonyx is of interest for several reasons. For example, considerable interest attaches to the specializations of signal and technique that go with adaptation of this mostly insect-catching genus to hunting at the surface of the water. Moreover, the great paucity of knowledge, relative to that of Noctillio, makes comparative pursuit studies of these different fish catchers (such as we have attempted for insect-catching bats) impossible until the hunting behavior and associated signals of Pizonyx have been more extensively studied. Its apparently symbiotic roosting, in rock crevices, with petrels (ref 34,44) raises a number of questions of ecology and possible inter-class communication or guidance relations. The evidence that the bat ingests insects leads to the question of whether or not it is a dual hunter--both insectivorous and piscivorous--rather than being purely a hunter of marine surface creatures.

Since increasing commercial development of the Gulf area threatens the balance of inhabiting fauna--possibly leading to the extinction of some--we have been anxious to obtain additional data on Pizonyx before major shifts of ecological structure interfere with its pattern of existence.

Our records have been limited to 35 mm flash photographs made at the roosting areas and recordings of pulse repetition rates made in the vicinity of the roosting sites and at the water areas where a few of the bats were hunting. Lack of portable high-fidelity recording equipment has made it impossible to obtain detailed pulse records at either location. A few high-fidelity recordings were made of bats flying in the laboratory at Cambridge, Massachusetts. However, we were unable to train the bats to come to a specific zone for multiple flash pictures and hence our photographic records are very limited. Better instrumentation and further search for high-density hunting areas will clearly be required if adequate records of the hunting behavior of these bats are to be obtained.

2. Observations

Pulse repetition patterns have been observed, with varying degrees of specificity, in connection with what appeared to be several distinctive types of activity. The following notes deal with the observations and associated inferences. At least partial information was obtained on five categories of activity. These were as follows:

(1) While remaining, after dark, in the daytime roosts; also during cage tests with simulated roosts;

(2) on the way to nighttime hunting areas, just after leaving roosts;

(3) while flying low over the water, occasionally appearing to touch the surface with hind feet, tail or wingtip;

(4) while apparently flying some distance above the surface and emitting pursuit-type signals, and,

(5) while flying in outdoor cage or laboratory flight space.

(1) Our first set of observations was at the joint roosting sites of <u>Pizonyx</u> and least petrels (along with a few black petresl) at Partida Island. The chief observation here was the prominent barrage of clicks emitted by bats remaining in the roosts, just after dark, while petrels were flying about over the roosts. Ornithologists had noted that during nesting season one of a pair of petrels would hunt food by day and the other by night--the exchange of mates being carried out just after dark and at dawn (see ref 38, pp. 640-642; also ref 1 and 2 cited in ref 38). Identification of its specific roosting location by each bird was supposedly achieved through identifying calls by the mate in the roost. However, it seemed possible that the clicks emitted by the bats--if audible to the birds--might also provide localizing information.

That some relation appeared to exist between the density of bat clicks and the number of birds flying over the roosts was evidenced by two sets of observations: First, one of our visits to the roosting location was made in sufficiently bright moonlight so that the birds were clearly visible while we were recording the ultrasonic clicks of the bats in the roosts. Although the correspondence was not absolute, there appeared to be a significant proportion of incidences where the appearance of birds was accompanied by an increase in the amount of clicking by the bats. Second, during a subsequent visit the birds had migrated from the Partida site, leaving only the bats at the roosts. In this situation, there was no clicking by the bats in the roosts--except for a few spasmodic clicks shortly before they emerged and flew away.

These tentative lines of evidence suggesting a relation between the flight of petrels over the roosts and the amount of clicking by the bats gave no indication as to the nature of the causal relations. One hypothesis, the "guidance hypothesis," was that the returning birds emitted weak ultrasonic clicks which induced a loud transponder-like clicking on the part of the bats. The birds were therefore tested for the emission of ultrasonic clicks. During flights in a confined dark space in the laboratory no such clicks were detectable, yet such an artificial test did not exclude the possibility of clicking under natural conditions. Moreover, it was noted that when apparently cleaning their beaks after eating, the petrels often did emit rather sharp clicks of relatively low intensity which contained distinctive components in the 20 kHz region. The guidance hypothesis did not, therefore, run counter to existing evidence (with the exception that no data were obtained to show that the birds could hear the clicks of the bats).

One collateral observation of possible relevance to the guidance hypothesis pertained to the capacity of the bats to locate their specific roosts. Bats were removed from their roosting sites and carried some distance away--leaving the roosts empty--then released. Under these conditions they appeared to have no difficulty locating their specific roosting site, even though the configuration of the roost entrance had been disturbed during removal of rocks to obtain the bats. Unfortunately, corresponding tests were not made with the birds.[12]

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[12] A further speculation regarding a possible symbiotic relation between the two sets of creatures was with respect to food location. It seemed possible that either the birds or the bats might be better able to locate marine food--for example, with the use of olfaction--and that the one might profit from the special sensibility of the other. One observation of some interest in connection with the location of food concerned the appearance of bats in the near vicinity of a finback whale. Because of the large discrepancy between the very small numbers of bats found hunting in the vicinity of the island and the relatively large numbers of inhabiting bats, question arose as to where the bats went to hunt and how they located small surface creatures at a distance. One obvious possibility was that since the blowing of whales could often be heard at a distance of a mile or more by human listeners (and that the sounds undoubtedly contained components within the audible range of the bats), the bats might use the blowing of whales for guidance to a likely source of food. One night when no Pizonyx could be located hunting in the near vicinity of the island, a finback whale was located (by

In order to make further observations on the clicking sounds made by bats on the ground, a simulated roost (a small pile of rocks with crevices) was placed inside the cage at Tucson. When the bats crawled about exploring the roost, they made the same clicking sounds as had been recorded at the natural sites. This observation suggested that the clicking might be related to various kinds of disturbances, of which the activity of nearby birds was apparently one.

(2) In the central section of Partida Island, a small valley leads up toward the main peak. The rock slide where most of the observations were made is on one side, only a few hundred feet in from the shore. Some distance further up the valley is a more extensive rock slide where some hundreds of Pizonyx roost. Bats leaving the upper site commonly pass over the lower site at elevations that probably range mostly from about 10 to 30 meters. It is thus possible to record the cruising pulses of the bats as they pass over. As is typical of most cruising pulses, these pulses are of relatively slow repetition rate, and are fairly regular.

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its intermittent blowing) near a small adjacent island. One or more bats were found to be hunting in the immediate vicinity of the whale. This observation, though suggestive, was in no way conclusive--in part because it was a single observation and in part because the bats might have independently located the high concentration of surface krill (on which both whale and bat were presumably feeding).

(3) A half-mile long lagoon on the north side of the island is frequently populated by several bats which appear to have two different modes of flight: surface flight and flight well above the surface. During the surface flights, the bats--often more than one, fairly close together--fly a few inches above the surface. They often fly this way for some time, making long sweeps over the surface of the lagoon. The search pulses here are of higher average repetition rate than the cruising pulses mentioned above. Moreover, there are intermittent bursts characterized by much faster, often rather irregular, repetition patterns. These are presumably associated with the detection of possible surface targets. Unfortunately, however, such targets were so widely separated in the lagoon that we obtained only one or two observations of surface touches, and were not able to observe or photograph the details.

(4) Because only two or three bats were hunting in a rather extensive area of search, we were seldom able to make visual observations of flight maneuvers. In one instance, we observed a bat that was flying perhaps 5 or 6 meters above the water make a sudden dive down close to the surface. Once or twice we heard (with the use of a Euphonics ultrasonic detector) what

sounded like typical vespertilionid pursuit buzzes. One of these appeared to come from a bat some distance above the surface. We thus suspected that the bats might be executing aerial insect pursuits as well as surface fishing.

(5) Some of the bats, brought back from the Gulf, flew readily in the outdoor cage at Tucson and also in the laboratory flight space. We were interested to note that the bats often deflected toward tossed targets in the laboratory. Although none were caught, the response of the bats suggested an inclination to pursue--thus lending additional substantiation to the impression that these bats do indeed carry out aerial pursuits as well as surface fishing. Pulse patterns during flights in the confined space of the cage or laboratory showed little difference from other vespertilionids tested. Rates increased with approach to a surface and often with the initiation of turns. Some difference in basic rates were noted with different individual bats. Our general impression is that, in normal aerial flight, pulse patterns did not differ significantly from those of various other vespertilionids. It was, however, noteworthy that pulse pairs--sometimes other pulse groupings--were often in distinct evidence.

3. Summary

(a) The fishing bat Pizonyx, although anatomically adapted for the capture of small marine animals at the surface of the water, appears also to retain the capacity to make captures of flying insects.

(b) The flight signals emitted by this bat resemble, for the most part, the signals of other vespertilionids. We did, however, note three characteristics of interest in the pizonyx signals: (1) the occurrence of irregular sequences of pulses, with bursts at relatively high repetition rates, while the bats were hunting over the surface of the water, (2) the intermittent preponderance of pulse pairs, sometimes other repetitive groupings, and (3) a relatively small amount of pulse-shortening with increase of pulse repetition rate.

(c) Some evidence suggests that when the bats remain in their rock-slide roosts after dark, they may emit clicks in some relation to the flight activity of petrels which share the same roosts.

(d) How the bats locate suitable hunting areas is not established. However, the only bats found hunting one night in the area around the roosting island were located in the immediate vicinity of a finback whale which was intermittently blowing as it foraged to and fro through a zone that was densely packed with krill.

SECTION VI

EQUIPMENT TRIGGER

A pulse repetition trigger has been designed by William F. Kelley of the Research Laboratory of Electronics, MIT, and constructed in large part by John Fairbanks of MIT. The trigger is designed to accept a certain number of pulses starting with a specified pulse interval and to transmit a trigger pulse, for the actuation of equipment, when the prescribed number of pulses occur. The chief purpose of the trigger is to make possible the use of specified average pulse repetition rates to activate cameras and recording mechanisms, on the one hand, and such experimental stimuli as masking noise, on the other.

Two situations where such a device is essential to the effective activation of equipment or stimuli are: (1) to trigger a source of masking noise at a prescribed phase of interception, and (2) to activate cameras in the field when a bat initiates pursuits of a natural target. Human reaction time is far too slow, in both of these instances, for useful activation of the equipment.

In its present form the trigger can be set to accept from 2 to 6 pulses, above a prescribed threshold and starting with an interval ranging from 5 to 99 milliseconds. Upon acceptance of a pulse, a blanking gate acts to exclude further acceptance for a specified time (usually 5 to 15 milliseconds), thus preventing the counting of spurious disturbances due to wall echoes, multiply-peaked pulses, etc., that may occur within an interval too short to represent a valid succeeding pulse in the situation under test. After transmission of the triggering pulse, the unit switches itself to "external reset" and will not trigger again until the reset switch has been activated.

The input to the unit is ordinarily derived from pulses received from an ultrasonic bat-pulse detector, normally operated in conjunction with a band-pass input filter. The pulses are amplified to the required level and applied at the input.

The present unit obviously takes no account of specific pulse pattern--for example, an accelerating as against an irregular or constant pulse rate. However, in the vespertilionid bats tested (see Section III) average pulse rates over a given interval have been found to define, to a relatively reliable degree, certain phases of a bat's response to a target. Thus, when flying in a clear space the bats seldom emit sequences of two or three pulses with less than 30-millisecond spacing unless they have detected a target which they intend to pursue, or at least to investigate. Active pursuit, with apparent intent to capture, or approach very closely, has normally been characterized by the initiation of a "terminal buzz": a sequence of brief pulses with spacings of less than 7 milliseconds. Two or three pulse spacings of 30 milliseconds or less can therefore be used as an indicator of the "approach phase" of pursuit, while two or three pulse spacings less than 7 milliseconds can be used as an indicator of the "terminal pursuit phase". Though refinements should eventually be incorporated, the present unit appears capable of more useful triggering of equipment than other methods thus far tested.

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13. ABSTRACT

Comparative pursuit studies carried out on three species (Myotis lucifugus, Eptesicus fuscus and Lasiurus borealis) revealed similar tactics of pursuit and capture in Myotis and Eptesicus. Detection and localization capacities of Eptesicus appeared equal to the other species, but discrimination between spheres and mealworms proved highly variable, and the capacity to capture small targets inferior. Though the measured pursuit signals of the three species had definable differences, the phases of pursuit exhibited common characteristics, adequate for real-time machine identification, and thus usable for pursuit-controlled triggering of stimuli or recording equipment. Echoes returned by objects discriminated by bats have been studied by oscilloscope and human listening. Due to the number of relatively nonfluctuating echoes from mealworms (projected into a sound field of ultrasonic pulses), other details must provide essential clues for the bats' observed discriminations. Human listeners could not discriminate clearly between echo categories clearly discriminated by bats, even with slow-down ratios up to 128X. Methods for accentuating significant echo properties are under development. Studies of the fishing bat Pizonyx vivesi suggest adaptation to both aerial pursuit and surface fishing. Symbiotic communication between these bats and the petrels that share the same roosts has been conjectured.

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