EXPERIMENTAL STUDIES ON TARGET DETECTION, EVALUATION AND INTERCEPTION BY ECHOLOCATING BATS

FREDERIC A. WEBSTER and OLIVER G. BRAZIER

SENSORY SYSTEMS LABORATORY

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FOREWORD

This study of the pursuit performance of echolocating bats was carried out under Contract AF 33(615)-1142, 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, Aerospace Medical Research Laboratories, Aerospace Medical Division, Wright-Patterson Air Force Base, Ohio. Work on the program was conducted between 1 May 1964 and 20 February 1965. The research was carried out by Frederic A. Webster, principal investigator, and Oliver G. Brazier in Cambridge, Massachusetts. Included are some findings from investigations initiated under a subcontract with M.I.T. Lincoln Laboratory.

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This technical report has been reviewed and is approved.

J. W. HEIM, PhD
Technical Director
Biophysics Laboratory
Aerospace Medical Research Laboratories

ABSTRACT

The echolocation techniques of bats provide functioning models with useful attributes: versatility of application, ultra-miniaturization of components, and processing methods capable of dealing rapidly and reliably with complex echo indications despite the inherent slowness of unit neural components. Present experiments, carried out on captive bats trained to catch natural and artificial targets projected into their flight paths, have quantified certain basic measures of performance. Spheres as small as 1/16 inch diameter were detected and localized at two or more feet, with resulting interceptions being accomplished in 1/4 second. Final localization accuracies of 1 cubic centimeter were sometimes achieved, even when resolution of up to 16 nearby targets was required. Massive or complex clutter backgrounds tended to reduce interception performance at short target-to-clutter distances, but some interceptions were accurately completed during actual contact with natural twigs or foliage; or when pursuit paths had to be radically adapted to background configurations. Interception scores for food targets sometimes exceeded 99% while like-sized negative targets of a different shape could be correctly discriminated roughly 95% of the time. Failure to make proper evaluation of trajectories tended to produce extensions of the terminal pursuit signal; but such modifications were not significantly increased in most clutter situations.

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SECTION I

GENERAL INTRODUCTION

Present studies are the outgrowth of investigations originally undertaken in collaboration with D. R. Griffin at Harvard University in 1958. The chief intent of the initial investigations was to develop methods which would permit accurate observations of the interception performance of echolocating bats and to discover essential details of the techniques used (Refs. 17 & 40). Included also is a brief survey of factors influencing the initiation and termination of pursuit.

Because the initial observations gave evidence of a precise and rapidly-acting system, and one that seemed capable at times of making effective predictions of maneuvering targets, M.I.T. Lincoln Laboratory undertook further sponsorship on a subcontract basis. Important foci of interest during this phase were as follows:

1) Further development of instrumentation for the observation of the actions and signals of bats (Refs. 3 & 23).

2) Experimental determination of the capacity of bats to identify and distinguish between different kinds of airborne objects approximating the size of natural targets (Refs. 14, 38 & 39).

3) Definition of sample relations between emitted signal and target pursuit, including more adequate descriptions of the signals themselves (Refs. 4, 5, 37, 38 & 39).[1]

4) Extension of the observations on interception techniques including observations on bats other than _Myotis_ _lucifugus_ (Refs. 38 & 39).

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[1] Studies of insect pursuit by non-vespertilionid bats have been carried out in the laboratory of A. Novick at Yale University, (Novick, A., "Pulse Duration in the Echolocation of Insects by the Bat _Pteronotus_", _Ergebnisse Biol._, _26_, pp 21-26, 1963; Novick, A., "Education of Flying Insects by the Bat _Chilonycteris psilotis_", _Biol. Bul._, _128_, pp 297-314, 1965; Novick, A. and Vaisnys, J. R., "Echolocation of Flying Insects by the Bat _Chilonycteris parnellii_", _Biol. Bul._, _127_, pp 478-488, 1964).

5) Collateral observations on action and signals associated with other activities than target pursuit (Refs. 13a & 39).[2]

Radical curtailment of the general research program at M.I.T. Lincoln Laboratory terminated the sponsorship in 1963 while most of these studies were still in progress.

The current program was designed to continue the investigations left incomplete at the termination of M.I.T. Lincoln Laboratory sponsorship and to extend the scope of the studies toward the eventual derivation of models which usefully formulated the echolocation procedures used by bats during the detection, evaluation and interception of airborne targets.

The first phase of this program was to attempt more complete definition of the full scope of the bats' system capabilities during pursuit. Such performance measures were to include evaluations of: true detection distances, localization accuracies (and precision of interception guidance, including prediction capabilities), quickness of response and speed of action, reliability of performance, versatility of application to a variety of interception problems, description of some of the diversity of methods used by different kinds of echolocating bats, discovery of the bats' capacities to deal with competing clutter echoes and with the constraints imposed by surrounding configurations, analysis of the types of interference introduced by different categories of interferring noise.

The second phase would attempt a useful analysis of the information-bearing properties of the emitted signals - particularly with respect to transformations produced by objects returning echoes. Relations to other processing systems, such as the human auditory system, were to be examined.

The third phase would attempt a synthesis of findings from performance measures, theoretical analysis and neurophysiological

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[2] Most of the investigations on aspects of the bat's system unrelated to target interception have been carried out in the laboratory of D. R. Griffin at Harvard University. These have included: 1) obstacle avoidance in the presence of noise (Ref. 16), and 2) studies of neurophysiological response to auditory stimulation (Refs. 18 & 35) also: Suga, N., "Recovery Cycles and Responses to Frequency Modulated Tone Pulses in Auditory Neurons of Echolocating Bats", J., Physiol. 175, pp 50-80, 1964 and, 3) investigations of bats other than vespertilionids (Ref. 13, also Suthers, R. A., "Acoustic Orientation by Fish-Catching Bats", J. Exp. Zool., 158, pp 319-348, 1965).

studies in an effort to formulate useful models of the important operating details of the bat's echolocating systems with particular reference to interception guidance and control guidance in general.

The material presented in this report is limited to aspects of the first phase. It forms part of the essential quantitative foundation on which any comprehensive undertaking of the bat's echolocating skills must rest.

SECTION II

DETECTION AND LOCALIZATION OF AIRBORNE TARGETS AND OTHER OBJECTS

This section on the detection and localization of airborne objects presents observations made during a considerable number of tests over the past 2 or 3 years. For the most part, these tests had one of the following primary objectives: 1) discovery of the bats' methods of pursuit and capture, 2) evaluation of the capacity of bats to identify and discriminate airborne objects, and 3) determination of the levels of interception performance in the presence of clutter. From roughly 5,000 multiple flash photographs, and perhaps 1,000 high-speed tape recordings, we have selected samples which illustrate certain relevant features of the response of bats to airborne objects. These samples relate chiefly to: distance of detection, accuracy of localization, evaluation of trajectory, reliability of capture, and some of the techniques used by bats in dealing with a variety of interception problems. Included also is a brief survey of factors influencing the initiation and termination of pursuit.

A. Detection of Small Spheres

Two lines of evidence indicate that some of our bats could detect and localize a vertically projected sphere of 1/16 inch diameter[3] at distances of 2 feet or more. The evidence comes in part from multiple flash photographs of bat and target, and in part from recordings of the emitted signals.

Multiple flash pictures typically provide indications of flight path maneuver, of head aim and sometimes of mouth action. When a bat detects an object of interest, it normally turns its head toward the object; and if it decides on further exploration, it directs its flight path either toward the object or toward where it expects the object to go. Decision to avoid a detected object frequently produces a momentary closure of the mouth and some degree of flight path deflection. Often, however, the shift of flight path is too slight for reliable observation.

Evidence of detection in the emitted signals is commonly

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[3] English system for measures is used here since the target spheres are commercial items fabricated in successive thirty-secondth inch sizes.

quite definitive for objects at close range. For example, when a bat detects an object a few feet ahead, it characteristically increases its pulse repetition rate. If, however, the object is immediately recognized as inedible and out of line with the intended flight path, the increase may be almost imperceptible. Objects that require maneuvering for avoidance, and objects that are judged to be edible targets, produce a definite rise in the repetition rate of the emitted pulses. With targets that are pursued, the rate tends to increase progressively and to end in a rapid sequence of brief pulses (the terminal buzz) just before the catch or final attempt. As will be discussed more fully below, objects that come within range of detection at greater distances may produce no detectable change in the emitted signal; yet the bat often appears cognizant of their presence.

Figures 1a and 1b show two different species of bat (Myotis lucifugus and Lasiurus borealis) catching a 1/16 inch sphere. Although the initiation of pursuit was outside the photographic field, the bats had obviously not only detected and localized the target while it was still 1-1/2 to 2 feet away, but were already following it at about that distance.

The evidence from analysis of the pulse repetition patterns of the emitted signal leads to similar conclusions. In one target discrimination test, for example, a bat (Myotis lucifugus) caught or hit four of the first five 1/16 inch spheres presented. The remaining six sphere presentations during this test produced little or no evidence of detection. Pulse pattern envelopes for the four approaches leading to target contacts were compared with the envelopes where no detection was evident (Fig. 2). If we assume that contact with the targets was made at the end of the terminal buzz (Fig. 36), we find that the divergence of the two sets of patterns occurs at least 200 milliseconds prior to the point of catch or hit. Since the flight speed of this bat was roughly 10 feet per second, and since detection must have taken place prior to the pulse-rate increase, it is safe to assume that detection had occurred by at least 2 feet from the point of contact. Of course, when the bat follows a target upwards, as in Figure 1, the target is relatively nearer to the bat at the point of detection than is suggested by the observed point of catch. In two of the present instances the bat followed the target slightly upward and, in the other two, the target came up toward the bat. Hence, on the average, no such correction was needed.

From both lines of evidence - photographic observation and signal analysis - we can safely conclude that a bat is capable of detecting and localizing a 1/16 inch sphere at a distance of at least 2 feet. To have achieved the localization, of course, detection must actually have taken place earlier. Current data are inadequate to say how much earlier, but our guess would be of the order of a tenth of a second, or a foot of flight distance. Determination of actual maximum distance of detection, and the echo strengths returned by such small objects at these maximum distances, will require further tests.

B. Detection as a Function of Target Size

Many experiments have demonstrated that a definite and progressive rise in pulse repetition rate is a reliable indicator that detection of an object ahead has taken place (Refs. 7, 11, 37). In experiments on the avoidance of wires, Grinnell and Griffin (Ref. 19) showed that fine wires were detected only at relatively close range (eg. 7 mil wires at roughly 1 to 4 feet), while wires of 3-1/2 times the diameter gave evidence of detection at about twice this range (ie, 26-1/2 mil wires were detected at roughly 2 to 8 feet). But with increasing wire size beyond this, the distance at which the bat increased its pulse rate no longer followed the increase in echo strength. For wires of 120 mils (4-1/2 times the previous diameter) the distances at which definite pulse changes occurred ranged from about 2 to 9-1/2 feet (averaging about 6 feet).

In these experiments the large variabilities in apparent range of detection from flight to flight, and the almost complete cessation of increasing distances of response with increasing size of obstacles, raised considerable question about the validity of pulse-rate changes as an indicator of initial detection. It seemed likely that the bat became cognizant of the objects but gave no overt evidence.

Our experiments with the smaller sizes of spheres produced rather similar findings to those of Grinnell & Griffin with small sizes of wire. Figures 3a and 3b, for example, compare the pulse pattern envelopes for two sphere sizes. The envelope for the 1/16 inch sphere is that presented in the previous section. The no-detection envelopes with this sphere are then compared with the pursuit envelopes for spheres of 1/8 inch and 5/16 inch diameters. When the time plots are converted to approximate distances, the definite pulse change associated with pursuit moves out from about 2 feet, for the 1/16 inch sphere, to 3 or 3-1/2 feet for the 1/8 inch sphere. Thereafter, however, the point of pulse-change virtually ceases to move out further as the size of the target spheres is increased.

The present findings with target pursuit thus raise the same question as did those of Grinnell and Griffin for obstacle avoidance: Did the bats detect objects of increasing size at increasing distance, yet give no evidence of such detection, or did they simply fail to detect the object? It would be reasonable to assume that somewhere in the course of early, low-level processing of echoes the bats' analytical system incorporated a range gate or time gate that was normally set to exclude, from further processing, all echoes beyond a certain time interval after the emitted pulse. The bats would then be spared the job of paying attention to a lot of items which did not call for action. A number of observations even suggest that such "attention gates" may sometimes be completely closed. For example, when an obstacle is suddenly introduced into a flight space that has long been unobstructed, a bat may fly straight into the obstacle with no apparent indication of detection. Thus, one bat long accustomed to flying without obstacles in our flight room, flew directly into a volley ball the first time it was tossed into the flight path.

On the other side of the ledger, however, are instances where bats turned away from unexpected moving objects at distances far greater than was evidenced by changes in their pulse rates. In one set of tests, we intermittently replaced our standard targets with a 9 inch sphere (volley ball) which was tossed up as the bat started its approach 10 or 12 feet from the target zone. Contrary to its usual behavior, the bat often turned away; yet we were usually unable to detect any shift of pulse pattern. During outdoor tests, moreover, bats have sometimes appeared to turn towards certain targets at distances as great as 25 feet. Currently, therefore, we cannot specify the distances at which initial detection actually takes place. We suspect that it may sometimes be further than measures of pulse-rate increase have suggested. Systematic outdoor tests will have to be carried out before any upper bounds can be assigned to a bat's true range of detection.

C. Localization and Trajectory Evaluation

1. Localization Accuracy

For objects at some distance from a bat, localization accuracy, at least in terms of elevation and azimuth relative to the bat, can sometimes be judged with reasonable accuracy from photographs. Furthermore, at close range, localization in three dimensions can often be judged to within fractions of an inch by noting the final precision of aim achieved with the flight membranes used to accomplish catches (Refs. 38, 39 & 40). Accuracy of range evaluation at a distance can be judged only indirectly by analyzing predictive trajectory evaluation. This will not be dealt with in the present discussion.

Accuracy of localization in elevation and azimuth is best judged when both bat and target are in a plane approximately at right angles to the line from camera to bat, and when the bat is seen either directly from the side or directly from overhead. Under these conditions, the accuracy with which an observer can judge the aim of a bat's echolocation system (mouth and ears) in a photograph is readily susceptible to test. For example, a second person can cover the actual target and move a test object until the observer says it is where the target ought to be. Angles to the bat from the actual target and the test target are then compared. To a rough approximateion, such tests indicate that an observer can commonly judge the head aim of Myotis lucifugus to about ±5°. Since the bat's errors and the human errors are compounded, the bat's actual accuracy of aim must be at least as good as this.

A striking feature of the head aim of Myotis lucifugus is the quickness and precision with which maneuvering targets appear to be followed in both elevation and azimuth (see, for example, Fig. 31 of Ref. 38). This holds true, at least, until the target is within a few inches. At very close range, head following often ceases and the bat appears to continue its catch maneuver by dead reckoning (see eg. Fig. 4). Our few observations with a totally different family of bats, Rhinolophus ferrum-equinum, suggest that these bats are also capable of quick and accurate head following (Ref. 38). Such detailed following with the head, however, does not appear characteristic of all bats. Red bats, for example, seem able to evaluate the position of a maneuvering target without the specific head following that is typically noted with Myotis lucifugus.

The final accuracy of aim achieved by bats is sometimes remarkable. Bats will often strike a number of ballistic targets in succession within a quarter of an inch of the center line of the tail membrane. When reaching with a wingtip, the very tip of the wing is often bent over to form a catching shelf or groove about half an inch square. A descending or ascending target is sometimes accurately seized on this small shelf. Figure 24 of Reference 38 illustrates this well. Our present Figure 4 shows a rather rapidly falling target about to be stopped in the bent-over tip. Figure 15, mentioned later under multiple target selection, shows an accurate separation of one target from another with the tail membrane. Likewise, Figure 6b from a high-speed film shows the separation of one target from a nearby one with the use of a wingtip. Since the bat's localization must be at least as good as the accuracy of physical aim, it is clear that bats are sometimes capable of achieving localization accuracies of the order of 1 cubic centimeter, or at least to within a zone represented by a sphere of half-inch diameter.

2. Trajectory Evaluation

Relative to observed accuracies of localization in angle, the accuracies of trajectory evaluation, as exhibited by the flight paths of the bats with respect to a target, show vastly greater variability and often strong components of learning. In the laboratory, bats commonly keep their heads accurately directed at a target though the aim of their flight path may be in such error that they are unable to complete the intended interception. The observed error often appears related to obvious features such as acceleration, high velocity or curvature of the target trajectory. Both the variability of such errors from bat to bat and from situation to situation gives evidence that other factors are often important. For example, red bats (*Lasiurus borealis*) appear much less prone to errors in evaluating vertical velocity and acceleration. We suspect that wingbeat may play a role in the evaluations made by big brown bats (*Eptisicus fuscus*). The little brown bat (*Myotis lucifugus*) seems remarkably proficient at judging the courses taken by small insects. Particular conditions (eg., motivation, perhaps external temperature, etc.) and surrounding configurations (particularly those which constrain the bat's flight path) also modify proficiencies of trajectory evaluation. In addition, conditions imposed by the laboratory modify the natural propensities of bats. Most bats, for example, tend to reduce their average flight speed and to make less vigorous pursuits as they adapt to laboratory conditions.

Perhaps the commonest error exhibited by new bats, in their evaluation of trajectories under present conditions of testing, is a failure to appreciate the acceleration of gravity. This is almost universal in newly captured *Myotis lucifugus*, though generally far less noticeable with *Lasiurus borealis*. *Myotis lucifugus* will characteristically aim several inches above the point where a vertical ballistic target will be at the intended time of catch. Very often the bats go through their catch maneuver without touching the target (Ref. 6). With perhaps a week of experience, however, they normally learn to make the proper corrections and to fly an effective intercept course (Ref. 38). During the process of learning, catches are frequently made by reaching downward with a wing and seizing the target with (or near) the sharply bent-over tip of the wing (see Fig. 4). Presumably, *Myotis lucifugus* tend, in nature, to concentrate their catching more on small, level-flying insects, while *Lasiurus borealis* make frequent pursuits of rapidly diving moths. *Lasiurus* also use flight speeds 50% to 100% greater (probably up to 35 feet per second) than *Myotis*, and are also capable of greater acceleration.

Maneuvering targets present bats with some obviously difficult interception problems (Ref. 38). For example, moths which hear the orientation sounds of bats, typically initiate one or more of a variety of evasive tactics (Refs. 26, 27, 28, 30, 32, 33, 33a, & 38). While the bat is at some distance, the moths often turn away and thus reduce their reflectance to the bat's emitted signals (Refs. 28 & 30). At closer range, they initiate various sorts of loops, spirals, and dives - often with abrupt and apparently unpredictable transitions from one to another form of tactic. We have observed that red bats sometimes make extremely accurate predictions of a moth's future point during spiral evasion (see Ref. 38: Figs. 2, 3b & 30). Whether the bat makes specific predictions of the form of the spiral or whether it evaluates the average trajectory, and uses a probabilistic estimate of specific position, is not known. It is clear, however, that sudden shifts of tactic (Ref. 28, Fig. 3c), if correctly timed with respect to the bat's pursuit, commonly result in highly effective evasion by the moth.

Evaluation of trajectories under natural conditions are often complicated by sound-emission, and perhaps other actions, on the part of certain moths (Refs. 2, 7, 38 & 39). Bats often veer away from mothswhich appear to make ultrasonic clicks in response to the bat's orientation sounds. The exact mechanism of the action produced in a pursuing bat, however, remains unknown. Too weak to produce actual jamming, the moth's ultrasonic clicks might serve as warning signals or they might generate some deceptive effect, such as the phantom divergence of a nonexistent target from the real one. The slow reaction time of moths, as well as the lack of evidence for deception-inducing time relations, suggests that the moth's clicks serve as some kind of warning. We have recently noted, for example, that when moths are placed in a fine-meshed cage with bats, the bats are often extremely cautious about the angle from which they attack the moths. Here the bats do not apparently use echolocation, but listen to the wing-sounds of the moths. Frequently they spend considerable time making sure that their attack will come from behind or above. The bats apparently attempt to seize and paralyze the moths (by crushing the thorax) before the moths can grasp the bats with their claws[3]. Such seizure with claws or spurs has been observed to cause severe interference with a bat's flight. In flight as well as under caged conditions, bats may try to assure themselves of proper relative orientation to the moth prior to capture, and wrong orientation may cause the bat to relinguish pursuit. Whether such an evaluation by a bat is accomplished by use of echolocation or whether the emitted sounds of moths sometimes give warning of obnoxious attributes or a wrong orientation remains to be discovered. There is also the possibility that the clicks which deflect one kind of bat may attract another. The relations between the sounds (and other characteristics) of moths and the pursuit tactics of bats, are as yet far from unravelled.

D. Other Observations Relating to Target Detection and Localization

1. Reliability of Capture

In the past, two kinds of observations have provided figures on the percentage of attempts on targets which resulted in

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[3] A. E. Treat (C.C.N.Y.): Personal communication

capture. One was inferential and the other direct. In an earlier study, for example, the number of fruit flies caught per unit time was approximated by weighing the bats before and after a given interval of pursuit; and this figure was compared with the number of pursuit "buzzes" which were heard by use of an accoustical monitor system or by ultrasonic recording (Refs. 17 & 23). Such comparisons lead us to the conclusion that the bats sometimes caught 90% or so of the flies they attempted.

When objects as large as mealworms were projected up into the flight-paths of bats, the results of the bats' pursuits could be directly observed with almost complete reliability. Marginal results could usually be evaluated with complete accuracy by observation of multiple flash pictures. During initial phases of familiarization with mealworm catching, the percent of targets caught sometimes ranged from zero to almost 100% (notably for red bats). After training, virtually all bats made good catch scores. In some instances, the levels achieved were impressive. During target discrimination tests one of our bats (a Myotis lucifugus) correctly selected and caught (or at least hit) 207 successive mealworms without a failure. During these tests, the timing of the experimenter was often far from perfect, and the bat sometimes had to made sudden dives or turnbacks to reach the targets. Such results indicate that under certain conditions, the interception proficiency of bats is extremely high.

Observations made in the field with moths that take evasive tactics have sometimes given quite a different picture (Ref. 33a). The maneuvering of moths sometimes presents interception problems of obviously great difficulty. We have also noted above that other considerations may cause the bat to relinquish pursuit deliberately. Because of these conflicting elements we cannot, at the moment, make a really adequate evaluation of a bat's true interception capabilities. We suspect that under many conditions the bats' interception skills are remarkably good, while under other conditions, the bats' problems are complicated by a variety of interfering elements which greatly reduce the reliability with which captures are achieved.

2. Speed of Localizing Performance

Since the interval between the images of our multiple flash pictures has been standardized at about ten per second, most of the observations on the localizing responses of bats are limited to this rather gross spacing. To some extent, however, we have been able to make collateral observations with the use of high-speed films (at 192, 384 and 768 frames per second) and with the aid of a signal-triggered strobe system. With this latter technique (see Appendix I) the strobe light is fired only when the bat emits a pulse. It is thus possible to follow the response to a target in terms of the bat's own echolocating pulses - with a small correction for the accoustical delay from bat to microphone.

Figures 5a and 5b illustrate very radical shifts of head aim between successive flashes. In Figure 5a, the bat appears to become suddenly aware of a moth coming down from overhead. Between the first two images there is a sideways turn and between the next two a sudden, and apparently accurate focus, on the overhead target[4]. In Figure 5b, the bat appears to become suddenly aware of a moth, roughly 90° to one side and about 18 inches away, which is flying into a mass of pine clutter. Between two successive tenth-second images, the bat appears to have made an accurate localization. From these and other like sequences, we believe it is safe to say that a bat can make accurate localizations of a target within a tenth-second interval. This is certainly in keeping with the rapid localizing action noted during pursuits of maneuvering moths (see, for example, Fig. 31 of Ref. 38).

More remarkable, perhaps, is the speed of the bats' physical action during the course of target capture. Figure 6a is a sequence made with the pulse-triggered strobe system, mentioned above. Here the tip of the wing was swept around in an arc of 6 or 7 inches, within about 22 milliseconds (roughly 1/45 second) to reach the precise point required for the capture of a falling mealworm.

3. Initiation and Termination of Pursuit

Whether or not bats pursue airborne objects they have detected depends on a number of factors, some of which are not specific to the objects themselves. Most obvious of the more general essentials, perhaps, are motivation and preparedness (or "set"). Even if a bat is motivated by hunger, it may pay no attention to insects along its path while it is headed for water - often a more primary need. The bat's state of alertness is also important. A torpid or tired bat will often not undertake pursuit. Moreover, a number of situations inhibit catching behavior even when the normal requirements for pursuit appear to be met. New or artificial situations, such as the laboratory flight space, often completely inhibit a bat's propensity to catch. An unpleasant experience with an obnoxious target may cause a bat to desist from all catching for some time. A bat's pursuit performance cannot be properly evaluated, in other words, unless the required conditions are suitably met.

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[4] A discussion of vertical localization is given in Ref. 1.

Important features which are specific to airborne objects themselves are discussed elsewhere (see Section II on Target Discrimination); hence, the present survey can be brief. The most immediately apparent feature is echo magnitude relative to distance. Objects giving faint echoes within normal ranges of detection very commonly induce pursuit, unless they are too small for adequate detection. By contrast, objects giving strong echoes at some distance are interpreted as obstacles and avoided. However, neither the echo magnitude nor the proclivity for pursuit is directly related to the physical size of the objects. For example, a hard-surfaced ping-pong ball (of 1-1/2 inch diameter) returns a relatively large echo from a bat pulse, while a soft-surfaced tennis ball (of 2-3/4 inch diameter) returns a relatively weak one. Ping-pong balls are seldom pursued, whereas tennis balls are quite frequently pursued and sometimes caught (Figs. 6c & 6d). It is also possible, of course, that the texture itself produces specific echo properties tending to induce pursuit.

Another feature which sometimes appears related to pursuit is wing-action, or perhaps flight-path. The wingbeat rates of insects commonly sought by bats probably range, for the most part, from about 20 to several hundred - with the wingbeat often producing marked shifts of echo reflectance within the span of a single bat pulse (Ref. 29). The nature of an insect's flight-path may also sometimes play a role in the initiation of pursuit.

The influence of passive listening on pursuits by bats remains only partially defined. An earlier study (Ref. 17) showed that - on the average - the rate at which bats caught fruit flies was not reduced when the flight sounds of the flies were completely masked by low frequency noise. At the same time, in the absence of masking noise, one of the bats in this study would often hang silently on a wall and await the hum of a passing fruit fly before emitting pulses and taking off in pursuit. Bats also appear at times to be attracted by the buzzing of insects in locations where echolocation cannot be used; they appear also drawn to areas containing insects by the hunting sounds of other bats. It thus seems probable that bats may often be drawn to the general location of insects by the use of passive listening; though actual pursuit - at least at close range - is presumably always guided by echolocation.

Not every pursuit undertaken by a bat leads to a capture or even to a serious attempt (see Sections II & III of the present report). Intensity of pursuit, and hence probability of capture of difficult targets, tends to fall off as a bat becomes satiated, tired or uncertain about the outcome of pursuit. Failure to complete pursuits often occurs when a target is recognized as inedible or obnoxious, or when the target's trajectory is too violent or is improperly evaluated. In addition, a number of pursuits appear to be discontinued when a target approaches an obstacle or clutter region too closely. The proportion of pursuits successfully completed varies over a wide range according to existing conditions.

It is important to note that the execution of an interception to the point of target contact is not synonimous with completed capture. Many targets are merely touched or hit while others are briefly retained and then rejected. In some cases, the failure to capture or retain is due to errors in inadequacy of technique by the bat. In other cases, however, the action appears to be deliberate (see eg. Appendix II). It seems likely also that bats may sometimes make use of tactile or olfactory evaluation prior to seizure with the mouth. Some insects, moreover, may emit warning sounds upon contact. Failure to retain clearly does not always indicate an "error" on the bat's part.

SECTION III

IDENTIFICATION AND DISCRIMINATION OF AIRBORNE OBJECTS

A. Introduction

Reasons of safety and economy suggest that a bat should be able to differentiate, by use of echolocation, between important categories of objects it encounters in flight. For example, the tips of small twigs must often give echoes which correspond in magnitude to the echoes of insects. Yet in the course of outdoor observations we had noted that bats made apparent catches of small insects close to the needles and twigs of evergreens. Were they unable to distinguish between the two, it seems likely that they might spend their time trying to catch the more numerous needles and twigs at the expense of insects. Likewise, maple "spinners" and falling leaves or petals must produce echoes corresponding in magnitude to those from moths - and they are sometimes more plentiful. It had thus seemed likely, from the outset of the studies, that bats could distinguish insects from other small objects they might encounter in flight.

Initial observations in the laboratory appeared to contradict this view. After being trained to catch mealworms projected up into the laboratory flight space, the bats seemed eager to attempt captures of almost any object - moving or stationary - provided that the portion they encountered was not too large. The bats attempted to seize: the upper tip of a 3/8 inch tube used for holding lights, two-inch lengths of chalk, metal washers, dead hornets, and small objects (such as 1/16 inch spheres) if close enough for adequate detection. Such indiscriminate catching, however, might simply be the result of the immediate laboratory situation. The bats' entire laboratory experience had been one of consistent positive reinforcement, where every airborne target had been edible. At the same time, Griffin (Ref. 10) had also found in earlier tests with wild Eptesicus fuscus in the field, that the bats would pursue small inedible objects tossed to them. Unfortunately, the outcome had not been discernible, and the question of whether final discrimination was made remained unanswered. To what extent acoustical recognition of objects might actually be achieved clearly needed systematic evaluation.

Simplest of the echo features, available to a bat for rough discrimination purposes, is the echo magnitude of an object relative to its distance; and the simplest test object which produces constant reflective properties, regardless of orientation, is a sphere. For this reason, spheres were used in the first set of discrimination tests.

Before any tests were actually carried out, however, certain constraining influences were recognized. First, at the upper end of the size range, all objects above a certain magnitude of reflectance would clearly be interpreted as obstacles and avoided. Second, at the lower end, objects too small for adequate detection would never be caught. Third, if simple echo magnitude (as a function of distance) were the basis of selection, a zone of confusion would exist whenever the echo magnitude of a sphere (negative target) overlapped the average echo magnitude of the positive targets which the bats were trying to catch. By contrast, if features other than average echo magnitude were the sole determinants of identification, no zone of confusion would be expected once the bats were familiar with the test situation.

In the first set of tests, the positive targets were mealworms (roughly 3/32 x 1/16 x 3/4 inches in size, Fig. 7), and the negative targets were spheres ranging in diameter from 1/32 to 1-1/2 inches. Presentation was sequential: either a mealworm or a sphere, but not both, being projected upward into the path of the bat as it approached the target zone. Sometimes the targets were tossed by hand and sometimes they were fired from the solenoid-driven "gun" described elsewhere (Ref. 38). Most tests consisted of 20 presentations: 10 of mealworms and 10 of spheres, with a number of different random sequences being used for the different tests. During a given test, only one size of sphere was used. The order in which the spheres of different sizes were introduced was not random: larger sizes predominating in the early runs. This ordering had been based on the supposition that early familiarity with the larger sizes would more rapidly acquaint the bat with the fact that the spheres were inedible, and hence negative targets, rather than potentially positive ones.

Results of the first series of tests were reported previously (Ref. 39), but should be reviewed briefly since they dictated the course of further tests to be reported below. With two exceptions - the downward extension of the error curve for spheres and the suddenness of improvement seen in one or two of the bats - the results were much as predicted. The general findings for all bats on all tests (involving over 1600 presentations) are given in Figure 8, based on Figure 6 of Reference 39. This overall set of curves illustrates two features. First, although large targets were discriminated best, the bats gave definite evidence of discriminating spheres from mealworms in the region where the average echo magnitude from a mealworm overlapped the magnitude of echoes from spheres: only about 30% of the spheres in the main zone of overlap being hit, as against 94% hits or catches for the mealworms. The zone of echo overlap was not precisely determined, but rough measures with artificial bat pulses had indicated that it might cover roughly the range represented by spheres of 3/16 to 3/8 inches diameters). Second, the errors of discrimination were not limited to the zone of overlap, but extended downward and showed a secondary maximum when the negative target was a sphere of about 1/8 inch diameter. These overall curves did not, however, tell the whole story and certain further findings of significance should be noted.

Two additional findings of interest concerned: 1) the effects of training and 2) the differences between bats. Figure 9 (based on Fig. 7 of Ref. 39) shows the results for four experimental bats on the first set of tests as against a final set of tests. This figure indicates that the bats initially tended to catch spheres of all readily detectable sizes within the limits indicated. Experience reduced the erroneous catches of spheres to a level of only 7%. With at least one bat, the shift from a predominance of errors to virtually no errors was almost instantaneous: as if the bat - though previously capable of discriminating the spheres - only belatedly became cognizant of the experimental situation. With most bats a small residual of errors tended to persist, the error zone being centered in the region where echo magnitudes of the spheres were suspected of being closest to the average reflectance magnitude of the mealworms.

Differences between individual bats were also striking. Figure 10 (based on Fig. 9 or Ref. 39) shows the initial curves for the best and worst of the four bats. While the worst bat at first seemed capable of very little discrimination between spheres and mealworms in the region of echo overlap, the best bat showed significant discrimination immediately and improved rapidly, even during the course of a given run. As implied in the previous paragraph, however, we sometimes suspected that such marked individual differences were more due to differences in appreciation of the experimental situation than to differences in echolocation skills as such.

The findings of the first series of tests still left a number of important questions unanswered. There was also the possibility that the early predominance of large spheres in the test sequences might have concentrated the errors (typical of early tests) in this region. Proper evaluation of the bats' capacity to discriminate targets of the present sort thus called for certain additional observations. These were as follows:

1) Sequential target discrimination tests with <u>one</u> size of sphere per run using a different ordering of sphere sizes from previous tests;

2) Sequential target discrimination tests with <u>all</u> sizes of sphere per run;

3) Simultaneous presentation of paired targets with one size of sphere per run;

4) Determination of the rough relation between shifts of signal pattern and target distance, with particular reference to distance of decision and target size;

5) Estimation of the relative echoes from mealworms and spheres of different sizes.

B. Sequential Target Discrimination Tests With One Size of Sphere Per Run

Sequential discrimination tests were carried out on two Myotis lucifugus using one size of sphere per test run. Eleven sizes of smooth spheres were used in all, the smallest being 1/16 inch diameter; the largest, 29/32 inch diameter. All eleven sizes were used in the first set of runs, but the size range of the second set was somewhat reduced. No further sequential tests were made with these bats. Test procedures were similar to those of the experiments already mentioned with three exceptions: 1) the ordering of the sphere sizes differed, 2) the target firings were almost exclusively from the mealworm gun (where previously most had been tossed by hand), and 3) more complete records (tape recordings and pictures) were obtained.

With the exception that one bat caught 4 out of the first 5 presentations of the 1/16 inch sphere (as against none for the other bat), the results for the two were essentially similar. Consequently, they have been combined and are given in Figure 11. The solid line shows the results for the first set of runs. By comparison with the previously reported tests, the error peak with the 1/8 inch sphere was accentuated with respect to errors in the overlap zone (eg. 3/16 - 3/8 inch spheres). Also, as already mentioned, one bat showed unusual initial propensity to catch very small spheres. Proficiency of mealworm catching was extremely good: one bat missing only 2 in 110; the other missing no mealworms in 110 presentations. Within the zone of overlap, the initial performance of these bats approximated the best of those previously tested: present error percentages lay between 20% and 30% as compared with the combined average of 60% to 80% for the previous bats.

The dotted line of Figure 11 gives the results for the second set of runs and shows there was an almost complete disappearance of the catches of small spheres. There was also a general reduction of errors, the largest error score being three hits of the 1/4 inch sphere by one of the bats. Performance scores with mealworms remained excellent, with only 1 mealworm being missed in

140 presentations.

C. Sequential Target Discrimination Tests With Mixed Sizes of Spheres Per Run

Two possibilities seemed likely in the responses of bats when presented with mixed sizes of spheres in a test. The first was that the selective ability of the bats might be viewed in terms of a "filter" set to detect the echo properties of mealworms to the exclusion of other objects; and the second was, in essence, that the bats would make separate evaluations of each single object detected. If the bats used some procedure akin to the first method, discrimination performance should not decrease significantly with increasing variety in the targets encountered; but if the bats attempted to make individual evaluations of each target, increased variety would present a more complex discrimination task - with corresponding likelihood of deterioration in performance.

Only three bats were available for the discrimination tests with mixed sizes of spheres. Two were the bats reported above which had already completed two sets of tests with a single size of sphere per test. The third bat was unfamiliar with the discrimination task. Recognizing that the data would necessarily be limited, we nevertheless thought it worthwhile to see how the findings might differ with different conditions of familiarization. The third bat, from the outset, was given the discrimination task involving mixed sizes of spheres. This was to permit comparison with the findings on bats which were previously trained to discriminate single sizes of spheres.

The bats previously trained with single sizes of spheres were given a total of 13 tests with mixed spheres. Combined results for the two bats are given in Figure 12. The results are obviously similar to those obtained on the second set of tests with single sizes of spheres. There was, in other words, no evidence that discriminating all sizes at a time was more difficult for these bats than was the job of discriminating each size in a separate test.

To permit comparison of the findings obtained on the third bat with those already cited, it was necessary to separate the familiarization tests from the tests which occurred after significant learning had taken place. Therefore, since only 8 tests in all were made with the third bat, they were divided into two groups of four, as illustrated in Figure 13. Although the numbers are too meager for anything but the most general conclusions, it is clear that the first 4 tests with mixed sphere sizes gave results similar to those of previous poorly discriminating bats during early tests with single-sized spheres, while the second 4 tests gave results similar to those of the final tests with single-sized spheres. This bat, in other words, instead of being confused by the problem of distinguishing mealworms from spheres of mixed sizes, actually acquired the capacity to make the distinction more rapidly. While we cannot conclude from these various observations that the bat's system of identification focuses on the properties of a given target (or targets) of preference - to the exclusion of other properties - the present results in no way contradict such a view.

D. Simultaneous Presentation of Paired Targets With One Size of Sphere Per Run

In these tests, two targets were presented simultaneously from two mealworm guns placed roughly a foot apart and at right angles to the flight-paths of the bats. Four categories of presentation were used: mealworm left and sphere right, mealworm right and sphere left, spheres of a given size in both positions, and mealworms in both positions. Firing heights were approximately equated, both guns being triggered simultaneously as the bat approached the target zone. Considerable variability in separation, commonly amounting to more than a cubic foot at the peak of the trajectories, occurred when two mealworms or dissimilar targets were presented. The trajectories of the spheres alone were relatively stable. Five sizes of sphere were employed: 1/8 inch, 1/4 inch, 3/8 inch - though sometimes this was replaced by a 5/16 inch sphere - 1/2 inch, and 5/8 inch. Test length varied according to the motivation and selective proficiency of the bats, the average length being about 18 and the range from 12 to 40 firings. The chief difficulty encountered during the simultaneous tests was a strong favoring of the targets on one particular side by two of the bats: one favoring targets at the left side, and the other favoring targets at the right side.

Tests with sequentially presented targets were interspersed near the middle and end of the simultaneous tests. These made use of the same bats that were being given simultaneous targets, and the same procedure as already described for sequential tests.

Results for simultaneous presentations of positive and negative targets are given in Figure 14. Data on the three bats are combined and the findings for the first tests are plotted separately from the findings for the last tests. We chose to show here the records of contacts-plus-attempts rather than contacts alone because of the observed tendency of the bats to make late decisions during these tests with frequent failure to reach the selected target. Although the three bats were introduced to the different sized targets in different orders, there was no evidence that the ordering modified the results.

For tests with <u>dissimilar</u> targets (mealworm and sphere) the results can be summarized as follows: During initial tests there was no evidence of discrimination between mealworms and spheres, either within or above the zone of overlap; but some evidence of discrimination did appear with paired presentations of a mealworm and the 1/8 inch sphere. During the fourth (final) set of tests, however, discrimination became evident for all sizes of spheres though it was least prominent in the zone of overlap. Finally, the improvement between the first and last sets of tests was erratic and at times retrogressive in constrast to the progressive and sometimes sudden improvement previously noted during sequential tests.

For tests with similar targets, that is with two positive targets (mealworms) or two negative targets (spheres), evidence of discrimination was more apparent. The bats made successful catches of over 90% of the 443 paired mealworm presentations, and showed a combined catch and attempt score of over 99%. By contrast, when two negative targets were presented, only 15% of the 425 presentations resulted in contacts, the corresponding catch-plus-attempt score being only 30%. With these paired presentations of spheres, the largest number of catches - 45 out of 65 - occurred with the small spheres of 1/4 inch and 1/8 inch diameter.

In comparing present findings with previous (sequential) results, the most conspicuous difference is the very large amount of residual error (i.e., small number of contacts) for mealworm targets when presented simultaneously with spheres whose size placed them within the zone of echo overlap. There is also a lack of significant error peak for the small (1/8 inch) targets when they were presented simultaneously with mealworms. This, however, was not apparent in the results with paired presentations of spheres, where large numbers of catches of small spheres produced a large error peak.

Results for the sequential tests on these tests follow the pattern of previous sequential tests on other bats; hence, no separate graph is given. As with previous tests, there were virtually no mealworm errors, almost all mealworms being caught. There was a peak of target errors in the zone of overlap and, for one bat at least, there was a prominent error peak with the 1/8 inch sphere. These results served as a control to eliminate the possibility that the differences noted with simultaneous presentation might have come from differences in the bats or from experimental details other than the pairing of presentations.

Present findings lead us to the conclusion that selecting the positive target becomes significantly more difficult for these bats when a nearby negative target is also present. It is possible that the lowered discrimination scores observed with the current sets of simultaneous presentations may reflect tendencies by the bats to use secondary clues - such as spatial relations - in the discrimination process. As previously mentioned, two of the present bats showed a marked preference for catching targets that appeared on one side or the other. In an earlier sample test it proved possible, by suddenly shifting relative positions of mealworm and sphere, to produce errors of selection in a bat capable of almost perfect selections with paired targets. For example, after four correct selections where the mealworm was presented above the sphere, the positions were reversed. The bat made its first error in many presentations most of which were of constantly varying spatial relations. Other tests with multiple targets (Refs.14 & 39) have shown that very great differences occur in the responses of individual bats, and according to specific conditions. Undoubtedly the speed with which a bat is forced to perform severely limits the amount of processing that can be devoted to single aspects of any complex problem. Certainly the many facets of responses to multiple targets involve complexities which will require much further investigation.

SECTION IV

INTERCEPTION PERFORMANCE IN THE PRESENCE OF CLUTTER

A. Introduction

The ability of bats to detect and utilize the faint echoes reflected from small objects along their flight paths has drawn increasing attention in recent years; and certain of the findings are significant. For example, in the presence of noise that fills the frequency band of their signals, bats sometimes detect objects at signal-to-noise ratios so low that the performance comes close to the optimum predicted by theory (Refs. 15, 16 & 18). Of equal interest has been the possibility that bats might resolve selected echoes when these were obscured or distorted by far more prominent competing echoes: those, for example, deriving from large objects in close proximity to an extremely small object of primary concern. Such competing echoes, in the terminology or radar systems, are known as "clutter echoes". For present purposes, all echoes from unwanted objects are defined as clutter echoes (Ref. 34)[5]. The clutter problem, however, involves more than the mere separation of signal echoes from clutter echoes. Frequently, for example, it involves the interpretations and evaluations which dictate permissible flight paths with respect to the clutter-producing configurations; and it may require fine discriminations between different kinds of objects. From the bat's viewpoint, there are thus many aspects to the clutter problem.

Most commonly stressed of the attributes of the bat's guidance system is its extreme miniaturization (Refs. 8, 12 & 37). Echo-processing is accomplished by mechanisms weighing less than a gram. The entire echolocation system operates at power level of the order of one ten millionth of a watt (Ref. 8) with the echo-processing functions calling for less than a tenth of that figure. From the point of view of the radar or computer engineer, however, the processing system of the bat has another significant feature: the slowness of sequential steps (Refs. 18 & 35). In any mammalian nervous system, the delay between the firing of one nerve cell and the firing of a subsequent one in series with it normally amounts to a millisecond or more. By contrast, the modern computer which processes radar data may carry out sequential steps over 10,000 times as fast. Yet, the bat achieves accurate and effective pro-

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[5] In sonar systems the term "reverberation" is commonly used (Ref. 21).

cessing of complex target data (including localization, identification, selection and trajectory evaluation) in less than half a second. In this interval, one unit volume (eg., a cubic centimeter) out of over 10,000,000 may be predictively selected and reached.

From these broad facts we can deduce features which are likely to characterize the bat's methods of processing. The processing system, for example, must perform many operations in parallel and it must link these together in ways that lead to well-integrated and effective action. In the bat's methods, there is no room for long trains of processing steps. Just what physical features are coded into the echo structure as to how the processing is actually done, and just what indications from the echo complex are converted into action-guiding messages, are matters for extensive investigation and careful measurement. Possibly no other area of performance calls so fully upon the bat's echolocating capacities as does the pursuit of targets in the presence of close-range clutter configurations. Initial measurement of performance in such situations was the primary intent of the present study.

Prior to these experiments, most known observations on the capacity of bats to detect and evaluate targets against clutter were non-quantitative. They did not specify the concrete physical situation encountered by the bat (in terms, for example, of relative distances and reflectances of target and clutter components). They gave no indication of the bat's specific actions (such, for example, as head aim, ear motion, flight maneuver or catch technique), and they made no attempt to indicate modifications of the emitted signal which might characterize the bat's methods of overcoming the clutter interference. Our own rough observations had shown that some bats, while in flight, were able to detect and seize stationary targets on surfaces and to make apparent catches of flying insects close to such natural clutter surfaces as evergreen needles, tall grass, bushes and the twigs of trees.

But besides the direct problem of detecting targets and their trajectories, bats were obviously faced with the need to recognize and avoid potentially dangerous components of clutter configurations such, for example, as sharp twigs or thorns. Observation showed that the bats sometimes gave themselves time and reduced their collision problems by slowing down. At other times, however, particularly with red bats, the targets were pursued at high speed (perhaps at 20 or more feet per second) in close proximity to clutter configurations. Though the bats quite commonly brushed swiftly past the surfaces, they never seemed to collide with them while up to speed. Clearly the bats had made rapid and excellent evaluations of essential configural features; and it might thus be more accurate to picture the problem in terms of two sets of signals: 1) echoes deriving from targets and, 2) clutter echoes that were relevant to the trajectories of the target.

Observations providing the required specificity for detailed measurement and analysis are difficult to obtain in the field. Initial detailed observations have therefore been made in the laboratory. Insofar as practicable, some of the situations encountered by bats under more natural conditions have been approximated. Eventually, of course, it will be necessary to supplement the kind of studies reported here with appropriate outdoor observations. We believe, however, that present laboratory observations provide worthwhile orienting data.

Two categories of experiments on interception performance with clutter have been made together with various measurements relating to the performance or its physical correlates. All experiments dealt with the detection, pursuit and catching of ballistically moving targets. In the first category of experiments the clutter echoes were produced by alternative targets which were moving along with the selected target. In the second category, the clutter echoes were produced by fixed clutter backgrounds. Some of these backgrounds consisted of natural clutter objects (eg., foliage), while others were artificial (eg., large spheres). Some were concave or diffuse in the sense that the targets were at times surrounded by clutter-producing structures, while others were convex so that the targets did not penetrate into the surface, and the bat's flight paths were less impeded by constraining configurations.

Two kinds of records were obtained during most of the tests: 1) multiple flash pictures at flash intervals of 10 per second (which showed the bat's approximate position with respect to target and clutter, and also indicated some specific components of the bat's action); and 2) tape recordings of the bat's emitted signals made at a tape speed of 60 inches per second. While additional details remain to be obtained from these recordings, the current analyses in terms of pulse repetition patterns provide much valuable information. Sample high-speed motion pictures, at 384 frames per second, were also obtained.

A preliminary effort was also made to measure the relative magnitudes of echoes returned by mealworms, target spheres and typical samples of clutter backgrounds. However, owing to limitations in the equipment available when the measures were undertaken, these results are only approximate, and serve chiefly as a general guide rather than as permanent findings, (see Appendix III).

B. Multiple Target Tests

1. Introductory Comment

In these tests, multiple targets (presented simultaneously in numbers ranging from 2 to roughly 200) were projected upward into the bats' approach path. Since we were not interested here in discrimination between different kinds of targets, the targets were normally all of one kind during a given performance. For the most part, the targets were mealworms, though for bats that would pursue other targets, we also used small spheres and sometimes small discs. In these tests we were chiefly interested in gaining approximate values for three measures of interest:

1) the closest spacing between two individual targets compatible with clear resolution;

2) the maximum number of closely-spaced targets from which a bat could accurately locate and physically separate a single, selected target, and

3) the precision of final aim, as compared with the final accuracy of aim noted in the absence of nearby objects.

We hoped also to gain some idea of the time relations involved in these procedures, and possibly to note clues as to the methods used by the bats in selecting a given target.

2. Resolution of Two Targets

Because of inevitable differences in processing mechanisms for range evaluation as against those providing indications of relative angle (elevation and azimuth) we might logically expect distinctive differences in range localization as against angle localization. Although our tests were not specifically designed to measure resolution in range as against resolution in angle, we made a number of observations in which closely-spaced targets were clearly resolved - apparently from some distance - in both range and angle. We gained no significant evidence that any differences of consequence existed. At the same time, we recognized that evidence for errors in range evaluation could not be so directly observed, and may well have excaped notice.

Several of our high-speed films suggested that a bat, trained to the selections in question, clearly resolved two targets from some distance and prepared to separate the desired one as the two were approached. These films lack triangulation, but a good deal of collateral evidence - such as the bat's striking the unselected member of a pair in a way that permitted measurement - indicated that targets as close together as one inch could be clearly resolved. Accuracies of aim, for the selected target, frequently appeared to fall within a volume of perhaps one cubic centimeter. There was, in fact, no evidence of any decrease in accuracy relative to the accuracies noted with a single target. A sequence from a high-speed film was shown in Figure 6b.

Several of our multi-flash pictures illustrate separations of closely-spaced targets with the use of the tail membrane. Figure 15 shows a red bat selecting one mealworm out of several (including, also, a 1/8 inch sphere). From the manner in which the streak lines are interrupted we note that the spacings here must have been very close. A far simpler selection of the nearer of two mealworms is shown in Figure 16. High-speed films also showed instances where two dissimilar targets were so close together that they were both scooped in by the tail membrane. However, the unselected target dropped out, while the desired one was quickly seized - the correct selection and aim obviously having been acoustically established prior to contact.

As mentioned earlier, the observations we have reported are based on selected individual bats. We presume, however, that they represent the typical capacities of the bat's echolocation system - even though many bats do not, under laboratory conditions, demonstrate like levels of proficiency. Recently, for example, we had a red bat which characteristically aimed for some acoustic "center of gravity" between any pair of targets that were spaced within perhaps 6 or 8 inches of each other. When the bat attempted catches of paired targets, it invariably failed. Many bats persisted in turning away from two or more targets; while still others spent so much time evaluating the configuration that their attempts came too late for capture. Typical performance under natural conditions, however, is undoubtedly far superior to the average impression gained during laboratory tests.

Details of technique are difficult to specify from our observations. We have noted a few instances in which a Myotis lucifugus directed its head at different members of a cluster of inedible targets (Fig. 17). Normally, however, any such shift of echolocating aim would be too subtle for reliable observation. Moreover, as already noted, red bats appeared to employ much less drastic shifts of head-aim, while following targets, than is characteristic of Myotis lucifugus. In general, the bats appeared to have made their decision in favor of a given member of a target group while still at some distance. At a guess, it was usually over one foot. The bats obviously attempted to seize the selected target in isolation from the others, though they often struck, or partially captured, other nearby objects.

3. Maximum Sizes of Target Clusters

Unless figures for mean density or density distribution are given, there is obviously no limit to the number of targets from which a bat can select a single target. In nature, bats undoubtedly capture isolated members out of very large swarms of insects - provided the spacings are great enough to preclude excessive clutter echoes from too many insects close to the one selected. In the laboratory, however, we have noted that some bats (*Myotis lucifugus* and *M. keenii*) did not habitually attempt catches of small insect targets (fruit flies) where high concentrations of the targets occurred. Certainly, if the mean spacings were as close as 6 inches, the bats appeared to seek locations where the flies were far more widely scattered. On the other hand, when large numbers of small targets ("jiffy-gems" of 1-2 mm diameter in clusters of perhaps 200) were projected upward into the bat's flight path, the bat occasionally appeared to approach the periphery of the cluster and possibly to attempt capture of targets that scattered out from the main focus (see Fig. 18). As will be shown in the next section, when bats are expecting small targets such as fruit flies, or even mealworms, in a certain zone close to natural clutter, they sometimes attempt to catch tips of clutter that project out close to them (see Figs. 19a, b, c & d). Both the action and the emitted signals in such cases normally resemble those noted with isolated catches of insect targets. We must conclude, therefore, that any small object or configuration which can be resolved and isolated at the edge of a clutter surface - no matter how large the clutter mass - can be selected and accurately caught or hit.

In most of our multiple target tests, however, the number of targets was kept below 20. When inedible targets or mealworms were projected upward in smaller numbers, the volume containing the cluster could normally be pictured as a sphere of one foot diameter or less. Though this was true for like targets, the target volume with *mixed* targets, became more of an ellipsoid; elongated on the *vertical* axis. It is quite possible that small clusters, within a small volume, are handled somewhat differently from large clusters. With large clusters, any distinct nearby object may be evaluated separately from the more massive background. In this latter situation the bat may gain a sort of figure-ground impression, while with smaller clusters, each object may tend to be separately evaluated.

Just how a bat selects a particular target is not clear. In general, an upper or nearer target is chosen. Figure 20 shows a nearer member out of 16 "jiffy-gems" being captured by a *Myotis lucifugus*, however, (Fig. 11 of Ref. 38 showed a red bat catching one out of 15 mealworms without such spatial selection). In our tests thus far we have gained the impression that bats which are good at selections out of compact clusters can readily deal with 8 and sometimes 16, targets. Above roughly this number, however, bats generally seem unwilling to attempt catches unless individual targets scatter out from the main group.

Even very small targets can be accurately isolated. Figure 21 shows the selection of one out of four 1/16 inch spheres. The selected sphere was actually hit, rather than caught, but such small hard objects bounce around in the membranes in a very different fashion from soft insects. The vertical downward motion also differs significantly from the flight motion of a small insect. Failure to catch, in other words, cannot legitimately be construed as an "error" by the bat.

Most of our observations have been limited to the vespertilionid bats Myotis and Lasiurus. Our few observations on the greater horseshoe bat (Rhinolophus ferrum-equinum) suggest good capacity to deal with multiple targets - with the use of an almost totally different signal system - as described elsewhere (Refs. 4, 11, 13a, & 38). Figure 38 of Reference 38 shows an erroneous selection between two targets. The sequence is of interest because it shows the bat first evaluating one of the pair of targets, a mealworm, and then quickly shifting to the other, a gelatin sphere, which it caught. In the one day of testing given this bat, it did not learn to select mealworms over spheres, but it did demonstrate excellent skill in selecting one out of as many as 8 or 10 targets in a cluster.

We can summarize our observations on the response of bats to multiple targets as follows: Bats are capable of selecting one target out of very large clusters provided that individual targets scatter out from the main mass. With more compact clusters, some bats appeared able to isolate single targets out of groups of 16 similar objects. Compact clusters of greater numbers have thus far been rejected. When the targets were presented in small groups up to four, for example, the bats were able to resolve a selected target, even when another target was within perhaps one inch of it. Accuracies of aim did not, in general, appear appreciably impaired by the presence of alternative targets close to the selected one. Target clusters were probably detected, for the most part, at 3-6 feet, and the desired target isolated well before the catch, perhaps at 1 foot or more. Approach selection and catch were completed normally in from 1/4 to 1/2 seconds. The catch maneuver itself was sometimes carried out within less than 1/10 second; major components of the action sometimes occuring in 1/50 second.

C. Preliminary Tests With Fixed Clutter Backgrounds

The first tests with fixed clutter backgrounds were initiated in connection with a thesis project by A. W. W. Clay[6] at the Massachusetts Institute of Technology. The plan of the thesis investigations was:

1) to determine, in a rough way, the capacity of bats to detect, locate and intercept ballistically moving targets close to clutter surfaces in the laboratory,

2) to make approximate measures of the relative magnitudes of target and clutter echoes in sample situations encountered by the bats being tested, and

3) to make preliminary observations on possible relations between observed performance and the echo problem in an effort to see whether the situations which appeared more difficult (on the basis of rough measurement) gave evidence of increased difficulty (as noted in the bats' detection or interception performance).

The clutter backgrounds in these tests consisted of: 1) smooth spherical surfaces (of 9 inch and 36 inch diameters), 2) a large toroid (of 10 inch cylinder diameter and 22 inch central opening), and 3) yew branches (a natural clutter with needles of roughly the same size and shape as the mealworm targets). The targets were not presented on standardized trajectories but were projected successively closer to the clutter in an attempt to bring the bats as close as possible to the clutter surfaces.

These tests demonstrated that the bats (Myotis lucifugus) could successively track a moving target up to the various clutter surfaces but that the probability of a successful interception decreased significantly as the target trajectories came close to the surfaces. The relative difficulty of interception appeared to increase in the following order: 9 inch sphere (easiest), 36 inch spherical surface, toroid, and yew clutter (hardest).

A number of measures were made of the echoes reflected back by various targets and clutter backgrounds from synthetically-

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[6] A. W. W. Clay, Jr.,: "The Effects of Clutter on the Echolocation System of Bats", M.I.T., Dept. of Elec. Engr., 1964.

generated "bat" pulses. Unfortunately, the equipment suffered from several defects and the results were not entirely satisfactory. Certain of the findings, with these limitations, are given in Appendix III.

With respect to the difficulties encountered by the bats in the presence of clutter backgrounds, significant details will be presented in a subsequent section. We noted, during tense initial tests, that bats often gave evidence of tracking difficulties as a target passed close to the yew clutter. Of particular interest was the occasional occurrence of burst of high repetition-rate pulse sequences (in the bat's emitted signal) much like the pulse sequences observed during the pursuit of maneuvering targets such as evasive moths.

D. Main Tests With Fixed Clutter Backgrounds

1. Equipment and Methods

a. Experimental Arrangement

The general arrangement of the equipment for these tests was much the same as in the initial tests just reviewed. The chief improvement was the construction of a standard clutter frame and its mounting on a track which permitted convenient adjustment of position. The purpose of the frame was to permit different kinds of natural clutter to be presented with the same over-all configuration and to be quickly adjustable within the field. Distinctive differences in response which the bats might show would thus tend to arise from variations in detailed characteristics of the different natural clutters rather than from variations in general configuration. Effects of over-all configuration were partially tested by the use of one or two natural clutters that were more or less similar in surface texture to clutters mounted on the frame, but were of radically different over-all form. These were shrubs grown in metal tubs which were positioned in the same clutter space with the use of pulleys.

The two configurations of clutter used in these tests might be categorized as convex forms and concave forms. The natural concave clutters were attached to the clutter frame in such a way as to provide a central clear space which was more or less surrounded by leaves, needles or twigs: the intent being to simulate the situation in nature where a bat is required to catch targets in the spaces between branches. The main frame was 4 feet by 2-1/2 feet in size, while the clutter depth (front to back) was roughly three feet. Concave natural clutters included: 1) maple leaves, 2) blue spruce, 3) hemlock twigs, 4) willow leaves, 5) red pine and, 6) white pine. Systematic tests were carried out only with the first three. Convex natural clutters consisted of potted shrubs (spruce and yew) corresponding roughly in size and curvature to the large hemisphere which constituted the convex artificial clutter. This hemispshere, which had a smooth surface and was of 3 foot diameter, was mounted from behind on a pole standing in a moveable frame on the floor. The concave synthetic clutter consisted of a pentagonal array of smooth 9 inch spheres mounted on a 6 foot ring. The spheres could be swung in or out to provide a central opening of variable size. Because bats seemed willing to venture into a central space of 3 foot diameter, but were hesitant to enter smaller spaces, this central diameter was used in the tests. No quantitative tests were made of the echo magnitudes produced by the array of spheres. We suspected, however, that from a distance these spheres gave an impression of size not too different from the concave natural clutters.

Routine target trajectories were set up with the use of a solenoid operated aluminum cup or "gun" mounted on a tripod with calibrated tilt head. During the routine tests three firing angles were employed, while a number of special tests made use of a fourth firing angle from a gun in a different position. Normally, these trajectories fell within the following bounds (as expressed in degrees of tilt toward the clutter):

Position 1 [Outer or Vertical (V)]	Position 2 [Middle (M)]	Position 3 [Inner (I)]	Position 4 [Sloping (S)]
0°-3°	5°-6°	10°-12°	20°-24°

The three routine trajectories were intended to present the bat with the following three situations. The vertical or outer trajectory kept the target sufficiently clear of the clutter so that the catches would be free of any significant interference of the bats' flight path by the clutter background. It also kept the target echo distinctly clear of clutter echoes. The middle trajectory brought the target close enough to the clutter so that the bat might have to adapt its flight path to the presence of the clutter behind the target; it frequently placed the target close enough to the clutter so that the echoes might not be distinctly separated (in echo-time) from the nearest clutter echoes. Targets on this trajectory sometimes made actual contact with the edge of the natural clutters. The inner trajectory was intended to require a catch that was either within the clutter space or so close to the clutter surface that mechanical interference was highly probable. Moreover, there would sometimes be intervals during which the target was further from the bat than the nearest clutter. In general, the timing of target release was such as to call for a catch close to the top of the trajectories. In some instances, however, the target had to be fired slightly earlier than this to prevent the bat from making a final upward or sideways turn, and thus produce a catch that was not directed toward the clutter.

Besides routine tests, a considerable number of special tests were carried out. These included:

b. Additional Clutter Backgrounds

Time did not permit the use of additional natural clutter backgrounds in the routine tests, but pilot observations were made on natural clutter backgrounds consisting of willow leaves, red pine and white pine. The original experimental plan called for backgrounds which varied along a continuum of obnoxiousness or danger. We intended to use, at the obnoxious end, clutters made up of profusely thorned branches of barberry and hawthorne. At the harmless end were to be willow leaves and white pine, both of which are very soft. However, our experimental bats were so limited in number that we decided against risking the wing injury that might have occurred had the bats failed to identify, and stay clear of, the very sharp tips of the thorns. The red pine clutter was used to produce a diffuse type of echo structure; the needles being longer and more sparse than those of white pine.

c. Multiple Target Tests

Very little sampling was done with multiple targets. We were chiefly interested in finding out whether nearby clutter introduced conspicuous increase in difficulty for the selection of one target out of several. We thus made a few observations on the capacity of bats to select one mealworm out of small clusters (mostly two or three) that were projected close to the clutter surfaces (Fig. 23f).

d. Moths as Targets

More extensive observations were made with moths as targets, since we suspected that the unpredictable nature of the moths' paths might produce responses related to tracking difficulties encountered in clutter situations. Because of the erratic paths often taken by the moths when projected upward by gun, the firing position was normally made a foot or two higher than with mealworms. Position relative to the clutter backgrounds could not, of course, be controlled (as with mealworms); neither could the moths be kept accurately within the photographic field. No complete records of the kinds of moths was kept. However, in isolated cases they were identified.

e. Fourth Trajectory

The fourth, more sloping trajectory was tested with two kinds of bats (Myotis sodalis and Lasiurus borealis), and two clutter backgrounds (white pine and hemlock twigs). It was intended to compensate, in part, for the suppression of detection observed with large clutter masses. Many of the failures, or late efforts, to pursue targets on the inner trajectory appeared due to inadequate detection. Since the target was relatively close to the clutter, it seemed possible that the target echoes might not have been distinct enough from the clutter echoes to make detection easy. In comparing clutter and non-clutter situations, we also wondered whether the problem of detection might not differ radically from the problem of tracking after automatic following of the target was established. Though a bat might have initial difficulty determining the presence and position of a target when the target was close to a clutter surface, it might be capable of accurate tracking once proper following was initiated.

With this in mind, the fourth trajectory was made to differ in the following ways: first, it started further away from the clutter along the course of the bat's flight path (thus bringing the target relatively nearer to the bat during the detection phase). Second, it went more closely along the bat's flight path, thus producing less rapid shifts of relative angle and velocity; and third, it arched up in front of the bat in such a way as to give more time for the establishment of effective following. An effort was made, however, to have it terminate in the clutter spaces as did the routine third trajectory.

2. Procedure for Routine Tests

The procedure for the routine tests was relatively simple. First, the clutter background was slid into position and lined up properly with the cameras: one camera directed upward from below and one directed from the side and about 30° ahead. A yardstick was then placed along the most typical flight path of the bats and photographed, along with a multi-flash picture of a sweep-second clock (for calibration of the strobe flash intervals). After this, the three firing trajectories were adjusted to the particular clutter backgroundin use. The bat was then weighed and allowed to warm up. When the bat came into orbit, it was normally presented with mealworms fired along a trajectory that sloped slightly away from the clutter. As soon as a successful catch was made, the recorder was activated and the test begun. Each test consisted of 16 flights, divided into 4 passes, by the bat for each of the three routine trajectories and a set of blank passes. During blank passes all details remained the same except that no target was placed in the gun. Several different randomized sequences were used to prevent possible familiarization with a given sequency by the bats. The targets here were single mealworms.

(In a couple of instances two mealworms were accidentally projected; but in each case a catch of one was made and the result tabulated as a normal catch).

3. Results of Clutter Tests

a. General Results

The general results of the main series of tests are given in Figure 22. These are divided into five clutter categories as follows: 1) no clutter, 2) 3 foot hemisphere, 3) diffuse (concave) natural clutters, 4) compact (convex) natural clutters, and 5) pentagonal array of 9 inch spheres. Certain distinctive findings appeared to be associated with each of these categories.

i. No clutter

The outstanding observation in the tests with no clutter backgrounds was the perfection of scores: all 72 firings producing catches or hits. Included in these tests were six different bats and the three routine trajectories. Because of this proficiency on the part of the bats, it was possible to exclude physical inability to reach the targets, in subsequent clutter tests, as a cause of failure to make contact - barring, of course, those cases where the clutter produced actual physical interference.

ii. Hemisphere

When presented with targets at distances of one or two feet from the hemisphere (ie., the outer or vertical trajectory) the bats did virtually as well as when no clutter was present. Only one out of 28 presentations was missed. Even with the middle trajectory (where the targets normally came within one-half to one foot of the surface) there was little decline in performance; only four out of 28 firings were missed. Only when the inner trajectory was used did a major decline in performance occur with 25 out of 28 of these presentations being missed. Here the targets usually came within 6 inches of the surface - many of them actually striking it close to the peak of their trajectory.

Several different responses were noted. Figure 23a shows a bat accurately tracking a target until the target hits the sphere. The bat, in close pursuit, cushions its collision with the use of its wings; then rebounds 2-1/2 inches off the surface and resumes flight. Sometimes, as in Figure 23b, the bat tracked the target to within some inches of the surface and then shifted its attention to the clutter - either losing the target in the massive clutter echo or deliberately preparing for collision with the surface. When practicable, the bats seemed to prefer a last-instant maneuver which resulted in a light brush, or total avoidance, of the clutter surface. Figure 23c shows a sudden turn, just off the surface, and an attempt to scoop in the target just as it reaches the surface. The bat's aim appears excellent, but mechanical interference evidently prevented a catch. Figure 23d shows much the same thing, but here the slightly greater distance from the surface permitted successful retrieval of the target. In Figure 23e the bat climbs steeply, then make a rather abrupt stop just off the surface. This catch was successful. Figure 23f shows catch of one out of two mealworms near the surface. Our general conclusion from the hemisphere tests is that the bats are clearly capable of tracking targets accurately right up to the clutter surface, but that the tracking may become significantly more difficult at close range and that mechanical interference, or the preparation for it, frequently prevents successful catches - and often results in failure of contact.

iii. Diffuse (concave) natural clutters

Although the outer (vertical) trajectory produced relatively little difference in the bats' performance, as compared with the hemisphere, very striking differences were noted with the middle trajectories. Of the middle trajectories, with the hemisphere, 86% (24 out of 28 presentations) resulted in contacts by the bat: while with the diffuse clutter, only 46% (32 out of 70) resulted in contacts. Because of the irregularities of the clutter surface and the variations in individual target trajectories, the targets sometimes hit the edge of the clutter; but such instances were too infrequent to account for the large discrepancy. There is a slight indication (not statistically significant) that bats did better with the hemlock twigs than with maple or spruce clutters (only two contacts each for maple and spruce as against 5 for hemlock). The hemlock formed a much less dense array, presumably with smaller echo magnitudes. Configural problems relative to the flight path, however, seem unlikely to have been very different. That a considerable discrimination problem may have existed is suggested by the fact that bats several times attempted catches of the outer twigs or pine needles (Figs. 19a, b & c).

The inner trajectories appeared to produce both fewer attempts and fewer contacts than did the hemisphere. With the inner trajectory, there were a number of instances where the target was further from the bat, at times, than was some of the nearby clutter. The fact that no contacts with the targets were made during these tests is perhaps slightly misleading. In special tests, where the trajectory was gradually moved into the clutter, or where the fourth trajectory was used, the bats did sometimes make successful catches, and a number of contacts, within the clutter (Figs. 24a, b, & 25). Uncertainty about the trajectory, and possibly the realization that easier targets would be forthcoming, may have contributed to the general failure of bats to pursue such targets during the routine tests.

iv. Compact (convex) natural clutter

In spite of the above suspicions as to why the bats did relatively poorly with diffuse natural clutters, some evaluation of effects that might be produced by details of the surface structure seemed in order. For example, it might be argued that the echoes from spruce needles resembled the echoes from mealworms, and thus confused the bat. Or, perhaps, more legitimately, it might be argued that the bats recognized the spruce needles to be sharp and potentially dangerous, thus warranting definitive evasion. These, in part, were our reasons for using yew and spruce in the compact clutter tests. The needles of yew are rather close in size and shape to mealworms (our standard target), while the needles of spruce are sharp. To permit more valid comparisons with the hemisphere, we selected shrubs which corresponded roughly to it in general size and curvature.

The results turned out to be much closer to those with the hemisphere than to those with the diffuse natural clutters. Outer trajectories resulted, as usual, in almost perfect scores. The middle trajectories produced results corresponding fairly closely to results with the hemisphere. The inner trajectories produced scores which were, interestingly enough, considerably better than those with the hemisphere. The bats attempted a number of catches quite close to the clutter and not infrequently struck both the target and the clutter. These findings suggested that neither the mealworm-like size of the yew needles nor the sharpness of the spruce was a major deterent. Configural complexity, the diffusely scattered echo indications and perhaps overall echo magnitude at at distance thus seem likely to have been more responsible for the fall-off in performance with diffuse natural clutters than were factors associated with the detailed structure of the surface.

v. Pentagonal array of spheres

The final set of tests represented an attempt to combine the open-center configuration, as well as the approximate overall size, of the diffuse natural clutters with the smooth spherical surface of the hemisphere. By the time this arrangement was set up there had been some changes both in the bats used and in their condition. The results may not, therefore, be strictly comparable. They are probably meaningful, however, in general terms. There were no failures of contact during the 16 outer (vertical) trajectories; while 11 out of the 16 middle trajectories resulted in contacts, with only one failure to attempt. This corresponded roughly to the results with the hemisphere and with the compact clutter. The results with the inner trajectory were closer to the findings with the hemisphere than to any others; the bats attempting roughly half the presentations, making contact with 2 and failing to pursue 7. Apparently the pentagon of spheres presented a rather less serious clutter problem than did the diffuse clutters of approximately corresponding general dimensions; it came much closer, in its effects on performance, to the single large spherical surface.

One additional note should be made. During the period of familiarization, there were a large number of early turn-aways as with the diffuse natural clutter. Undoubtedly detection was more greatly impaired from a distance than was true with the more compact clutters, and the existence of an obviously large obstacle during early familiarization may have tended to inhibit the initiation of pursuits. Once the situation became familiar, however, the problems of tracking and interception seemed to be relatively easily mastered.

b. Examples

A few examples of representative clutter situations will serve to illustrate some of the quantitative relations. For these records two cameras were used to triangulate the bat's position with respect to the target and the clutter backgrounds, while tape recordings of the bat's signals were used to plot the pulse intervals. Some of the distances in the plots are fairly approximate, since precise measures of distances to irregular configurations of natural clutters were impractical. Relative to actual variations that occurred during different clutter pursuits, however, the approximations of measurement do not introduce deviations of any significance.

Figure 27 illustrates a typical set of time-distance relations for outer, middle and inner target trajectories in front of the 3 foot hemisphere. The target gun is shown as 5-1/2 feet lower than the center of the clutter surface and a couple of feet out from it. The firing angles illustrated are roughly 1°, 5°, and 11° toward the clutter and represent the trajectories #1, #2 and #3 respectively. At 1/10 second intervals along the trajectories sample positions of a target (mealworm) are indicated. Such targets are damped by air-resistance by 1-1/2 to 2 feet of elevation relative to an undamped target (eg., steel ball). Sample sequential positions are also given for a bat approaching at a rate of 10 feet per second. Such a rate is typical for Myotis lucifugus and Myotis sodalis, although the speeds of individual bats have been measured from a minimum of approximately 5 to a maximum of about 20 feet per second. Lines are drawn from bat to target at the successive tenth-second intervals. Since the intent was to have the bat reach a roughly corresponding point in the trajectory for each of the firing angles, the firing was made slightly later for the inner trajectory than for the outer. The trajectories of mealworms were subject to considerable spread: the ellipses at the top of the trajectories indicating a volume within which perhaps 90% of the firings might be expected. From the size of these ellipses it is clear that the three trajectories were not totally separate, but only statistically so. Possibly a fifth of the firings for one trajectory sometimes overlapped an adjacent zone.

In Figure 28, measurements from Figure 27 have been converted into approximate time-distance curves. The base line (abscissa) represents the position of the clutter surface closest to the bat. Below it are arcs which designate the distance of the portion of the clutter surface which is in-line with the target as observed from the bat's position. Since the surface of the hemisphere slopes rapidly away, echoes from that portion of the hemisphere directly behind the target are of little consequence when the target is almost straight in front of the surface - though with the diffuse natural clutters, of course, this situation does not hold. Sloping down from the upper left corner are three lines which represent the uniform approach of the bat to the clutter surface. Zero reference is the point of catch (shown at 0, 11 and 20 inches from the surface for the three trajectories). The curved lines which intercept these approach lines represent bat-to-target distance: these distances being most simply pictured as drawn down from the approach lines to the target lines. Photographic evidence suggests that a bat often directs its head down toward the rising target when the target is between 1-1/2 and 3 feet above the gun - quite commonly, for example, at roughly the -0.5 second position of the present illustrations (and representing a bat-to-target distance of about 5 feet).

As already indicated, these lines are sampling approximations only. If the target rises higher relative to the sphere, the slope of the bat-to-clutter line tends to curve toward the horizontal as the bat flies upward along the surface. When a large and diffuse clutter mass replaces the hemisphere, several differences appear. For example, the irregularities of the clutter surface make definition of a fixed clutter distance at the point of catch difficult. In certain cases, also, the bat-to-clutter distance may go negative in that a bat may pursue a target behind a near piece of clutter or may deflect the clutter to achieve the catch (Figure 30). In a number of instances, as in Figure 25, the bat brushed a clutter projection as it proceeded to the target beyond. Another difference from the hemisphere is that the bat-to-clutter distances, for nearest clutter projections, are generally not uniform: the bat, for example, may fly upward after a rising target while passing clutter projections that generate an irregular sequence of distances. In addition, the in-line distance of the clutter beyond the target does not rapidly flare off, as with the hemisphere; the bat, in other words, is dealing with clutter echoes directly behind the target for a longer time. Finally, the clutter echo-structure has greater complexity.

Figures 29 and 30 illustrate the distance relations and pulse patterns for two catches: one very close to the surface of the hemisphere, and the other at the edge of the hemlock clutter. The hemisphere catch was made a couple of inches off the surface with the bat turning in such a way as to avoid collision. With the hemlock catch, the target actually went into the edge of the clutter configuration, and the bat had to deflect some of the twigs to make the catch. In neither instance was there any evidence of tracking deterioration, nor were there any significant deviations of the emitted signal.

Figures 31 and 32 illustrate, respectively, a successful catch and an unsuccessful wingtip attempt, with targets that came close to a background of maple leaves. The catch sequence appears typical of non-clutter catches in all respects except for the unusually abbreviated terminal segment of the emitted pulse. The sequence showing a wingtip attempt could be interpreted as an error in localization and timing due to the close range clutter echoes; or it could have been due to a conflict between an acceptible flight path past the clutter and the intent to catch the target.

4. Other Observations Relating to Pursuit Performance

a. Techniques of Pursuit

Our general impression, both from observations in the laboratory and in the field is that bats seldom, if ever, collide at full pursuit speed with obstacles along their flight paths. At the same time, they frequently brush past twigs and foliage on their way to a target, (Fig. 25), and they not uncommonly attempt catches as they slow down close to, or even in contact with, a clutter surface (Figs. 23c and 24). When practicable, they appear to turn parallel to or away from the nearest clutter. A number of attempts at catches (eg., Figs. 26a and b) were made so close to foliage that contact was inevitable. When bits of foliage as well as target were scooped in, the catches generally were not successful.

b. Accuracy of Tracking

For the most part, little deterioration was evident in the accuracy of tracking against clutter backgrounds. Occasionally, when the backgrounds were evergreen needles or hemlock twigs, a bat would suddenly shift from tracking the correct target to a focus on a nearby clutter protrusion. In Figure 19c, for example, the first image shows the bat tracking a mealworm that is about a foot above. In the second image, the bat's aim is directed toward the tip of a pine needle directly ahead. The bat then executes a catch maneuver and flicks the needle sharply upward (the upward curving needle being clearly visible in the space between the two clusters). In come instances, the bat appeared to direct its aim in different directions in an attempt to pick up a target that had gone behind some nearby clutter. When a target came very close to a clutter surface (as in Fig. 23b), the bat sometimes shifted its echolocating focus to the clutter - apparently in an effort to prepare for inevitable contact with the surface.

c. Simultaneous Pursuits

Of interest in connection with catches in the presence of strong echoes are observations on simultaneous attempts at a single target by two bats. In these tests, two bats were induced to circle in opposite directions within the flight space. It was then possible, at times, to project a target midway between the two bats as they approached from opposite directions (Fig. 33). Once in a while, when the placement was precise, the bats would collide as they made simultaneous attempts on the same target. Figure 34 is a two-flash sequence of such a collision. In the second set of images, the mealworm target can be seen starting to fall out from between the two bats.

It is significant that no loss of tracking accuracy was noted during such attempts even though the bats were now contending with three sets of sounds: 1) echoes of their own signals reflecting back from the target (weakest), 2) echoes of their own signals reflecting back from the other bat, and 3) the signals being emitted by the other bat (strongest). This is another instance demonstrating the capacity of bats to focus on a particular set of weak echoes in the presence of vastly stronger signals of a like type.

d. Emitted Signals

Perhaps the most striking feature of the typical signals emitted by bats during pursuits in the presence of clutter is their lack of noticeable deviation from non-clutter pursuits. Most commonly, in other other words, even severe clutter problems produce no appreciable adaptation of the pursuit signals (Fig. 35). A typical pulse sequence for Myotis lucifugus with its associated action tracing (from multiflash pictures) is given in Figure 36. Elsewhere, the pattern of such sequences are discussed in more detail for different kinds of bats (Refs. 11, 13, 13a, 25, 37 & 38). Most records we have obtained during the present tests have been of the type illustrated in Figures 35 and 36.

In some instances, however, three modifications of interest have been noted. The first modification was an increased average pulse repetition rate during the approach phase. Following detection, there is normally a rather gradual build-up of pulse rate and then a final rapid uniform pulse sequence (terminal buzz). Occasionally, the present records showed an earlier and more uniformly progressive rise in rate, with a less sudden transition into the final buzz sequence.

The second modification was in some respects opposite to that just indicated. Here the rise of pulse rate during approach often did not increase progressively but tended to be characterized by plateaus. There was then a very sudden rise in rate and, typically, a shorter-than-usual terminal segment. Present Figure 31 illustrates such a pattern. Sudden transitions into a brief terminal segment are sometimes also seen, in clutter-free situations, with small targets. It is conceivable that such a pattern indicates a last instant focus on the target's precise position.

The third modification was basically a prolongation of the terminal buzz. In non-clutter situations, prolongation of the terminal buzz is characteristic of extended pursuits where a bat has misjudged the position or path of a target. In the laboratory, when trained *Myotis lucifugus* catch mealworms, the terminal buzz typically ranges from about 50 to 100 milliseconds in duration. But when new bats dive after mealworms whose trajectories they have misvaluated, the buzz may be extended to 500 milliseconds. Sometimes such long buzzes are continuous; and sometimes they have one or more brief interruptions (possibly while the bat catches its breath). In a few instances, when bats attempted to track targets moving closely past configurations of natural clutter, prolonged buzzes were noted. In certain instances such buzzes were broken into smaller segments or bursts of half a dozen to a dozen pulses.

SECTION V

RECOMMENDATIONS

Based on our observations to date we believe that studies on the interception performance of echolocating bats should be extended in the areas broadly outlined below:

1) Greater diversity of observations under conditions that simulate natural conditions. For example, bats other than *Myotis lucifugus* and *Lasiurus borealis* should be given similar tests of performance. Tests in a larger, controlled flight area, as a large outdoor cage, are clearly indicated as are additional tests under natural field conditions.

2) Systematic analysis of the effects of interference on interception performance. In particular, we suspect that much important information could be gained on the bats' utilization of signals and echoes by selective interference in time and frequency bands with the bat's reception of echoes.

3) Study of the information-bearing features of received echoes (in terms of the bat's reception system, its requirements and the theoretical data-content of the signal and echoes). Special analytical methods, such as an "analog ear" and human listening with modified bat-type pulses, should be used.

4) Development of data-telemetering methods from bats in flight. A number of questions about signal generation and important physiological aspects of the methods used by bats cannot be evaluated without such methods. In addition, telemetering methods may offer important adjuncts to training and to observations under field conditions.

APPENDIX I

FACILITIES AND EQUIPMENT

The facilities of the laboratory include an integrated system of equipment designed to permit the study of the many aspects of a bat's performance. Generally this equipment consists of two types; systems to record photographically the bats' actions, and systems to record on tape the bats' ultrasonic sound signals. These systems are so interrelated that a reconstruction of the bat's performance may be studied at a later time. The flight room is a space (35 feet x 14 feet x 14 feet) near one end of which is the target firing zone. A separate camera room, facing on the target firing zone through a glass partition, serves to remove any camera noise from the flight room. The cameras and their associated lights, along with the recording microphones, are all aimed at this zone where the bat's action takes place (Fig. I-1).

Three kinds of records were made during these tests: 1) tabulations of observed action and results, 2) tape recordings of the bats' emitted signals, and 3) multiple flash photographs of some of the details of performance. Only the tabulations of action and results were made in all cases.

The recording arrangement is shown in block diagram form in Figure I-2. The microphone, constructed by Dr. L. P. Granath of the Worcester Polytechnic Institute, was of the general design of Kuhl, et al (Ref. 22). This was followed by a pre-amplifier, with D. A. Cahlander's modification of the original Granath design (Ref. 23). The received signals were further amplified and transmitted to an Ampex FR-1100 recorder operating at 60 inches per second. The bat's signals were also passed through a bandpass filter (20-100 kc), rectified and sent to a loudspeaker for human listening. In some cases oscilloscope traces were also available.

To record the details of the bat's action, multiple flash photographs, at a rate of 10 flashes per second, were taken by a 70 mm Beattie-Coleman, Varitron camera. Stroboscopic flashes of about 1/10,000 second duration, at 70 or 200 watt seconds, were produced by a flash unit constructed by D. A. Cahlander.

A 16 mm Fastax high-speed movie camera, capable of speeds of 100 to 3000 frames per second is available, and is combined with a specially designed speed control unit whereby the correct speed is reached in 0.1 seconds with an accuracy of ±1% (Ref. 3). Two Edgerton, Germershausen & Grier type 501 strobe control units provide synchronous illumination of 2-4 watt seconds each (Fig. I-3). In playback these pictures result in the so-called "slow motion" pictures whereby the bats' continuous flight may be examined. A sample of such a film is shown in Figure 6b.

In order to obtain a record of a bat's flight positon in relation to his own pulsed sound pattern, a control system has been designed to provide illumination for the Varitron cameras in synchrony with the bat's sound pulses, making use of a Tektronix pulse generator and the Edgerton, Germershausen & Greier strobe units (Fig. I-4). An example is shown in Figure 6a.

APPENDIX II

HYPOTHESES FOR SLOW RECOGNITION OF INTERMEDIATE-SIZED SPHERES

There are at least four obvious hypotheses for the tendency of some bats to require many trials prior to clear-cut avoidance of the intermediate-sized spheres: 1) failure to discriminate, 2) a natural catching proclivity, which over-rides discrimination, 3) non-recognition of the experimental situation, and 4) a propensity for confirmatory testing of the targets (by tactile means). Since these different possible explanations may incorporate elements of general significance to any analysis either of motivation or of technique and performance during interceptions, a brief review of each will be given.

1) Failure to discriminate. A logical first conjecture might be that, without fairly extensive experience, the bats simply could not discriminate mealworm shapes from spheres of the same general size or slightly smaller. With certain bats, however, such an explanation clearly did not hold. One bat (FB), for example, even at the start made only a few errors with the most difficult spheres. Another bat, during some sampling tests, proved capable of distinguishing almost any alternative target that did not too closely resemble a mealworm. Finally, in certain instances (bat BE, for example), very sudden changes were noted in the responses: on one test it would catch or attempt all of the spheres of approximately mealworm size; on the next test it would attempt none of them. These three instances obviously contradicted the hypothesis that long and gradual learning was required for targets as different as spheres and mealworms.

Basic to any overt evidence of discrimination, there seemed to be a factor operating in the manner of motivation or attention. To the bats it seemed rather immaterial, for the most part, whether or not they caught the non-edible targets. Either the attention required to discriminate or the motivation to avoid was insufficiently activated to suppress capture. It may be significant that the bat (FB) showing the quickest discrimination had previously been tested with cylinders (of insulated wire) which seemed obnoxious to the bat, when caught. Had some form of punishment been associated with the catching of intermediate-sized spheres, all the bats might have learned the discrimination much more rapidly.

2) Natural Catching Proclivity. In view of the great difficulty commonly encountered in persuading bats to catch anything at all in the laboratory, the idea that a bat's natural catching proclivity must be actively suppressed, to prevent the capture of

even insect-sized objects, may seem contradictory. The laboratory space itself, however, initially seemed to impose one of the most severe forms of suppression on catching activity. Perhaps bats normally interpret the space as a cave for roosting or as an imprisoning region from which escape must be made before catching can be undertaken. The change in behavior of those bats which started to catch was sometimes very sudden: after a single catch of mealworms, they would often begin to pursue almost any reasonable sized object within reach. Perhaps they simply became cognizant of the experimental situation (see 3) below).

The next problem was to obtain selective suppression. At the upper end of the size scale this was easy: most bats learned rather quickly that items only slightly larger than mealworms (eg., spheres of 3/8 inch diameter) were not worth bothering about. At the lower end, however, the situation seemed very different: most bats tended to continue catching objects (notably spheres) down to the size of 1/8 inch or smaller. An obvious interpretation of this downward trend of the sphere-catching curve for *Myotis* is that the preferred natural targets of this bat are in the size range corresponding to spheres of roughly 1/8 inch diameter. If suitable small positive targets (such as insect eggs of 1/8 to 1/6 inch length) were used as the positive target, there should (according to this hypothesis) be little or no upward skew of the curve above this target size. Thus far this has not been tested though we found that bats would readily catch and eat insect eggs of about this size. Another reasonable explanation could be that smaller targets are detected only at close range and thus permit inadequate time for evaluation. It is quite possible, also, that such small airborne objects are seldom as obnoxious when caught as are some of the larger targets. As mentioned in the text, the arctiid moth *Halysidota tessallaris* has been observed to cling to a bat and seriously interfere with its flight.

3) *Non-recognition of the Experimental Situation*. An indication of the capacity of some bats to size up the situation was given just above: a bat which was first tested with unpleasant-seeming targets was the quickest to avoid spheres, and another bat (during some sampling tests with obnoxious-seeming targets) avoided virtually all targets but mealworms. The implication was that these two bats somehow recognized that they were being presented with a dichotomy of choice: 1) edible mealworms or, 2) inedible miscellany. Perhaps their logic might be stated: if not a mealworm, avoid it; while the early logic of the other bats took the form: if not a mealworm, catch it anyway (since it might be edible and no punishment was attached). Certain bats simply became frustrated (and refused to take part in the experiments) when the nature of the situation was not clear to them. Such bats, in other words,

became so disproportionately disturbed by finding that much of what should have been edible was not that they seemed unwilling to learn the nature of the test situation.

4) Propensity for Confirmatory Test.

a. Possible reason for confirmatory testing by bats: Before defining what is meant by this last explanation for the bats' tendency to keep catching (or hitting) the intermediate-sized spheres, it might be profitable to consider a hypothetical hunting situation. We shall assume that early in the evening a certain Myotis goes to a hunting area frequented by large numbers of mosquitoes. Along with these mosquitoes are some inedible beetles of a slightly larger size. The bat can readily distinguish between the two simply on the basis of average reflectancy. All the bat need do in other words is always to catch objects below a certain size range. In this way it saves itself a large amount of effort and trouble. Gradually, however, the mosquitoes become scarse and the beetles become admixed with many edible insects within the same size range. Failing to recognize the existence of new, edible insects the bat would either go hungry or be forced to seek another hunting area. At the same time, however, a more exploratory companion bat finds a different solution. Not satisfied with the initial observation that most targets just above mosquito size are inedible, this bat elects to test such targets at frequent intervals. But rather than making full-fledged catches, involving the biting of an unpleasant target, this bat makes the evaluation by touch: since the unpleasant targets also have a different feel. The bat thus keeps testing its acoustical evaluations with tactile confirmation: constantly monitoring its acoustical decisions and keeping them up to date with the shifting structure of the insect population.

b. Evidence for confirmatory testing: Was there any evidence in the data on spheres that bats made such "confirmatory touches"? Since last-instant acoustical discriminations could presumably not be definitively distinguished in the laboratory from intentional touches of a target, present evidence is inconclusive. It was noted, however, that bats hit or touched occasional targets even though previous tests had indicated that they seemed able to distinguish such targets perfectly from mealworms by echolocation alone. In many such instances no attempt at catching seemed to be made. To gain some idea of where, in the sequence of tosses, such suspicious hits or touches fell, a tabulation was made of the sequential position of all target contacts that occurred after learning was essentially complete.

The method of tabulation was as follows: Learning was assumed to be essentially complete when the number of hits of undesired targets fell to 2 (in the usual series of 10 spheres and 10 mealworms per test). In a given test there were thus three possibilities: no hits, one hit, or two hits. (Tests with 3 to 10 hits were excluded). 70 tests involving 1400 tosses (700 of spheres and 700 of mealworms) were used in the compilation. In 27 of the tests no spheres were hit; in 15 tests one sphere was hit, and in 3 tests two spheres were hit (ie., 6 hits in the three tests). This gave a total of: 15 plus 6 equals 21 touches. To remove irrelevant detail, the sequential positions of the "erroneously" touched targets were reduced to five (ie., first and second presentations were lumped, likewise second and third, etc.). The next step was to see where in this five-stage sequence the erroneous hits tended to occur. The results were: 13 hits for presentations 1 and 2, none for presentations 3 and 4, 2 for presentations 5 and 6, 2 for presentations 7 and 8, and 4 for presentations 9 and 10. This trend of touches suggested that when uncertain about target the bats were likely to touch it on the first or second presentation; but then, recognizing the nature of the target, they did not bother to touch it again until they felt inclined to recheck their acoustical evaluation. Presumably the inclination to recheck such evaluations varied greatly (during the early tests) in different bats, leading in some cases to the appearance of almost complete failure to discriminate.

A conspicuous omission from the breakdown just given was the situation where no spheres were hit. This category included 27 tests, as against 18 for category a above (a hit on the first or second presentation). This perfect-discrimination category, over several test runs, was not unique to any one bat. Moreover, it did not occur entirely after the 1 and 2 hit tests. In other words, regardless of their experience with the situation, the bats either failed to acquire perfect discrimination or were inclined to check their acoustical discrimination. If this latter interpretation is correct, it would follow that even when a bat was capable of perfect discrimination, a residue of "errors" might always remain and that this residue might be more evident within certain size ranges or for certain types of test targets.

d. Application to Acoustical Testing. Before leaving the data on sequential sphere discrimination in *Myotis*, one final speculation should be appended. Just as tactile confirmation may be used intermittently to check acoustical evaluations, so close-range acoustical analysis may be used intermittently to check long-range acoustical impressions. Thus, one bat (BE) often appeared to eliminate pursuit, even of a mealworm-sized sphere, at distances as great as three feet (1 meter) or further. Yet at other times, the decision appeared to be reached at much closer range. In the interests of economy, it would certainly behoove a bat to eliminate unnecessary pursuit as early as possible. At the same time, unvarying elimination on the basis of marginal clues could result in loss of edible targets. The distance of final recognition may thus shift, not only as a function of learning in a given test situation, but also in accordance with a bat's natural tendency to confirm or modify the reference clues which are given by partial sets of acoustical data.

APPENDIX III

ECHO MEASUREMENTS

The chief intent of our observations on the echoes produced by targets and clutter used in the tests was to gain a rough idea of relative amplitudes and configurations of the target echoes as compared with the clutter echoes. A block diagram of the equipment is given in Figure II-1. A signal generating portion of the system had three components as follows: first, an ultrasonic sweep generator capable of producing electrical signals that correspond roughly to the signals produced by various kinds of bats during their different phases of pursuit; second, an electrostatic transducer driver (which amplified the electrical signal up to 200 volts peak-to-peak and imposed a 300 volt bias); and third, a flat electrostatic speaker of 1-1/2 inch diameter (which followed the design of Kuhl et al) (Ref. 22). The speaker was mounted adjacent to the microphone used for receiving the echoes (Fig. II-2). Both speaker and microphone were directed toward the target and sometimes partially partitioned from each other by a thin plate (to reduce acoustical feed-through).

The receiving microphone was designed by L. P. Granath, and was followed by two stages of amplification. The echo signal was then passed through an Allison 2C bandpass filter, set for 20-100 kc before being displayed on a Tektronix 502 oscilloscope. (In later tests, the Allison filter was replaced with a Krohn Hite 310 filter).

The transducer-microphone portion of the system was mounted adjustably at the center of a bar which formed part of the frame of a cubical booth five feet on a side. Another bar ran longitudinally along the top of the booth, from a point over the speaker to the center of the opposite side. This bar permitted convenient suspension of targets and clutter at variable distances in front of the speaker and microphone. Targets were suspended on fine wires (1 to 3 mil diameter), which produced negligible echoes. Most of the inner sides of the cube were lined with 6 inch thick fiberglass insulation. The fiberglass attenuated the ultrasonic pulses to such an extent that no echoes of consequence were returned to the microphone by the back or side surfaces.

For the observations and measurements, pulses of both constant frequency and downward swept frequency were used. Three downward swept frequency ranges were used: 100 kc to 50 kc, 100 kc to 20 kc, and 50 kc to 20 kc. Pulse duration was routinely kept at 1 millisecond.

The selection of pulse frequency ranges (except from 100 to 20 kc) and a duration of 1 millisecond was based on approximations to the pulses commonly used by *Myotis lucifugus* when at distances of one to two feet from an object. Actually, this is an oversimplification; but we felt it gave convenient approximations adequate for the present purpose. As a *Myotis lucifugus* approaches an object, its pulses shorten from an initial length of 2 or 3 milliseconds to about 1 millisecond before any significant change occurs in the range of frequency sweep. With closer approach, the pulses shorten markedly (eventually down to 1/3 millisecond), the repetition rate goes up (to nearly 200 per second), and the frequency range slides down until it is of the order of 35 to 25 kc. With other vespertilionid bats, considerable differences may exist. For example, the pulses of *Lasiurus borealis* tend to be longer, until a point of close approach, and they never exhibit the marked fall in frequency range that is seen in the pulses of *Myotis*. In *Eptesicus fuscus*, the fundamental frequency is, for the most part, only about half as high as that of Myotis pulses. Still different variations are seen in other bats (Ref. 4, 10, 11, 13 & 25).

The system available to us had several defects. Most conspicuous was a marked resonance that was peaked in the vicinity of 50 kc (see Fig. II-3). Troublesome, also, was the marked nonlinearity of the waveform below 30 or 40 kc. In addition, the initial and terminal portions of the pulses were characterized by further distortion. For pusposes of very rough comparative evaluations, however, the system proved useful.

The limitations of the synthetic echo system were such that we decided that quantitative evaluation of frequency swept pulses would be unprofitable. We limited our observations to a rough attempt to determine three things:

1) How does the average reflectance of a mealworm compare with the reflectance of a more uniform target such as a sphere?

2) How much variation in average amplitude and amplitude pattern is a mealworm likely to exhibit during the approach of a bat?

3) How does the reflectance of a mealworm to a bat pulse compare with the pattern of reflectance given by some of the clutter backgrounds used in the tests?

Figures II-4 and II-5 show the relative echo amplitudes returned by a mealworm and several sizes of smooth spheres to a constant frequency pulse of 100 kc. According to their shape, orientation and size, mealworms give a reflectance corresponding to spheres that range, for the most part, from about 5/32 inch diameter to about 3/8 inch diameter. The reflectance of the fruit fly tested corresponded roughly to that given by a 1/8 inch sphere (Fig. II-4c).

Figures II-6 and II-7 give examples of the echo reflective patterns from a mealworm and from three sizes of sphere (1/8 inch, 1/4 inch, and 5/16 inch) to a pulse which sweeps from 100 to 20 kc. (This represents the full range of frequencies used by Myotis lucifugus but is, of course, greater than is incorporated in any single actual bat pulse.) Far greater variations of amplitude pattern are often seen in the echoes from mealworms (see eg., Ref. 14).

Figure II-8 shows the echo pattern returned by a 100 to 20 kc pulse when a mealworm was suspended just in front of a typical yew branch. Most of the low amplitude disturbance to the right of the central axis is due to the mealworm, while the large amplitude disturbance to the left is due to the clutter. As the mealworm is removed into the space between sprigs of clutter, visual detection of a static mealworm echo is usually impossible. However, when the mealworm is swung to and fro within the space, the shifting position of the mealworm echo becomes clearly visible. Undoubtedly, target motion relative to the clutter background is often essential to the bat's detection and localization.

APPENDIX IV

EFFECTS OF ULTRASONIC NOISE ON THE PURSUIT PERFORMANCE OF BATS

Observations on the effects of interfering ultrasound, synthetically produced, have been very limited. These have formed part of a study in our laboratory by D. C. Dunning of Tufts University, and some initial results have been recently published (Ref. 7). Noise of 50 db (re 0.0002 dymes/cm^2) or more within the signal band of the bats, when introduced at the time of detection or early pursuit, produced distinctive responses that were obviously unrelated to pure jamming. They mostly consisted of abrupt turn-aways, even when the noise level was relatively low. Such responses may be related to the sudden terminations of pursuit often noted with moths capable of emitting ultrasonic clicks. Such clicks are clearly much too weak to produce direct jamming; and they do not appear to bear time relations to the bat's emitted signal compatible with the generation of phantom echoes diverging from the actual echoes of the target. The effects of noise on pursuit require further investigations with carefully worked out experimental procedures.

APPENDIX V

COMPARISON WITH OTHER SYSTEMS

Informal consideration has been given to the attributes of the bat's echolocation methods, as a system of pursuit guidance, relative to other systems. Perhaps the closest natural system is that of the porpoise - possibly 100,000 times as large. The system of the porpoise undoubtedly has to deal with far more complex configurations of both targets and surrounding objects and with vastly greater ranges, but it does not have to function nearly as fast. Echolocation systems in general suffer from the requirement of having to convert essentially one-dimensional sequences into indications of three dimensional reference. Visual systems have increased initial dimensionality. Yet, relative to visual systems, echolocation methods may gain an advantage in the evaluation of range. Further study will be necessary to define comprehensively and accurately just what the performance capacities of natural echolocation systems really are.

APPENDIX VI

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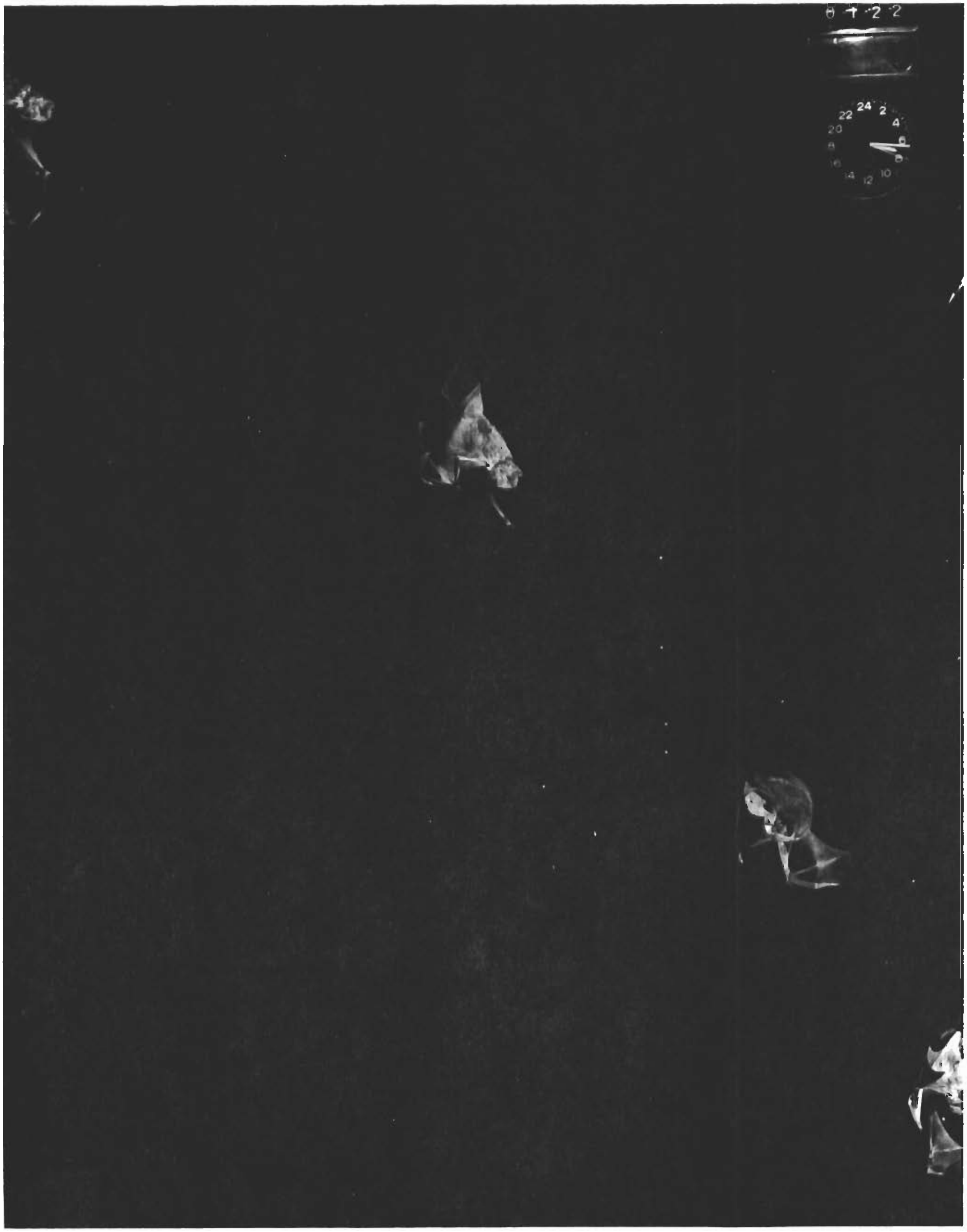

FIGURE 1a. Catch of a 1/16 inch nylon sphere by _Lasiurus borealis_.

FIGURE 1b. Catch of 1/16 inch nylon sphere by *Myotis lucifugus*.

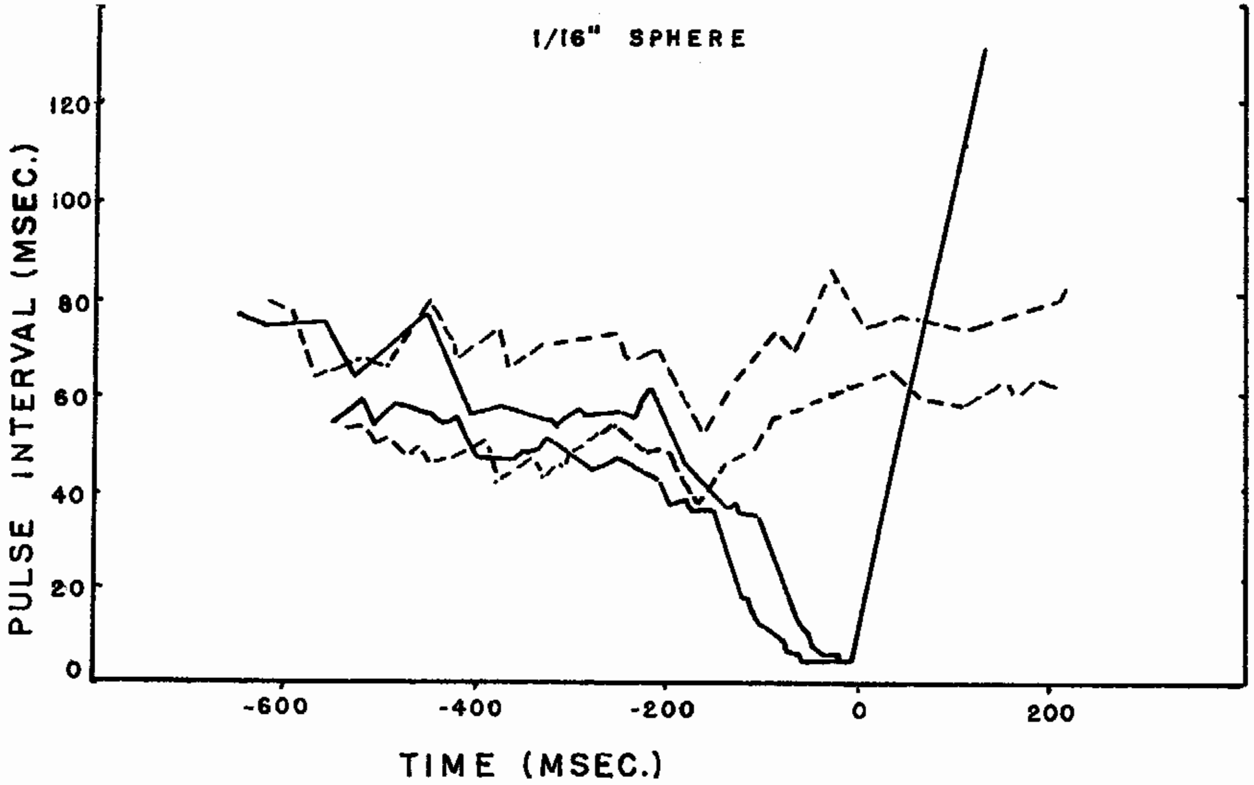

FIGURE 2. Pulse pattern envelopes for *Myotis lucifugus* when presented with 1/16 inch nylon sphere. Solid lines enclose pulse repetition sequences for 4 catches, while broken lines enclose repetition sequences for 6 non-pursuits. Separation of the two sets of patterns occurs at about 200 milliseconds prior to the end of the terminal buzz (for catches). (In Figures 3a & 3b the lines also enclose all deviations of pulse patterns obtained during the tests illustrated).

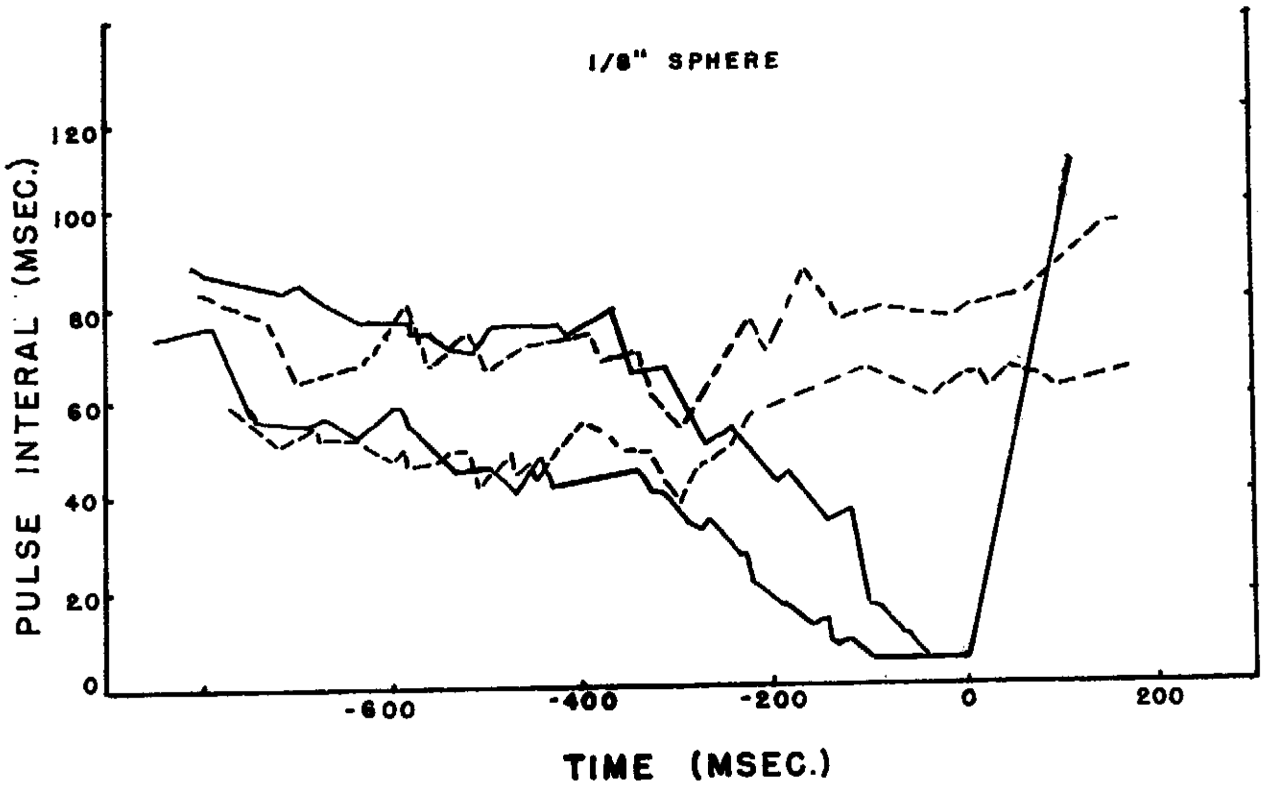

FIGURE 3a. Comparison of non-pursuit pattern of Figure 2 with pursuit pattern associated with pursuit of 1/8 inch sphere. The non-pursuit pattern apparently represents the bat's response when no significant detection takes place: the dip in the curves representing the point of decision beyond which active search is relinquished. Since the separation of the curves takes place about 300 milliseconds prior to the end of the terminal buzz (for catches of the 1/8 inch sphere), detection of this sphere must have taken place by this point.

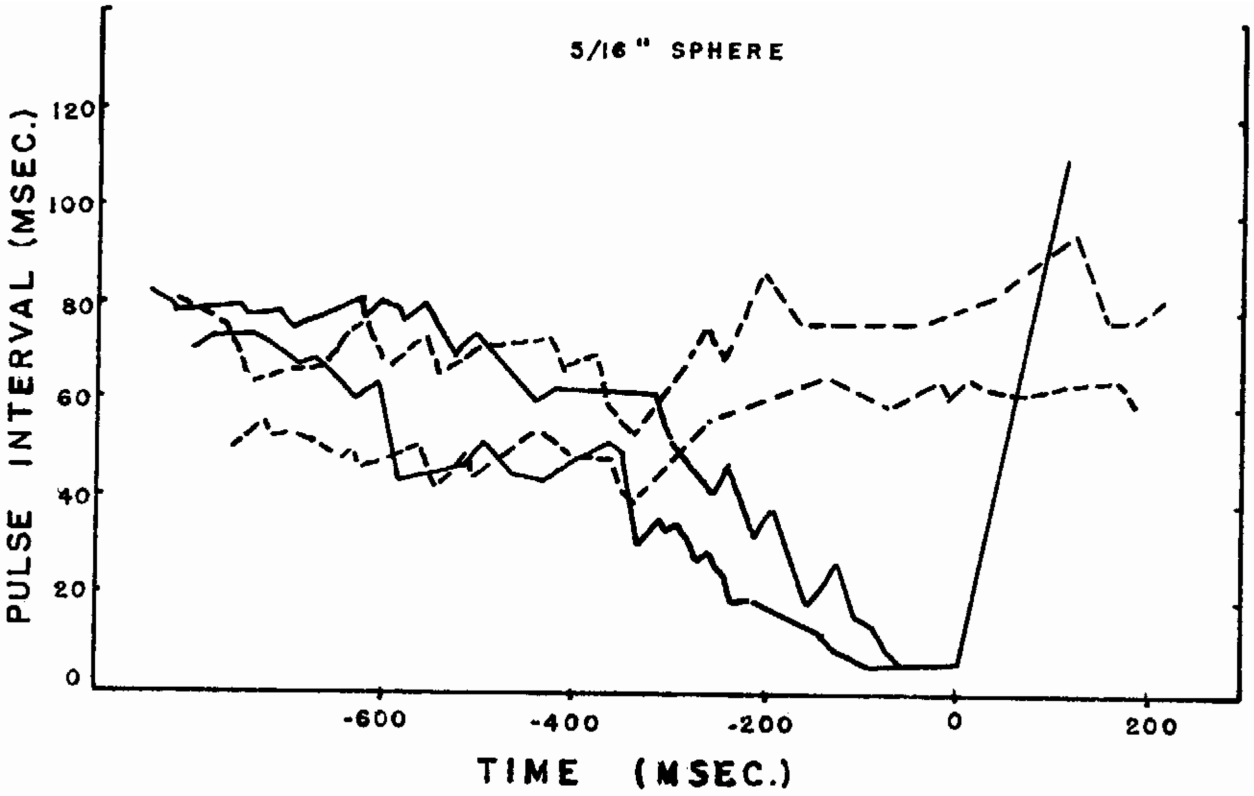

FIGURE 3b. Comparison of non-pursuit pulse pattern of Figure 2 with pursuit pattern associated with pursuit of 5/16 inch sphere. Although the cross section area of the target is about 6 times as large as that of the 1/8 inch sphere, no significant difference in the point of separation of the curves is evident.

FIGURE 4. Capture of falling mealworm with the use of downward extension of wing. Although the target appears to fall more rapidly than the bat seems to have estimated (as judged from the too-high aim of the approach path), the wing is extended accurately downward; and it is obvious that the target will lodge in the groove formed by the sharply bent-over wingtip. (From there it will be transferred into the pouch of the tail membrane and then to the mouth.)

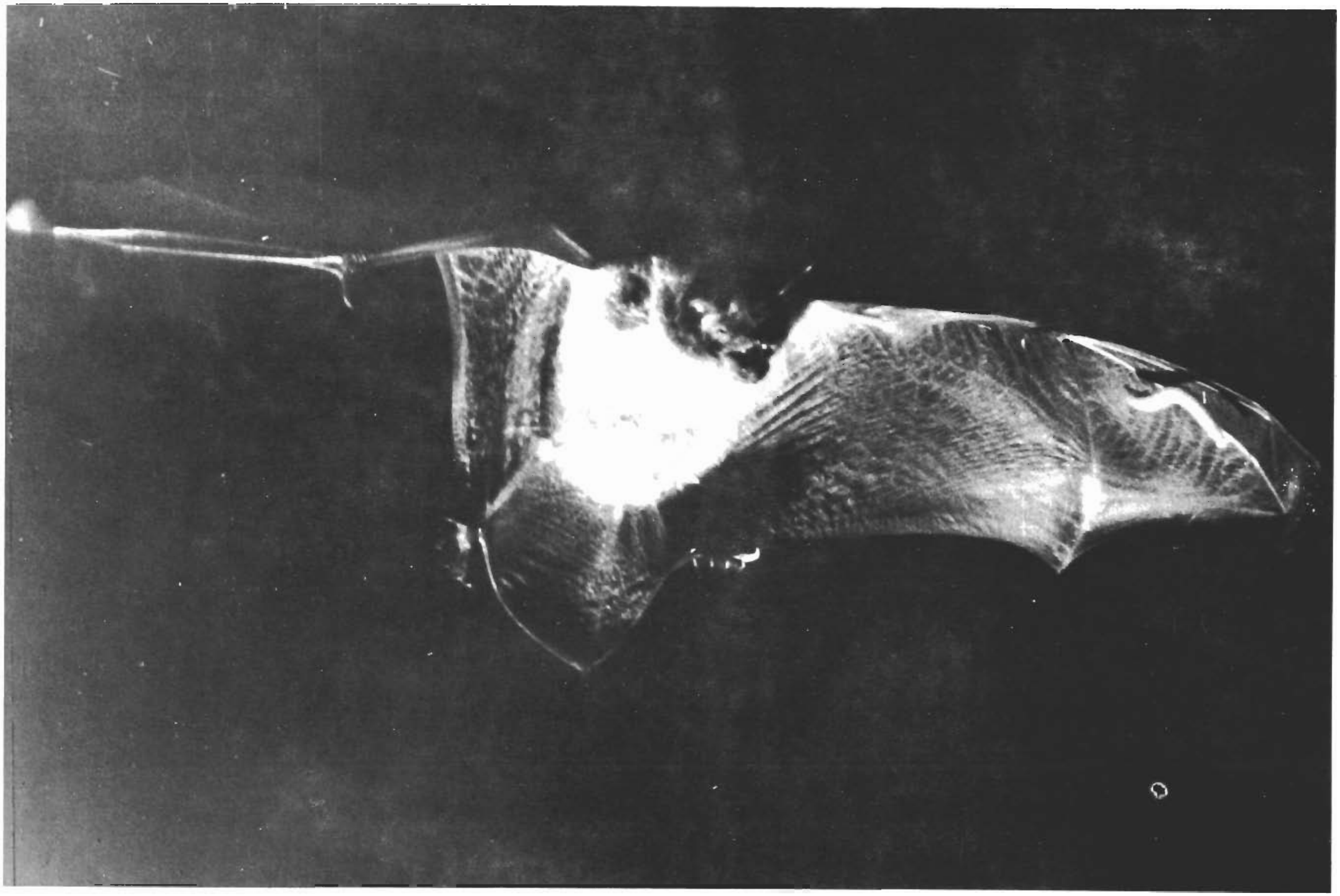

FIGURE 4 (inset). Detail of wing capture. Note target about to make contact with wing just above bent-over wingtip. Bat's head no longer follows target as final catch maneuver is initiated.

FIGURE 5a. Apparent sudden detection and localization of overhead moth. At first image, bat is flying down past red pine clutter with no apparent awareness of moth above. At second image, bat's head is turned toward right. At third image, it is directed overhead toward descending moth. At final image, bat is following moth as it dives down below level of bat.

FIGURE 5b (inset). Detail of head action of Figure 5a.

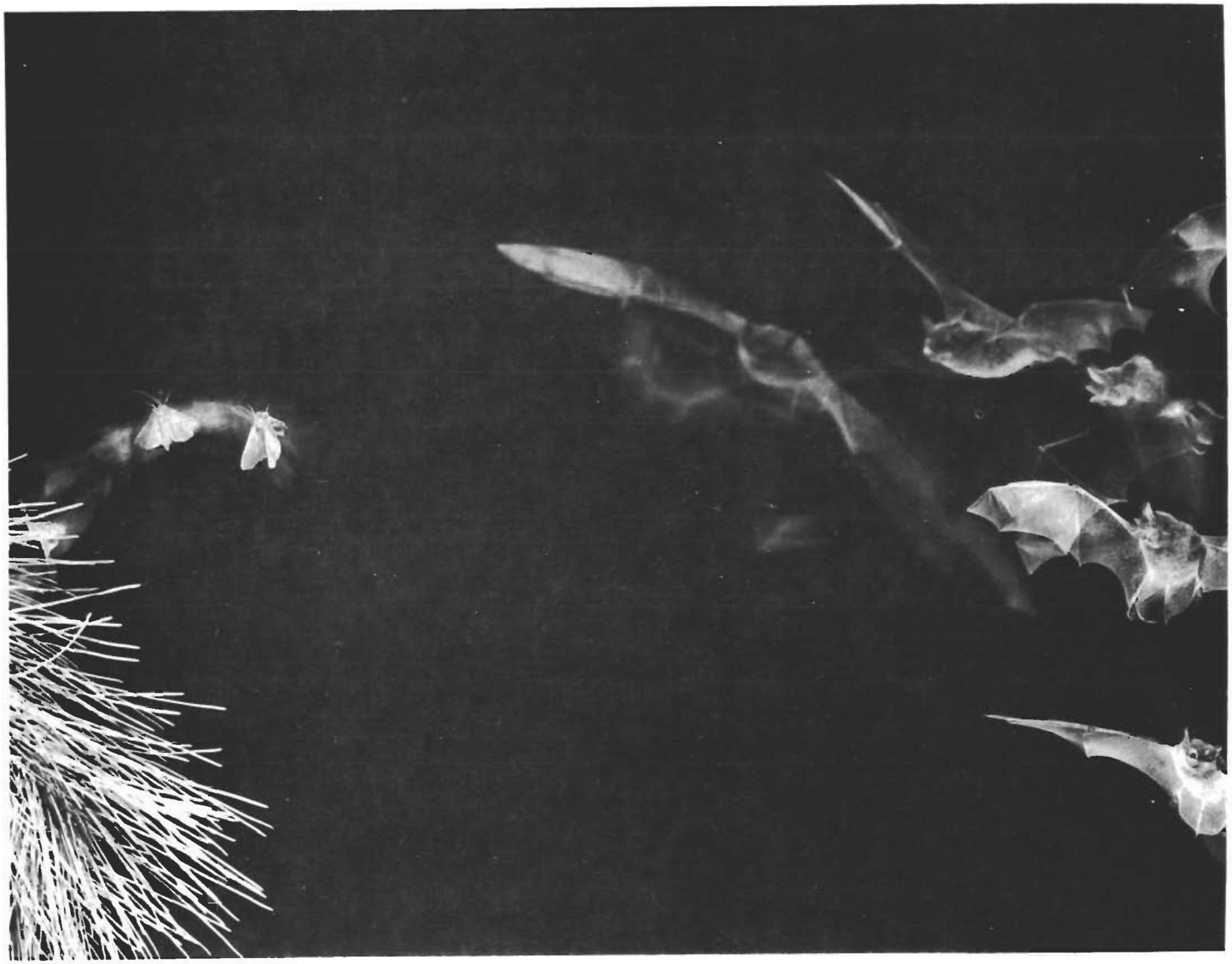

FIGURE 5c. Apparent sudden detection and localization of moth against clutter to right of bat. The bat's head is suddenly directed to the right between the first and second images. By image #3 pursuit is initiated, but as moth flies into clutter, it is promptly given up.

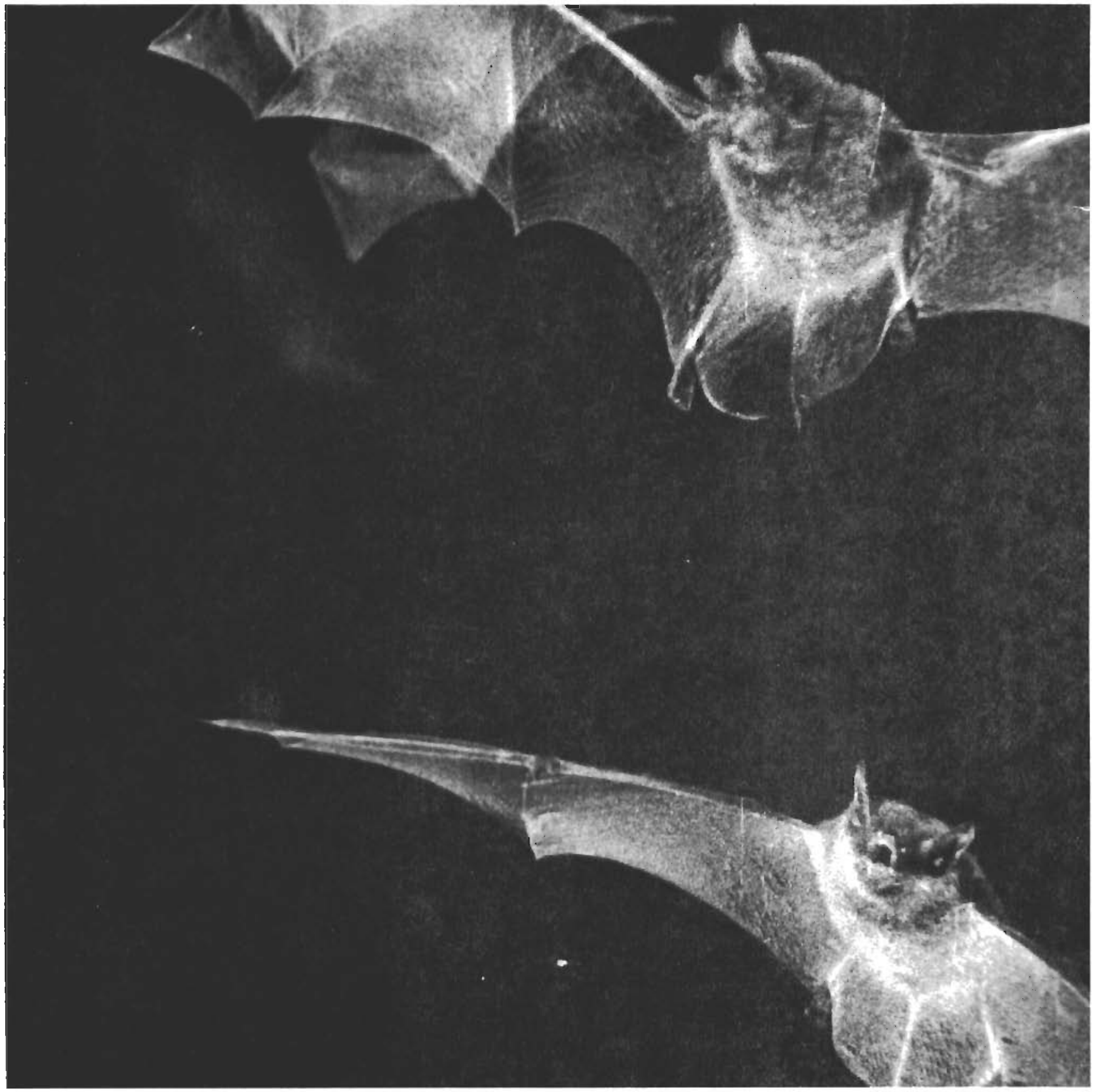

FIGURE 5d (inset). Detail of head action of Figure 5c.

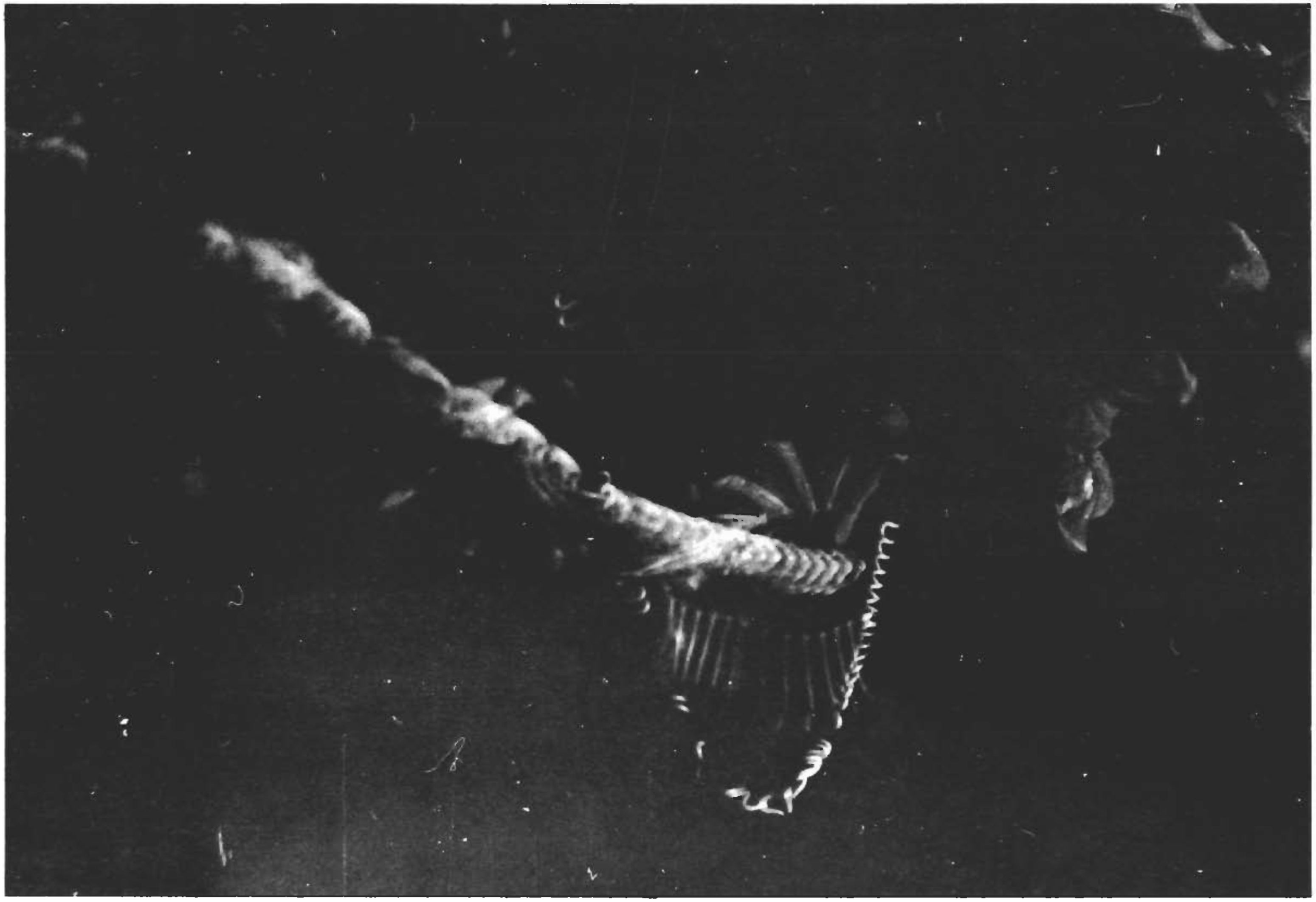

FIGURE 6a. Wingtip catch of mealworm, photographed by pulse-activated strobe light. The most striking feature is the extremely rapid final action of the lower wing (used to catch the target). Terminal pulse rate was about 185 pulses per second. In the last 4 intervals, the tip of the wing was swept around in an arc of over 6 inches to reach precise point required for catch. (Acoustical delay to strobe trigger equalled one pulse interval at end of approach). (Double images during early portion of approach are due to wall echoes, which produced double triggering).

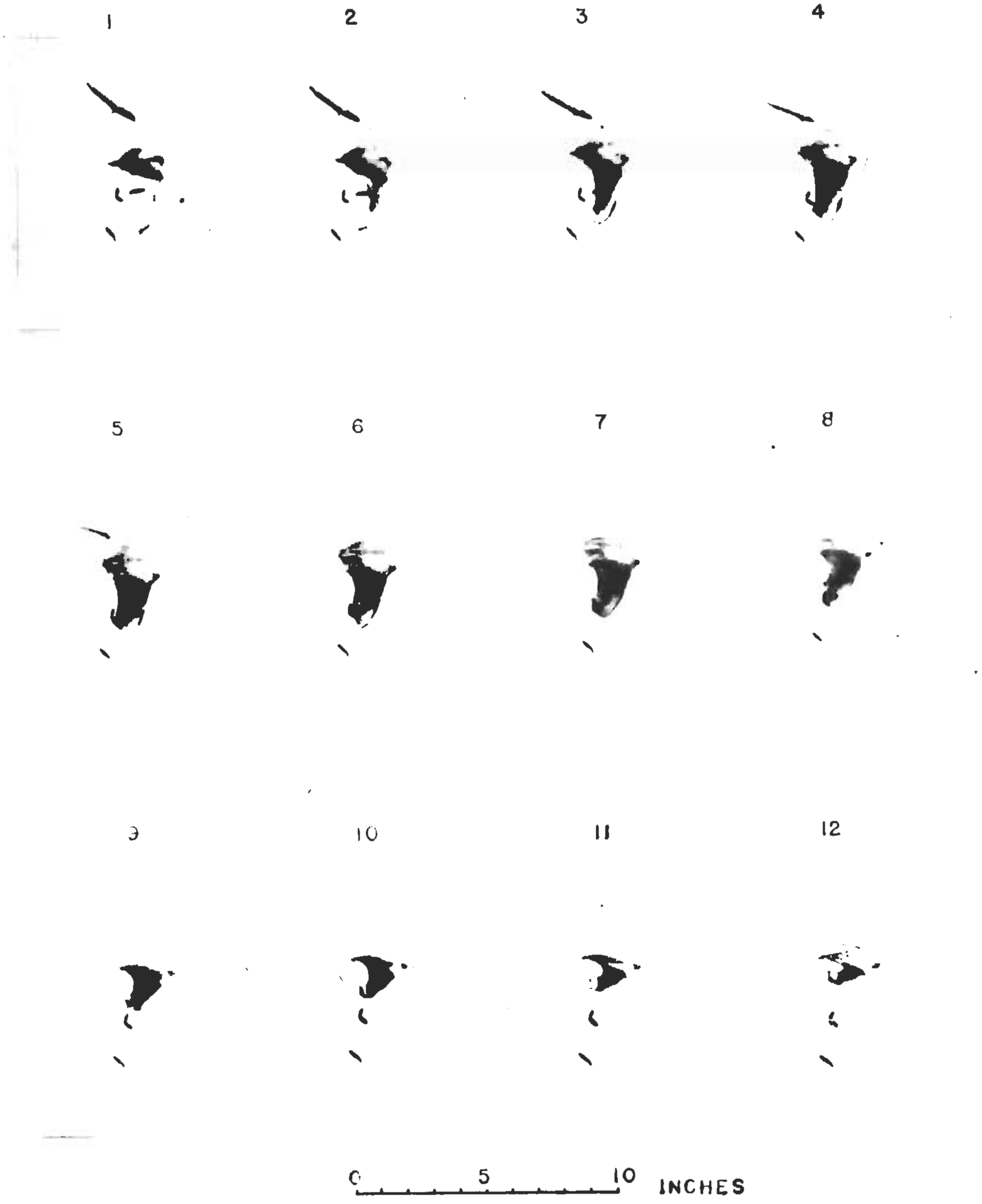

FIGURE 6b. Seizure of one out of three nearby mealworms with the use of a wingtip. Upper right mealworm is carefully selected and pulled away from closely adjacent one. (This sequence is printed from a high-speed motion picture film, originally taken at 768 frames per second. Images shown here are separated by 2.7 milliseconds, the whole sequence occupying less than 1/30 second.)

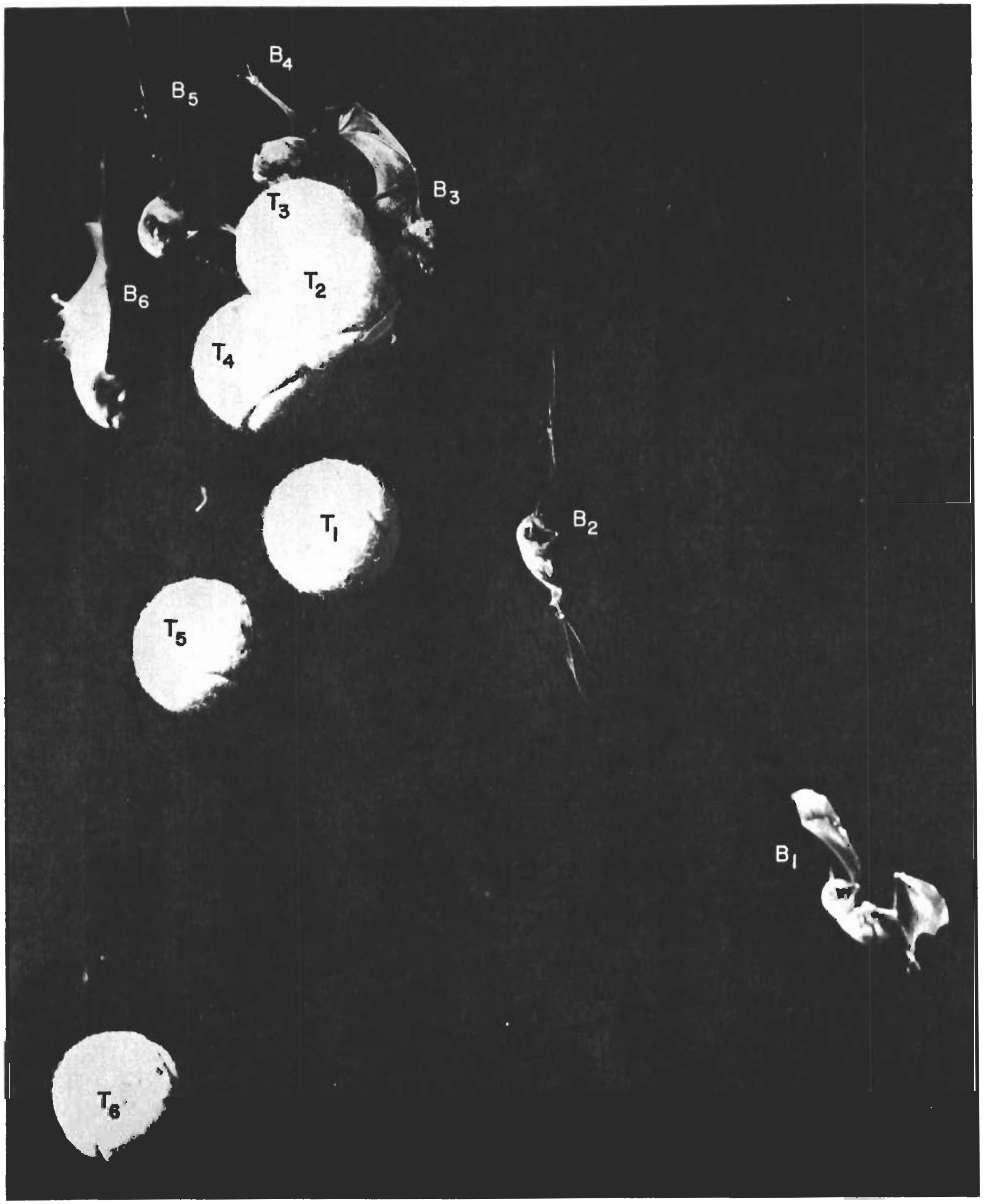

FIGURE 6c. Touch of tennis ball by Myotis lucifugus. Correspondingly numbered images of bat and tennis ball show bat approaching and extending its wings partially around ball in preparation for capture. At fourth image, the bat is passing just to the right of, and above, the falling ball having displaced it slightly by a light touch. (In another sequence a Myotis keenii seized a tennis ball and dropped about a foot with it).

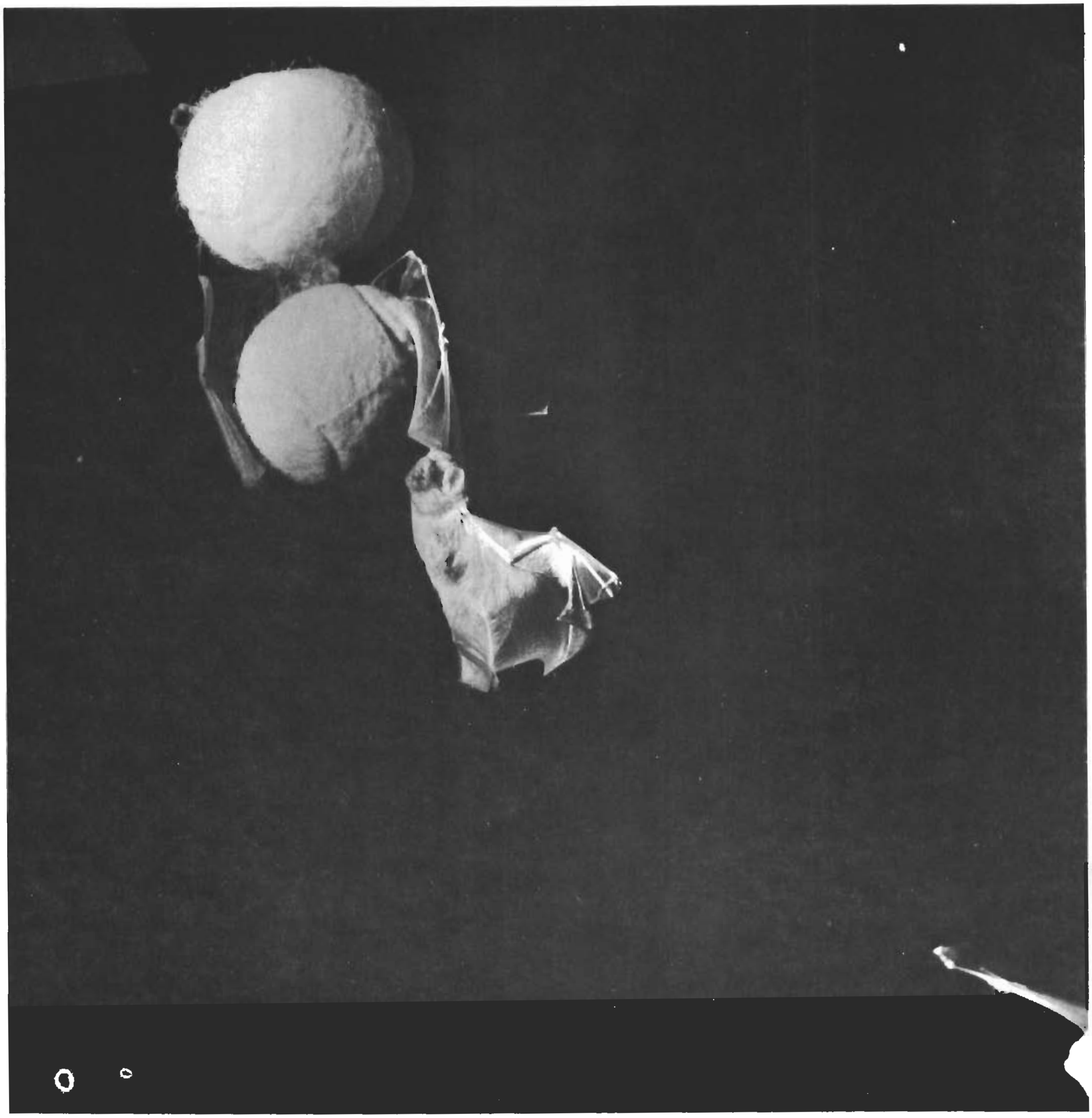

FIGURE 6d. Catch and drop of tennis ball by *Lasiurus borealis*. Images of tennis ball corresponding to first two images of bat are at top. At image #3 bat is behind tennis ball, with wings extended and ball partially in tail membrane. Another sequence shows wings and tail membrane wrapped around ball.

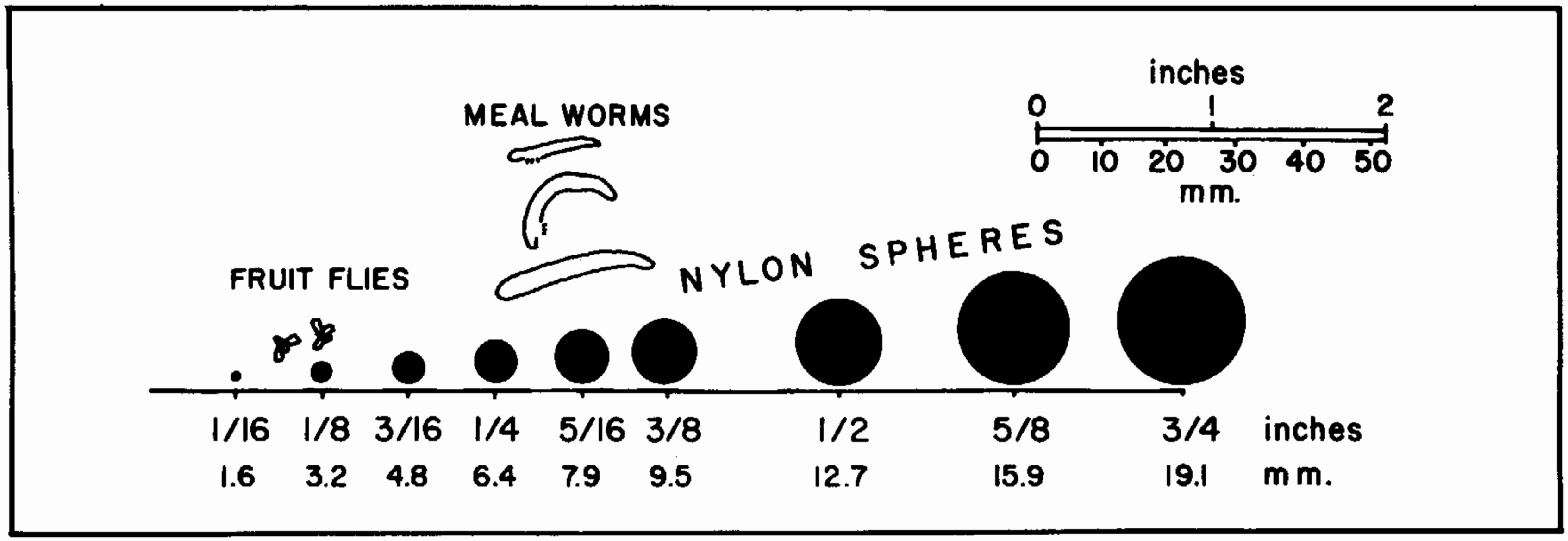

FIGURE 7. Targets used in discrimination tests. The diameters of spheres used in most of the discrimination tests ranged from 1/16 inch to 3/4 inch although larger sizes were also employed in a number of instances. In pilot tests, lead shot of roughly 1/32 inch diameter gave only rare and marginal evidence of detection and, hence, were eliminated from further use. The mealworms illustrated cover the total range of sizes: the curved worm being most representative. At times, a number of fruit flies were present in the flight space - the bats often catching them.

FIGURE 8. Average error percentages for spheres vs. mealworms for all bats on all tests during first series of discrimination tests. (Adapted from Fig. 6 of Ref. 39).

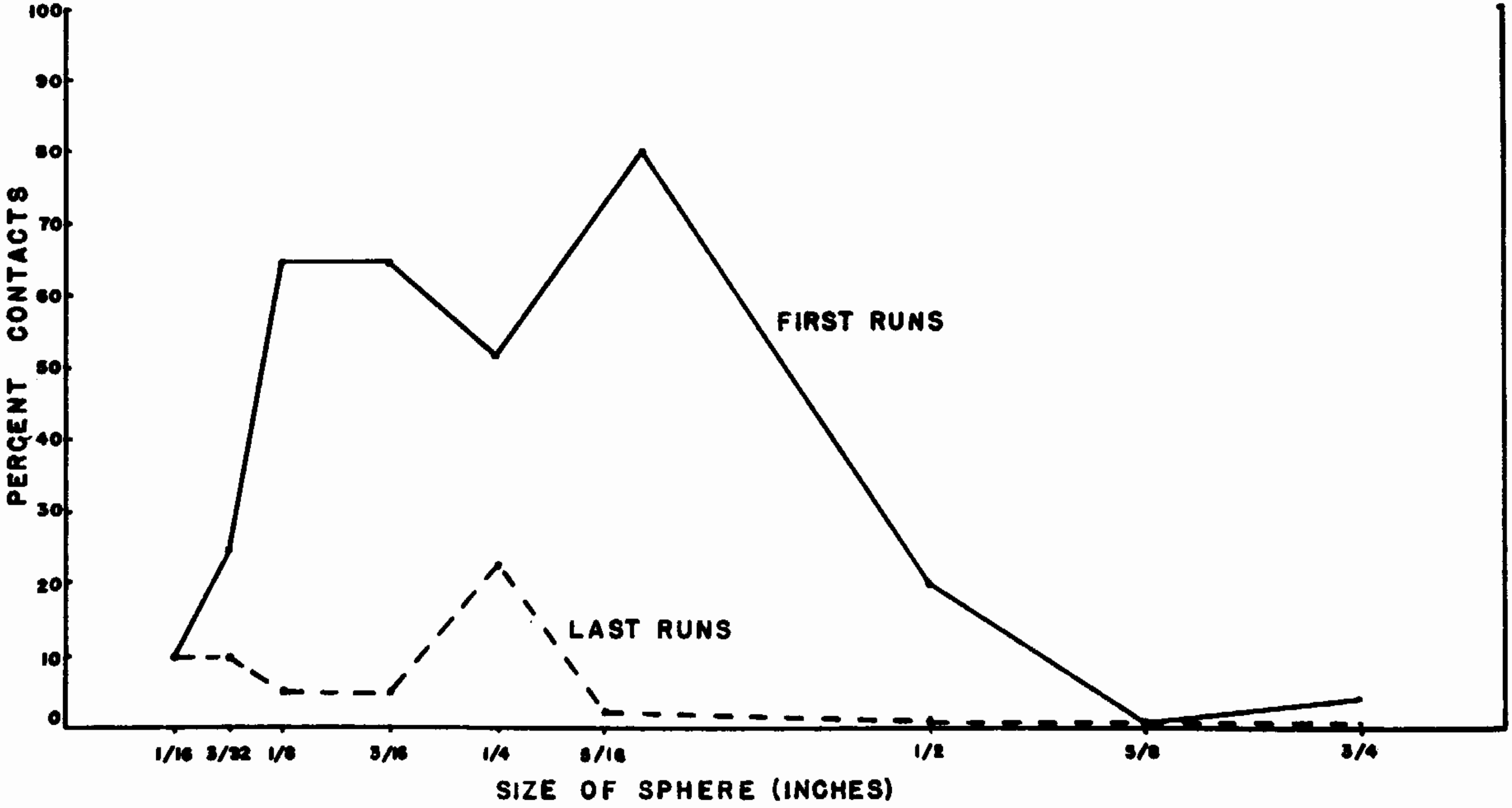

FIGURE 9. Comparison of errors with spheres on first and last runs. (Adapted from Fig. 7 of Ref. 39).

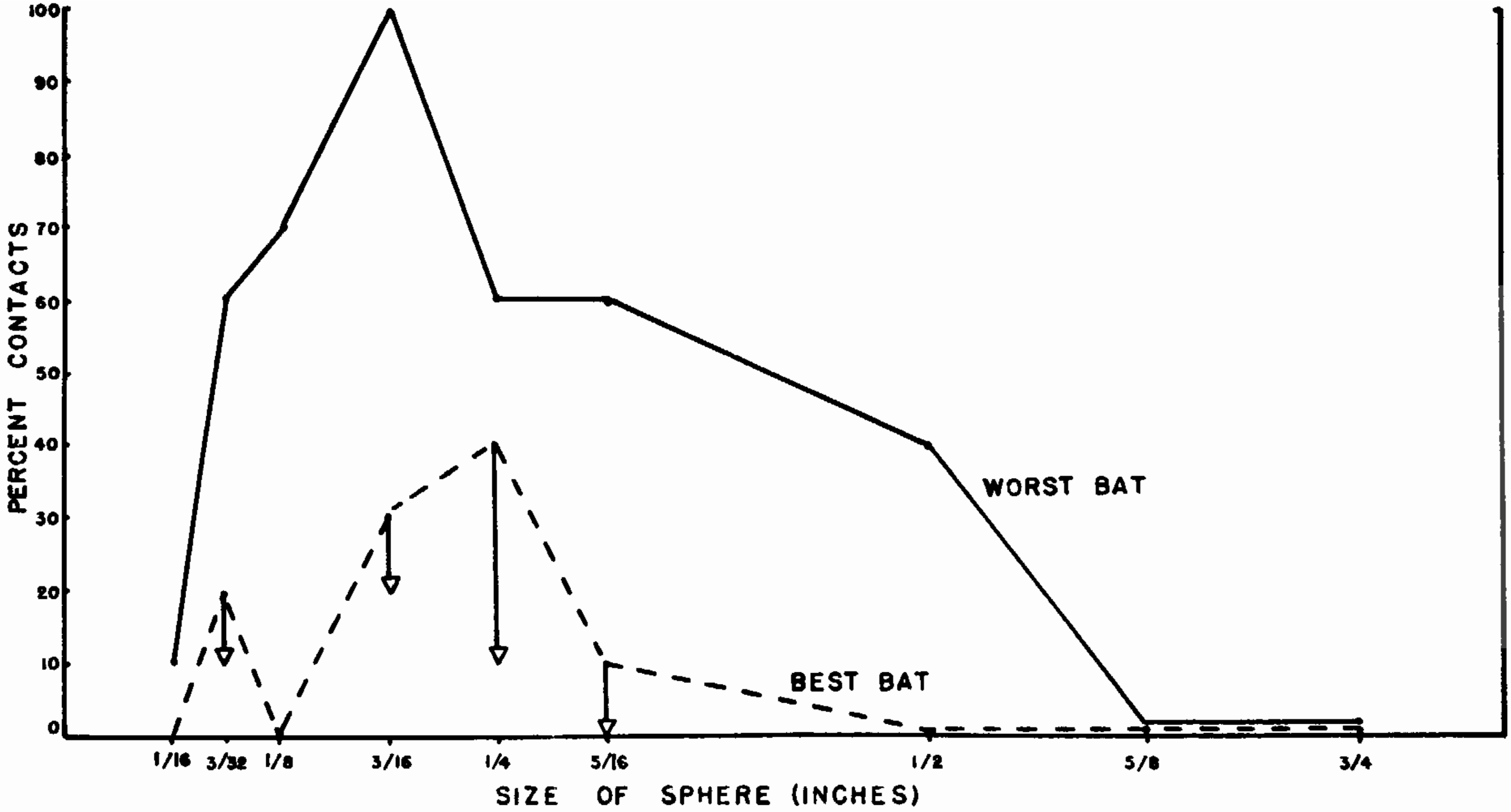

FIGURE 10. Comparison of errors with spheres on first runs for best and worst bats. Downward pointing arrows show improvement of best bat during second half of (extended) tests. (Modified from Fig. 9 of Ref. 39).

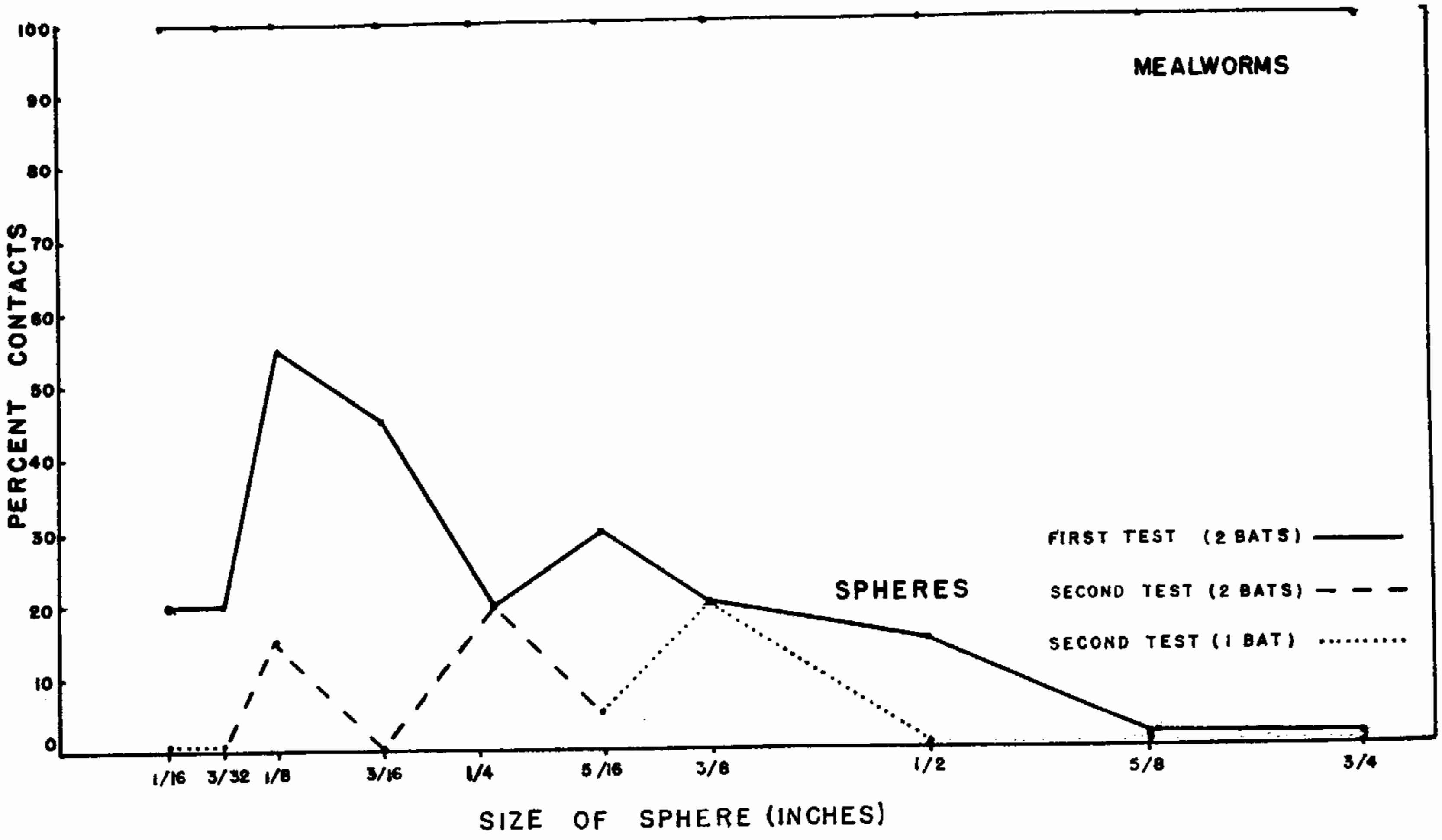

FIGURE 11. Comparison of errors with spheres on first and second sets of runs for two bats with sequential presentation and one size of sphere per run. In the total 360 mealworm presentations there were only three misses.

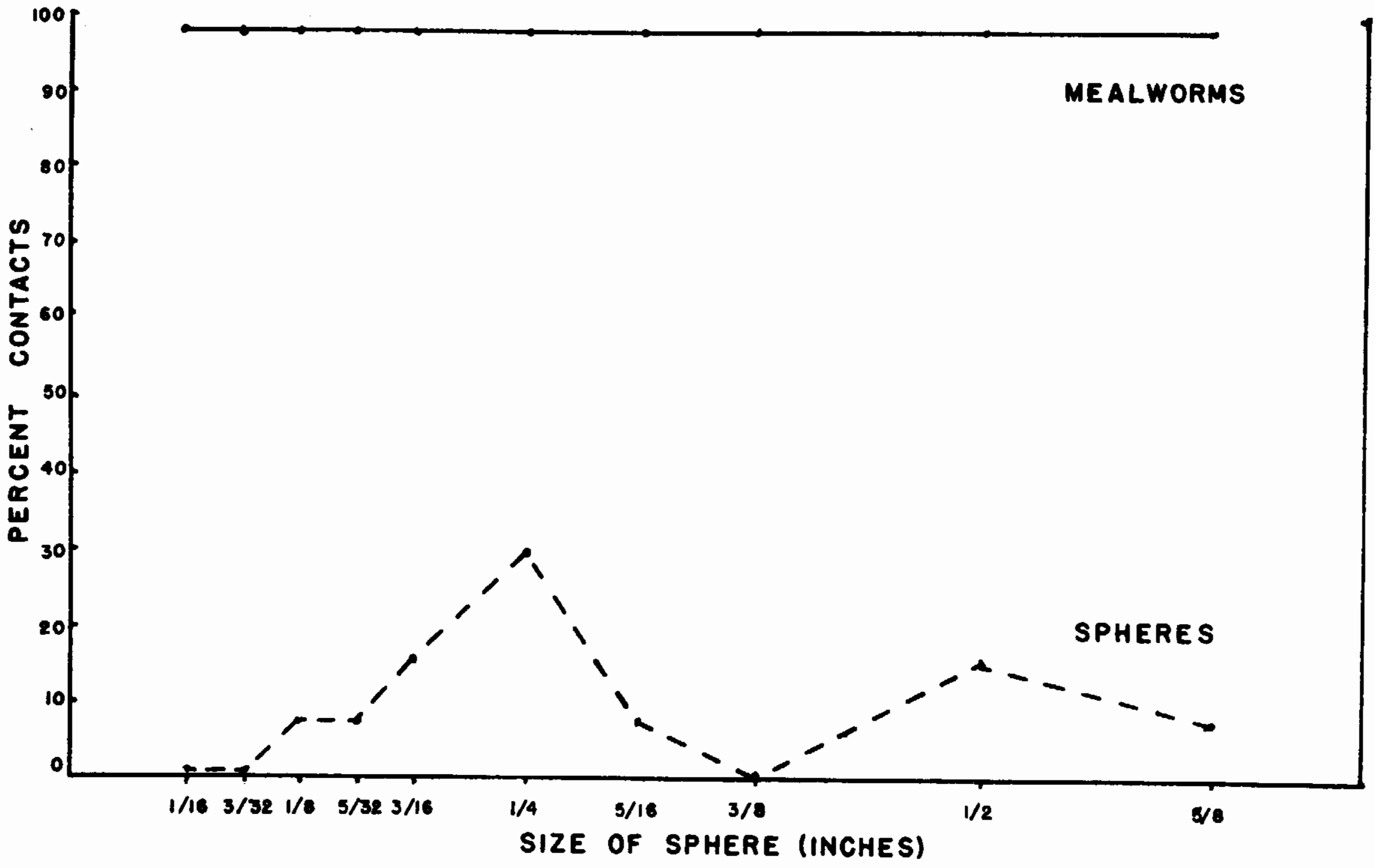

FIGURE 12. Error percentages (for same bats as in Fig. 11) with sequential presentation and mixed sizes of spheres per run. Three mealworms were missed in 130 presentations.

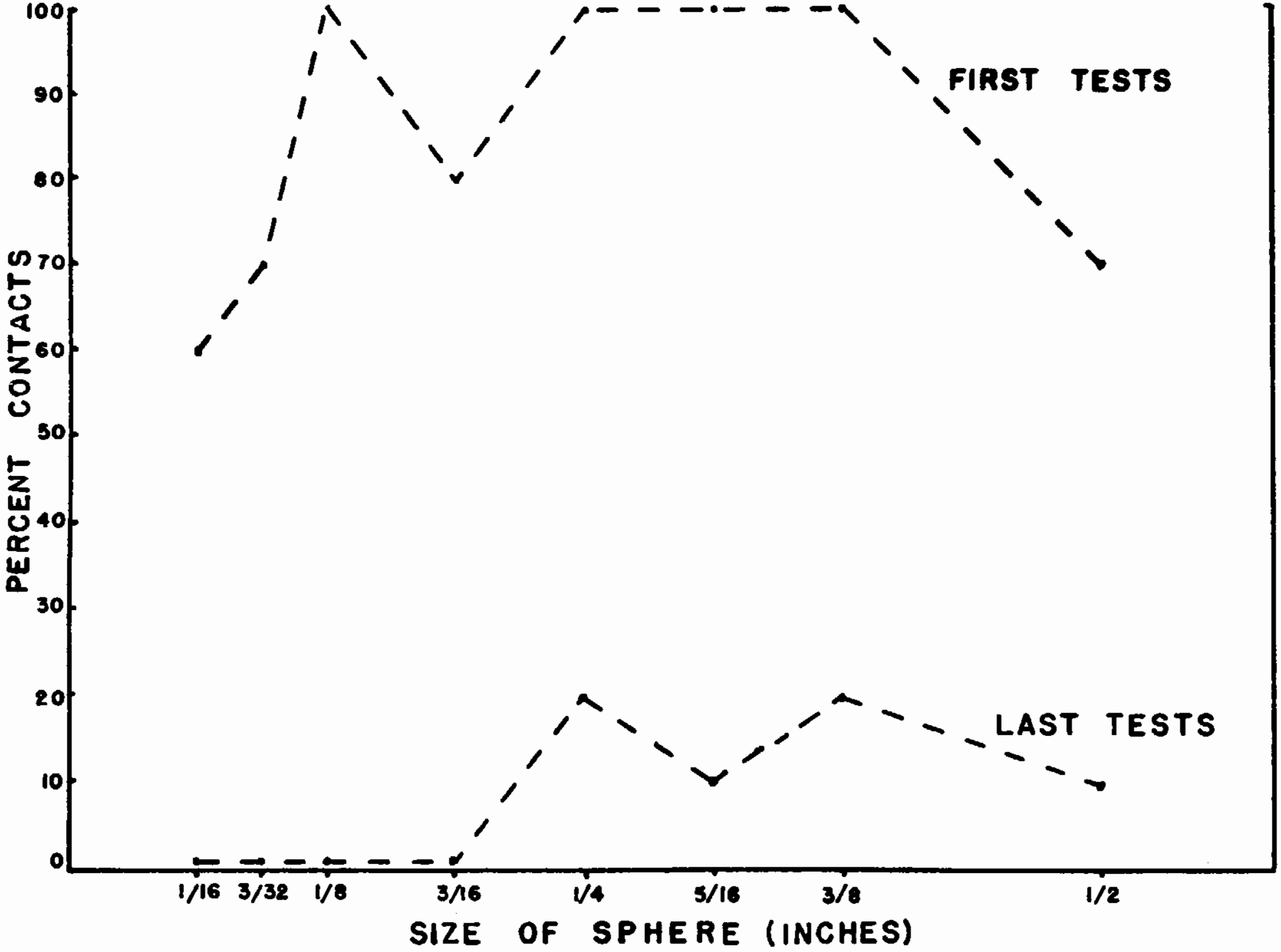

FIGURE 13. Comparison of first four runs and second four runs on one bat with sequential presentation and mixed sizes of spheres per run. No mealworms were missed during these tests.

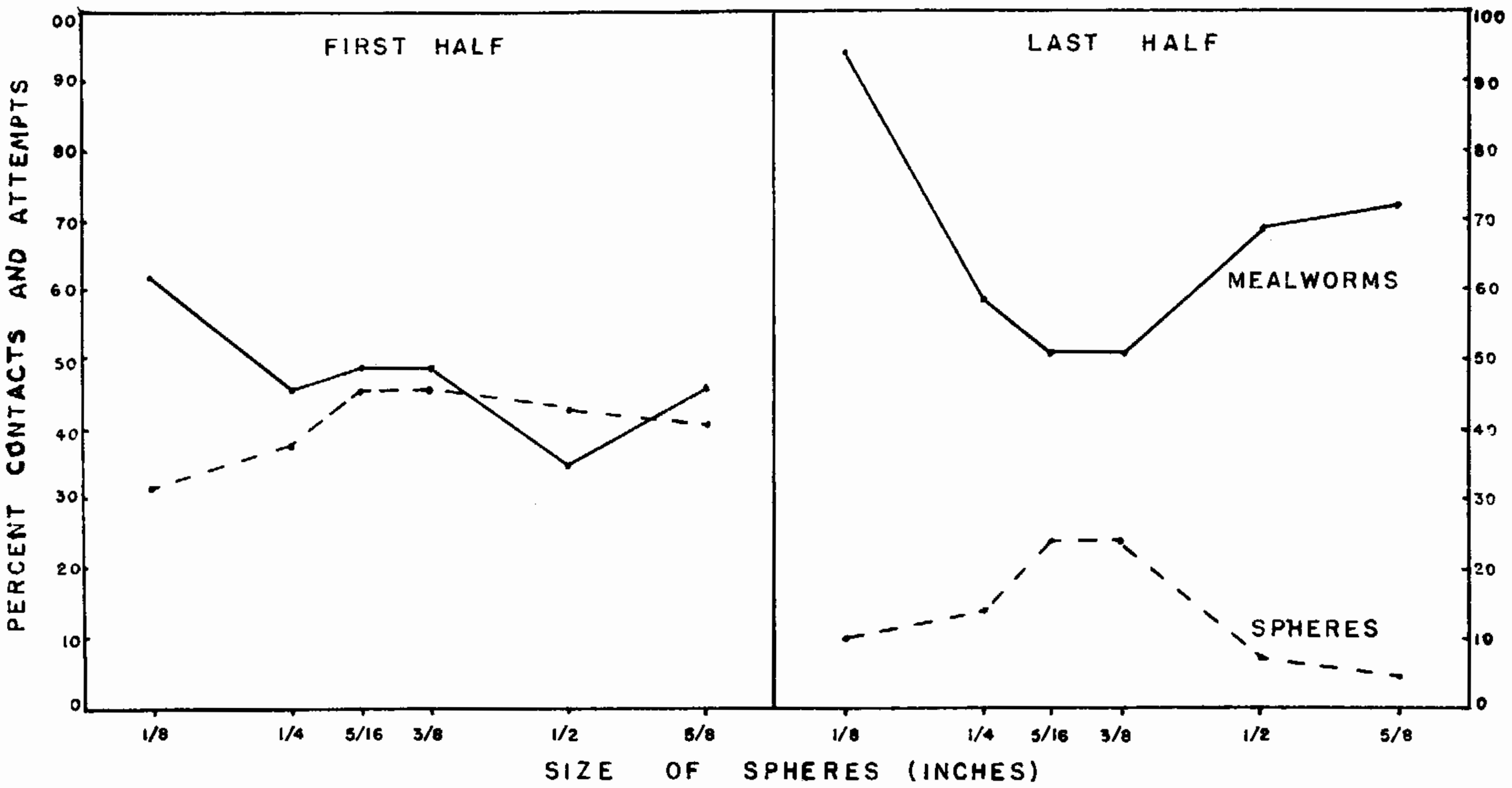

FIGURE 14. Comparison of first and last sets of runs for three bats, with simultaneous presentation (of sphere and mealworm) and one size of sphere per run.

FIGURE 15. Selection and catch of mealworm out of cluster consisting of six mealworms and a 1/8 inch nylon sphere.

FIGURE 16. Somersault catch of one out of two mealworms by *Lasiurus borealis*.

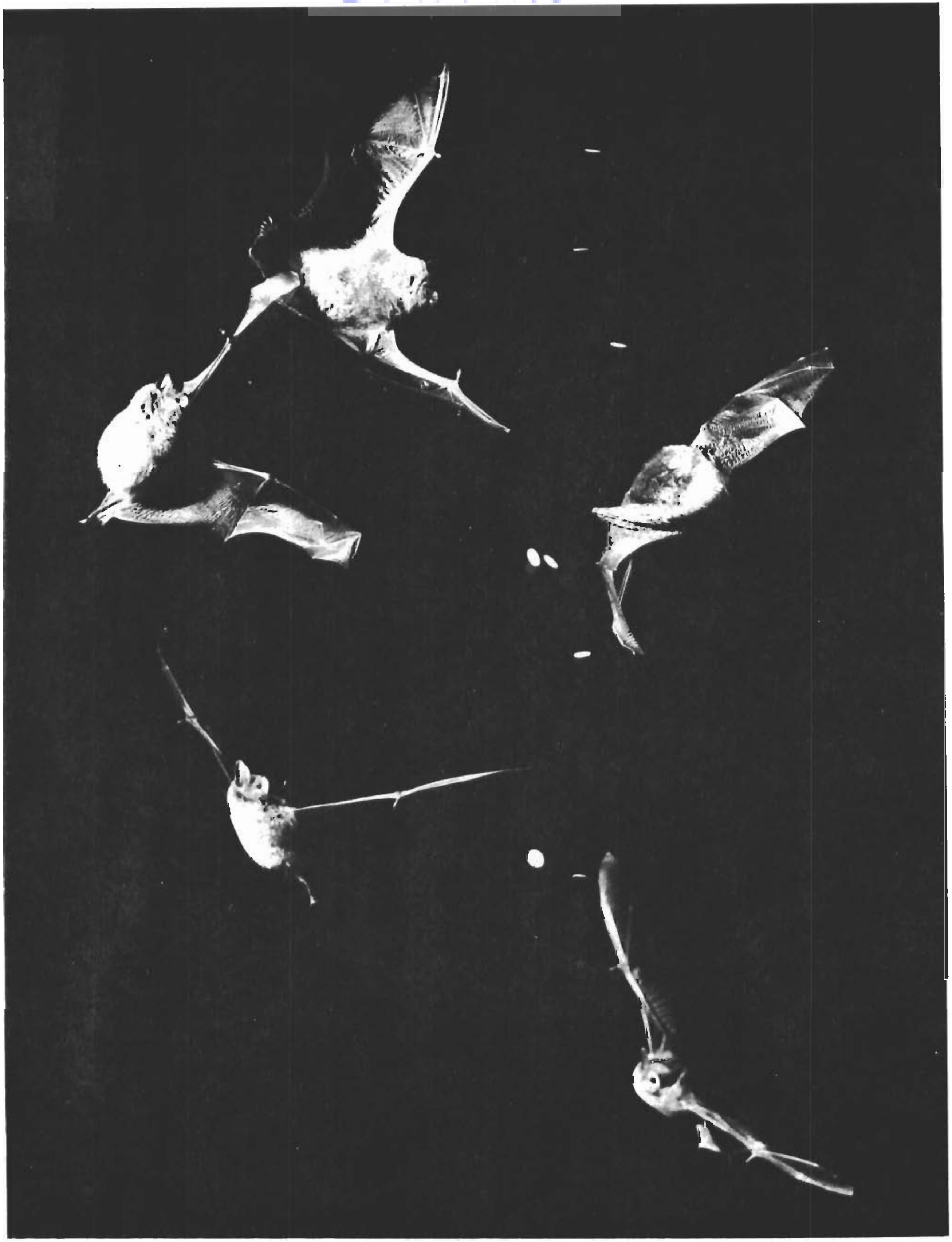

FIGURE 17. Approach of Myotis lucifugus to lower small disc with subsequent shift of attention to upper disc which is being caught in lower portion of downward-extending wing at last image.

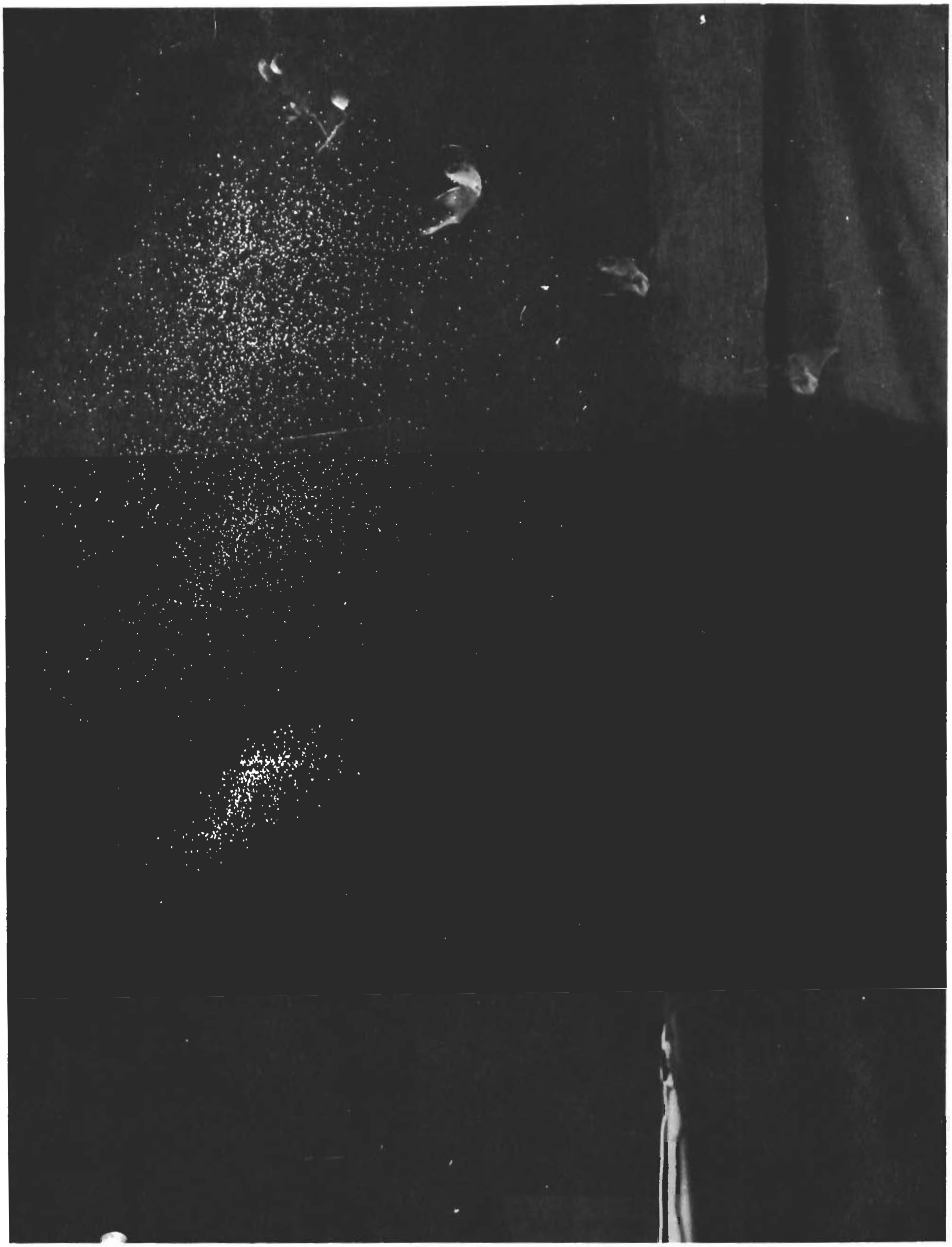

FIGURE 18. Approach to edge of large cluster (200 or so) 1/16 inch "jiffy-gem" candies by _Myotis lucifugus_.

FIGURE 19a. Attempt to catch tip of hemlock twig by Myotis lucifugus.

FIGURE 19b. Attempt to catch tip of pine needle. At next to last image, needle is being deflected upward by tail membrane; at final image, it has sprung back past its rest position. Mealworm which was originally being tracked is coming down at top of picture.

FIGURE 19c. Sudden shift of attention from overhead mealworm (not shown) to tip of pine needle. The bat's catch maneuver flicked the needle upward. It is curved up into space between the clusters at the last image.

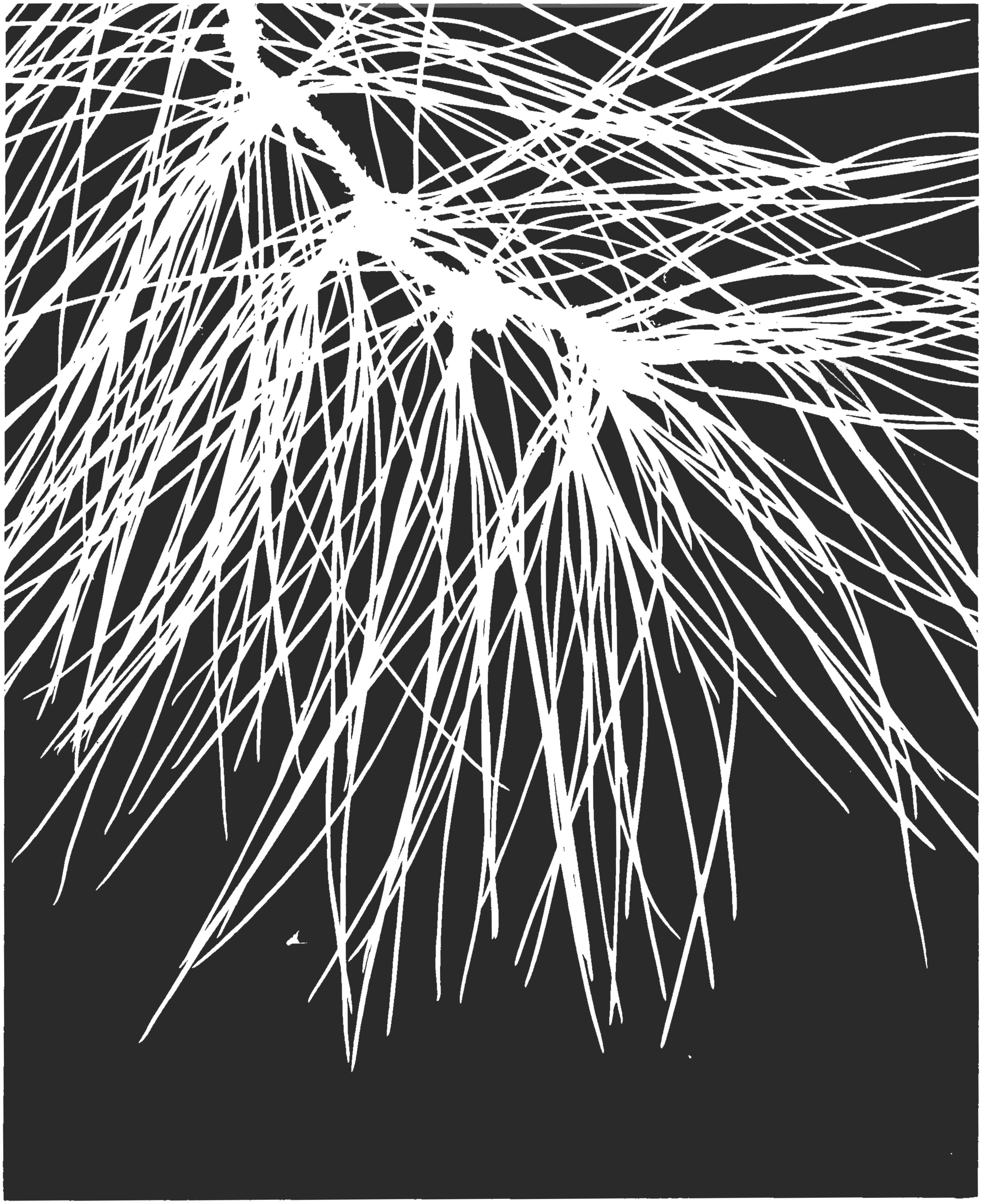

FIGURE 19d. Size comparison of fruit fly and tips of pine needles. Since a number of fruit flies were present during these tests in the vicinity of the clutter backgrounds, it is possible that the tips of the needles were occasionally mistaken for small flies.

FIGURE 20. Selection and capture of one "jiffy-gem" out of cluster of 16 or so. Although selected target differs from others, in that it is double, it seems unlikely that this individual target was selected from so large a group because of its shape.

FIGURE 20a.(inset). Detail of portion of catch maneuver of Fig. 20.

FIGURE 21. Selection and hit of one out of four 1/16 inch nylon spheres. (Sphere was knocked upward by tail membrane and shows at top of picture in last image).

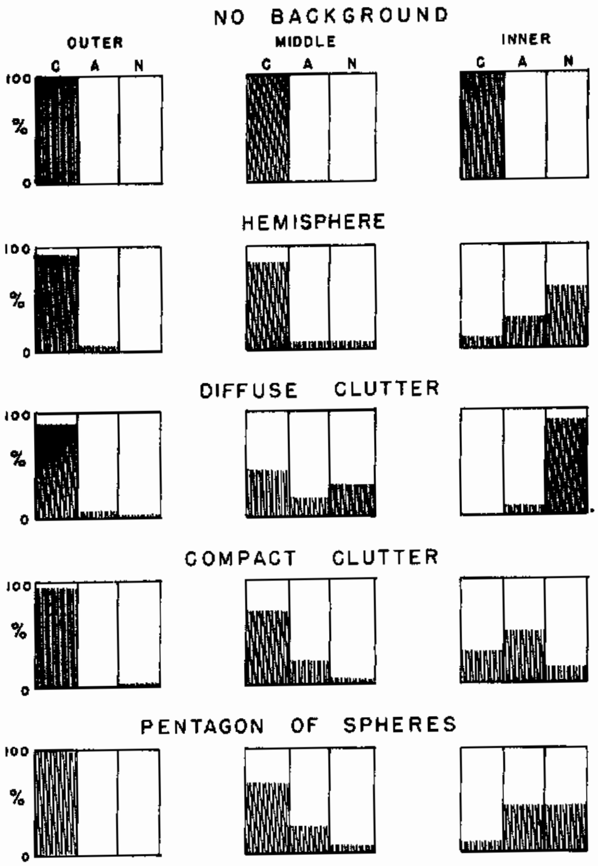

FIGURE 22. General results of systematic clutter tests. In each block the first column (C) gives precentage of contact s (catches, catch-and-drops, hits-and-touches) with the target. The second Column (A) designates the attempts (tries at the target with failure to reach it). The third column (N) indicates no attention or no attempt.

The first row (no clutter background for the three trajectories) shows that all targets were successfully reached.

The second row (three-foot, smooth hemisphere) shows that with this clutter background deterioration of performance occured only with the inner trajectory, where the targets normally reached the clutter surface.

The third row (diffuse natural clutters of maple leaves, hemlock twigs or blue spruce) showed dignificant deterioration of interception performance when the targets came within perhaps a foot of the surface (middle trajectory).

The fourth row (cmpact natural clutters consisting of convex surfaces of yew and spruce bushes) shows less serious deterioration, even when the targets were projected very close to the clutter surfaces.

The fifth row (pentagonal array of 9-inch spheres with 3-foot central opening) shows somewhat greater deterioration when the targets went into the central space and close to one of the spheres. (See text for further details).

FIGURE 23a. Collision with hemisphere at end of pursuit of mealworm. Mealworm is accurately tracked to surface, but at last instant bat cushions impact with use of its wings, then bounces backward before resuming flight. (Last three images of falling mealworm parallel last three images of bat).

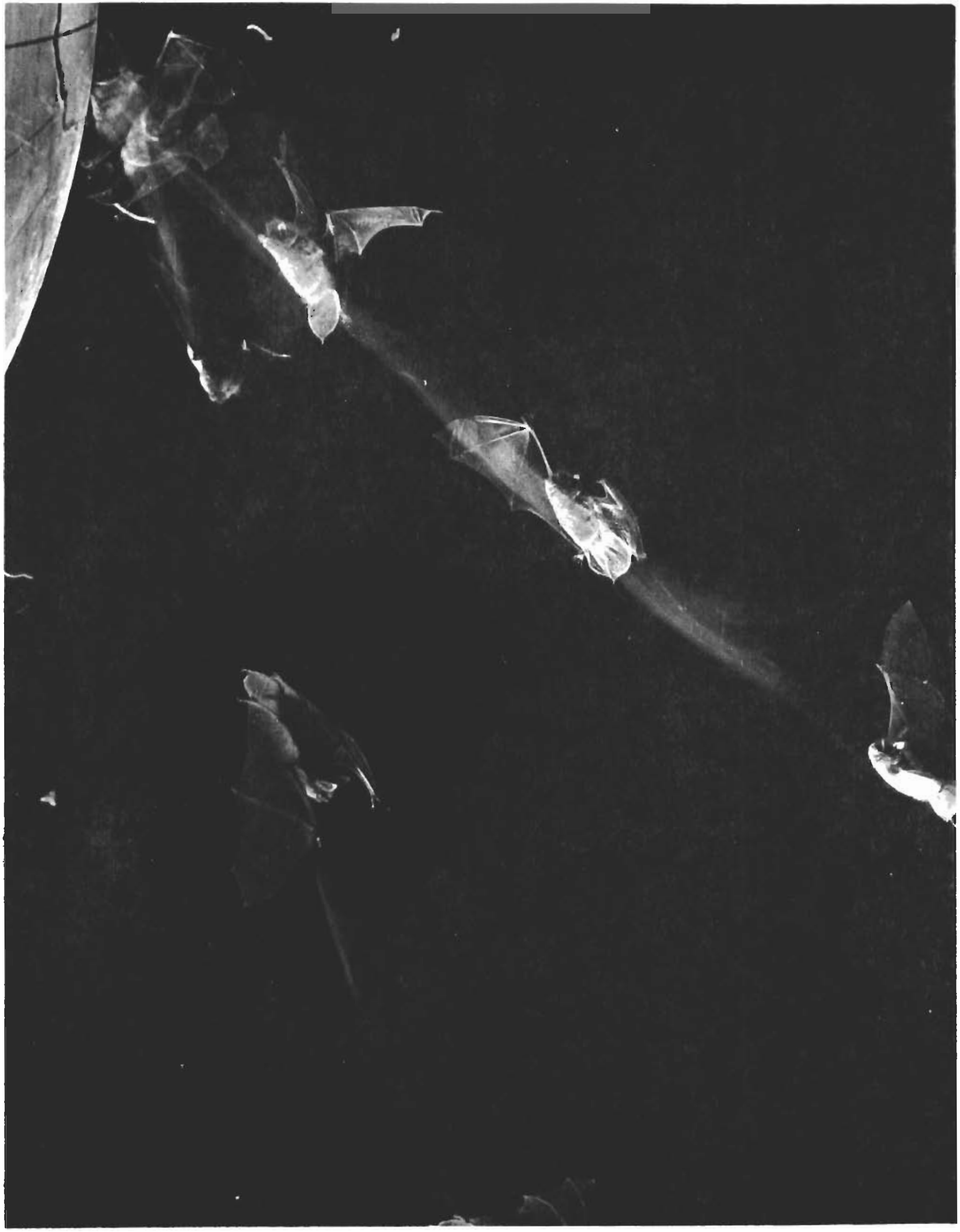

FIGURE 23b. Collision with hemisphere after giving up pursuit of mealworm just before contact with the hemisphere. (At third image bat's head is directed above mealworm and toward surface of hemisphere ahead).

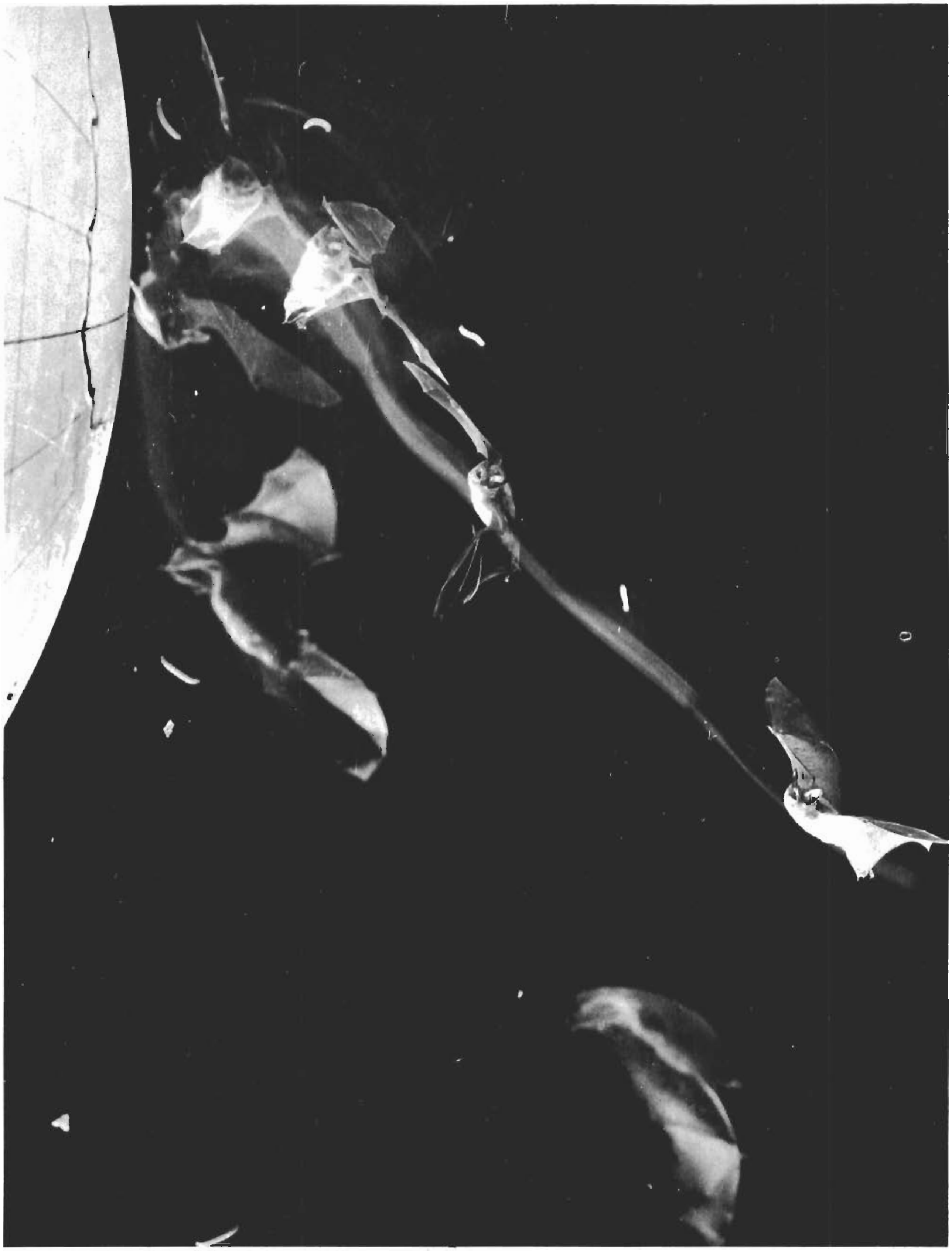

FIGURE 23c. Accurate tracking of mealworm to surface of sphere, but mechanical interference prevented successful catch.

FIGURE 23d. Successful catch of mealworm just off surface of hemisphere with use of final turn to permit a catch parallel to the surface.

FIGURE 23e. Successful catch of mealworm close to surface of hemisphere with use of sharp climb to avoid collision.

FIGURE 23f. Successful catch of one of two mealworms just off surface of hemisphere. Bat made climbing catch and stopped against surface of hemisphere, then dropped downwards with mealworm in mouth.

FIGURE 24a. Successful catch of moth at edge of hemlock twig clutter. Immediately after catch, bat struck hemlock twigs (as shown by multiple vibration images).

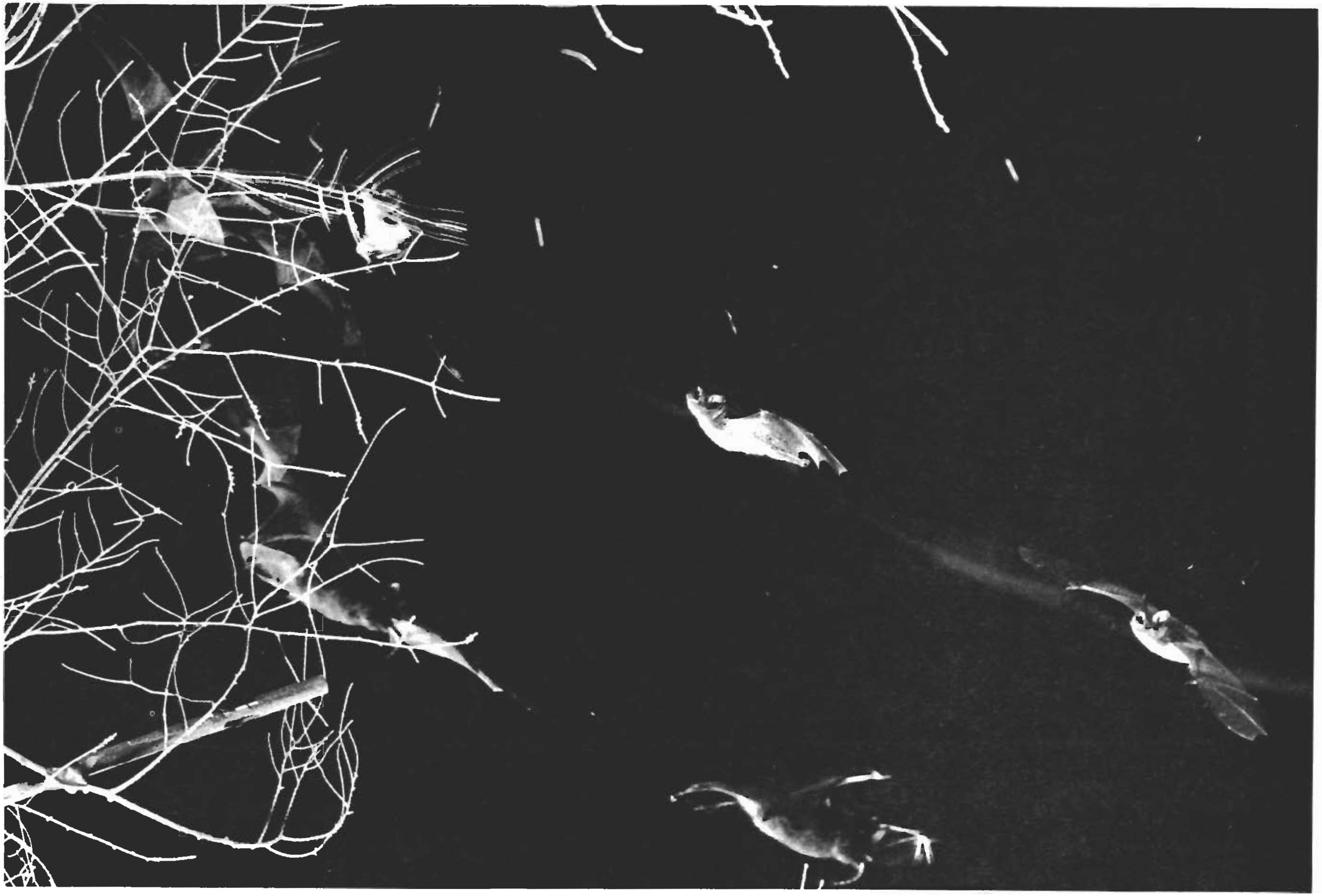

FIGURE 24b. Successful catch of mealworm at edge of hemlock twig clutter. The bat apparently strikes twig as it completes catch in fourth image. (In some instances, such collisions interfered with successful catch).

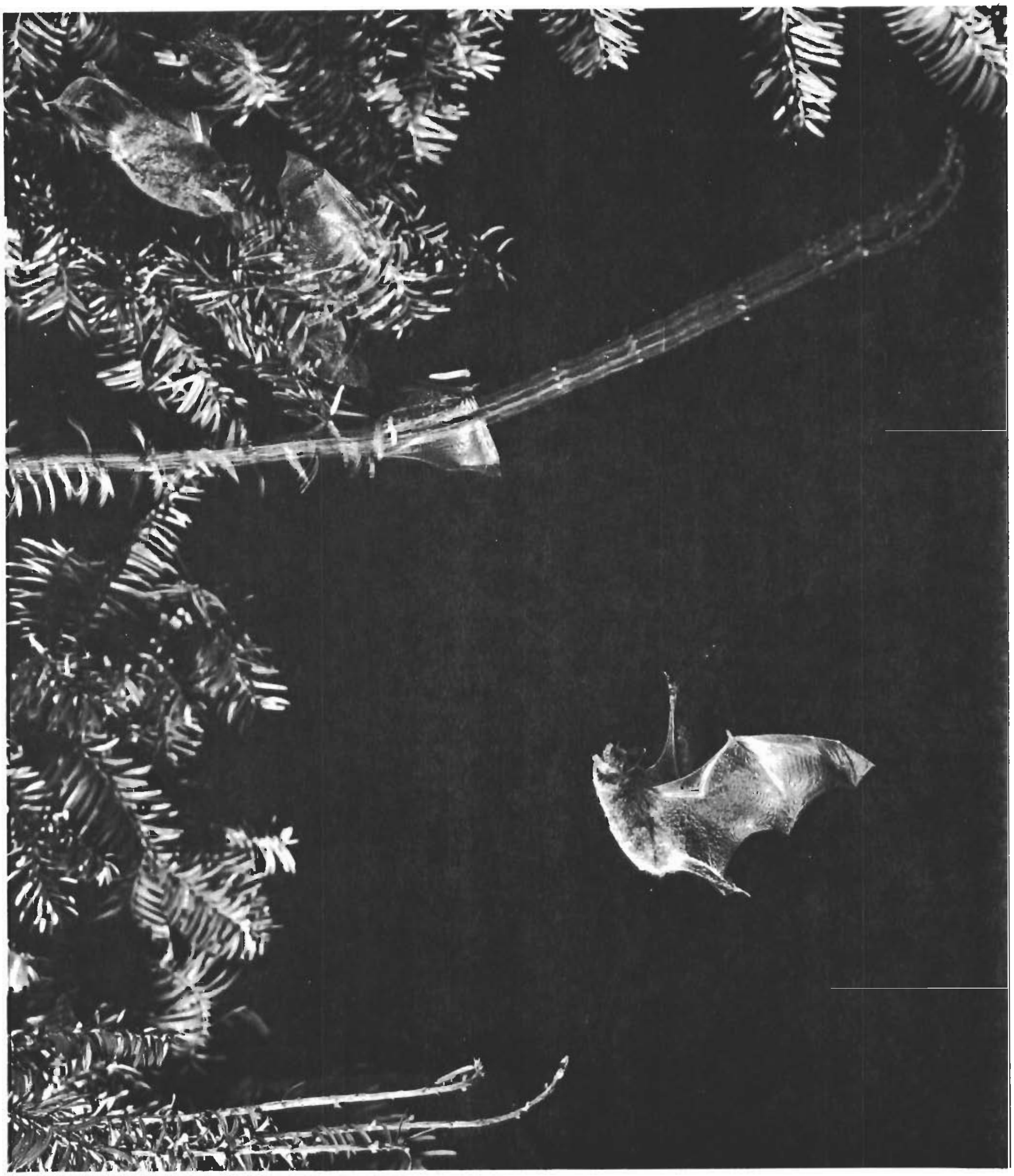

FIGURE 25. Successful catch of mealworm within yew clutter. Bare twig is being brushed with wing in second image, as bat pursues mealworm into space between yew needles. Final image shows bat coming back out with mealworm in its mouth.

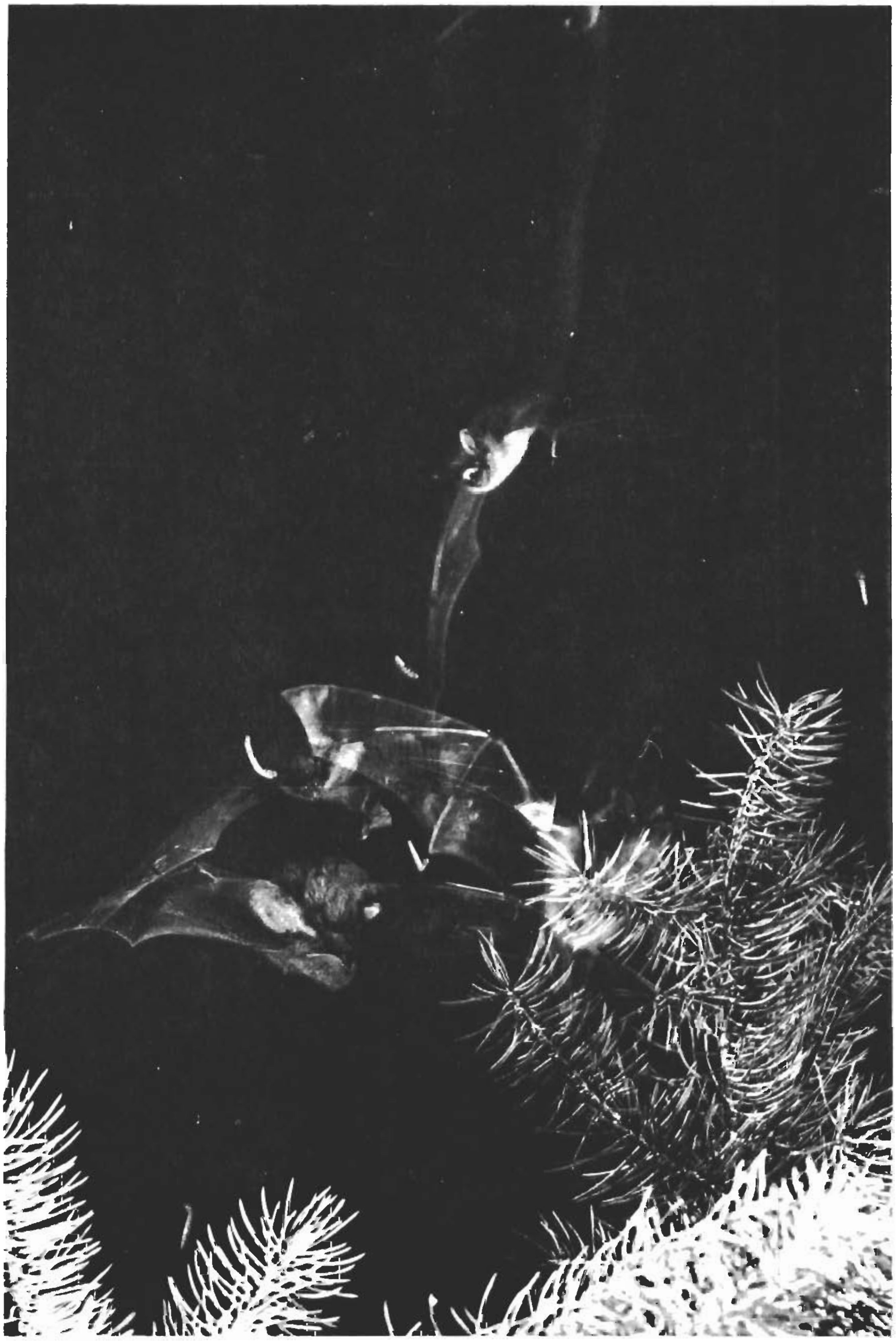

FIGURE 26a. Unsuccessful attempt at mealworm close to needles of blue spruce. Snap of tail membrane is just too high and knocks mealworm ahead (see mealworm image at upper left) rather than retaining it for seizure. (Multiple images of needles show that bat was very close to clutter).

FIGURE 26b. Unsuccessful attempt at mealworm close to willow clutter. Third and fourth images show mealworm being seized in tail membrane; but apparently contact with clutter disturbed the catching process, for in subsequent images mealworm is dropping through clutter space.

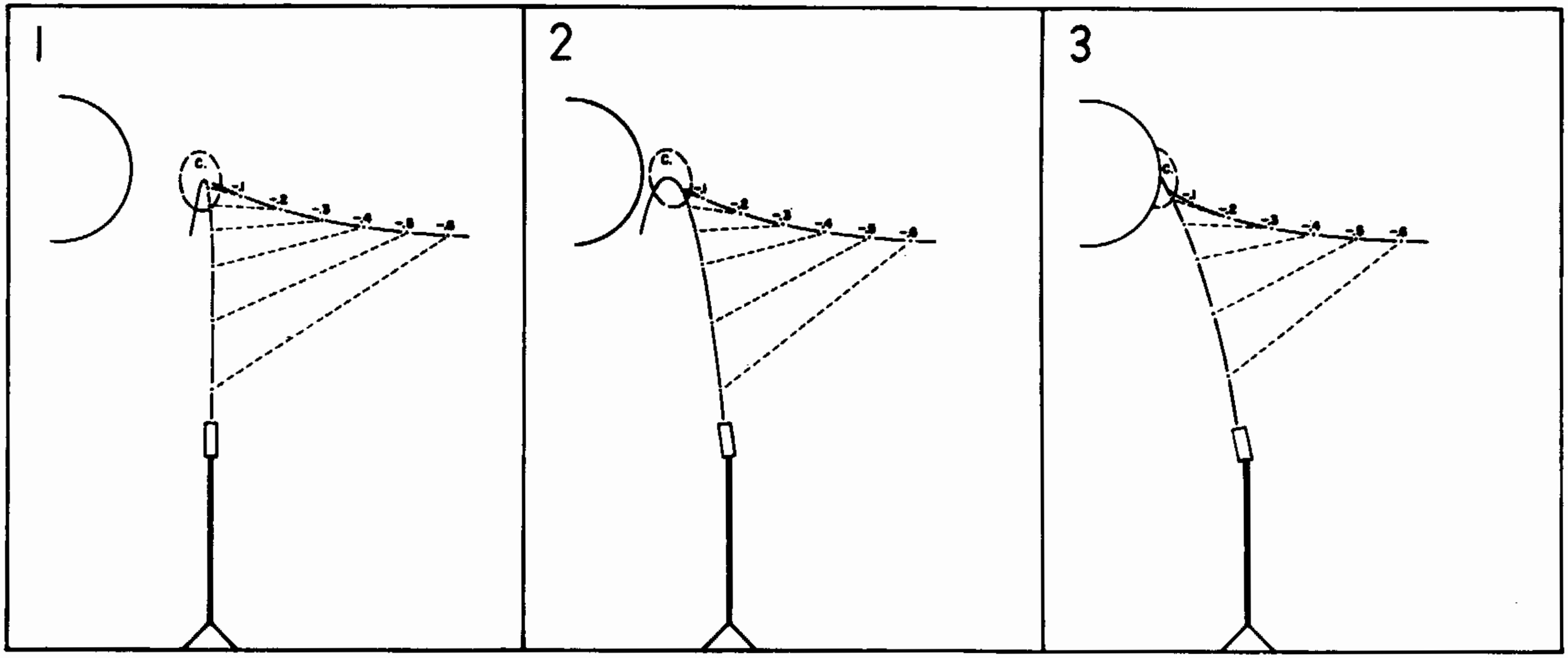

FIGURE 27. Samples of trajectories used in the systematic clutter tests. The outer, middle and inner trajectories were initiated with the gun tilted towards the clutter at angles of roughly 1°, 5° and 10° respectively. With the hemisphere (shown here) the inner trajectory was normally adjusted so that the target reached its peak roughly as it hit the surface, and for this adjustment the hemisphere was sometimes moved back from the position shown. At successive tenth second intervals, the corresponding positions of bat and target have been connected with a line. The bat's flight speed is indicated at 10 feet per second.

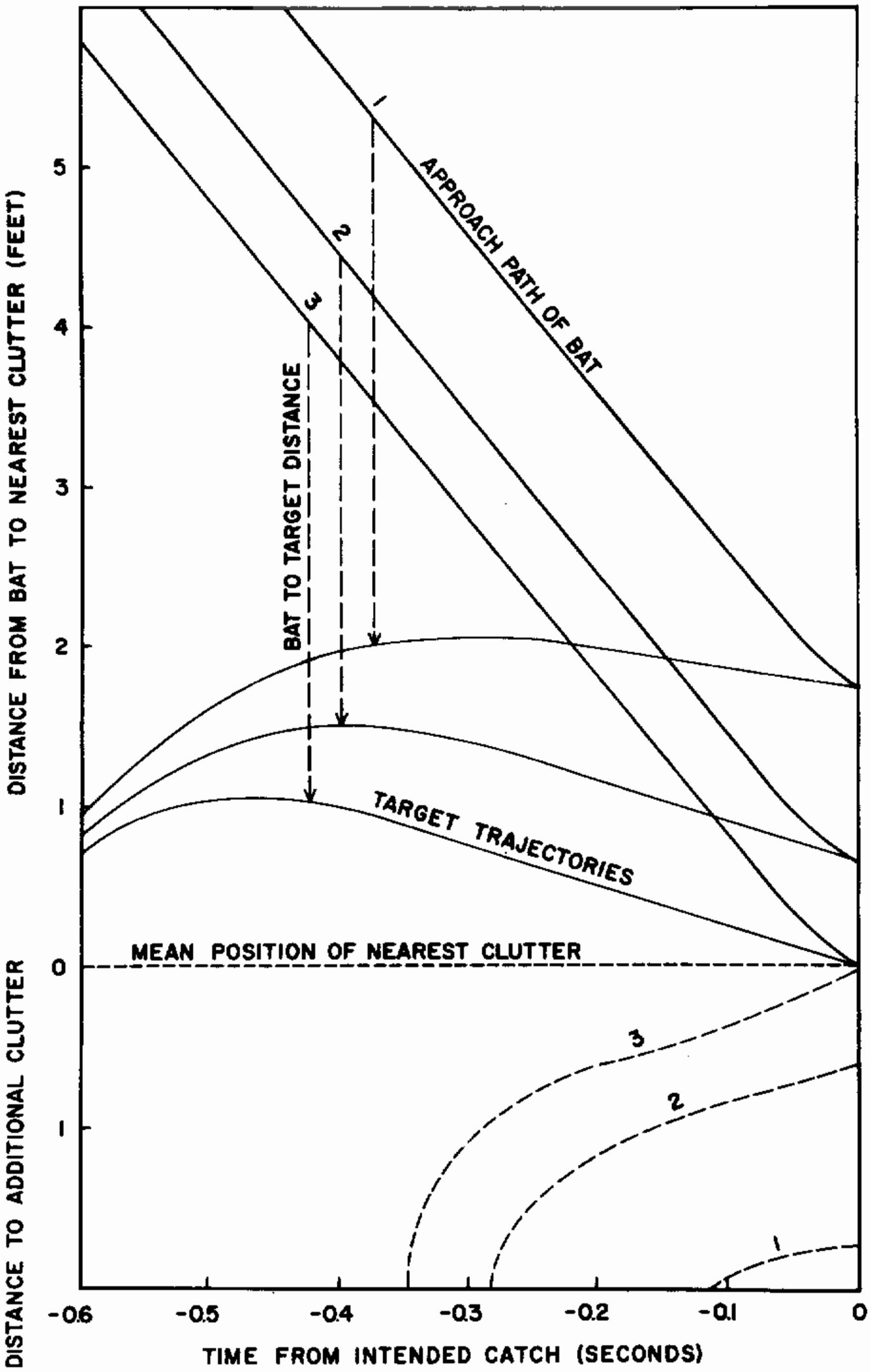

FIGURE 28. Approximate distance plots for the trajectory samples of Fig. 27. Lines extending down from upper left corner represent approach paths of bat in terms of distance to surface of hemisphere. Upper line represents outer trajectory; lower line represents inner trajectory. The lines coming in from the left to intercept them represent the target trajectories, the distance between these lines and the approach lines representing the bat-to-target distances. The curved line segments below the line of zero reference indicate the additional distance (ie. further than the nearest clutter) that the clutter surface is beyond the target as observed from the bat's position.

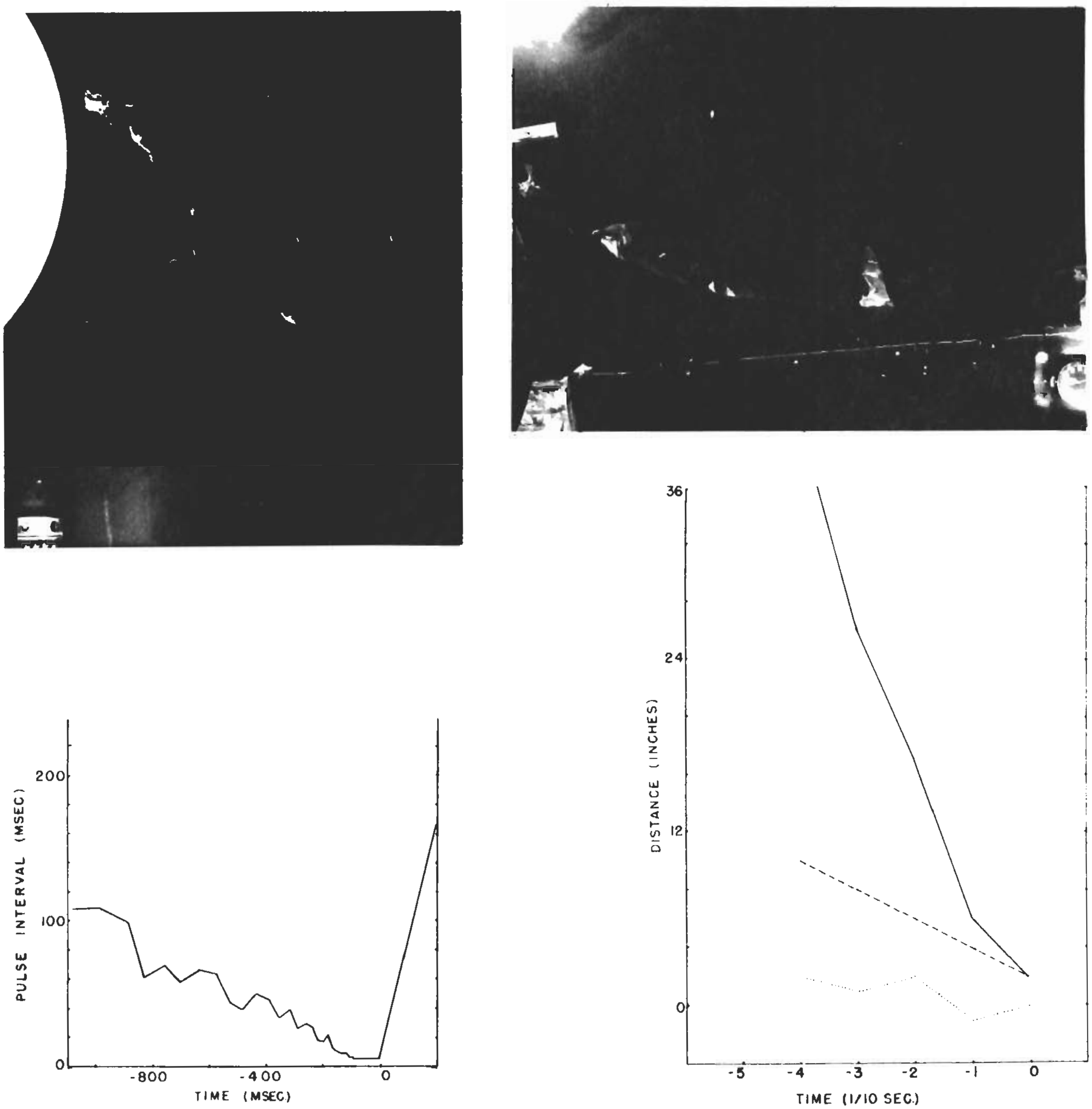

FIGURE 29. Example of catch near surface of hemisphere. For full explanation see text. In Figures 29 through 32 the upper left picture is taken from the side, while the upper right picture is taken from below. These pictures permit the construction of approximate distance plots (lower right). The pulse pattern plot (lower left) is made according to the method described in References 17 and 38. In the distance plots, the spacing between solid and dashed lines represents bat-to-target distance, while the spacing between dashed and dotted lines represents target-to-clutter distance.

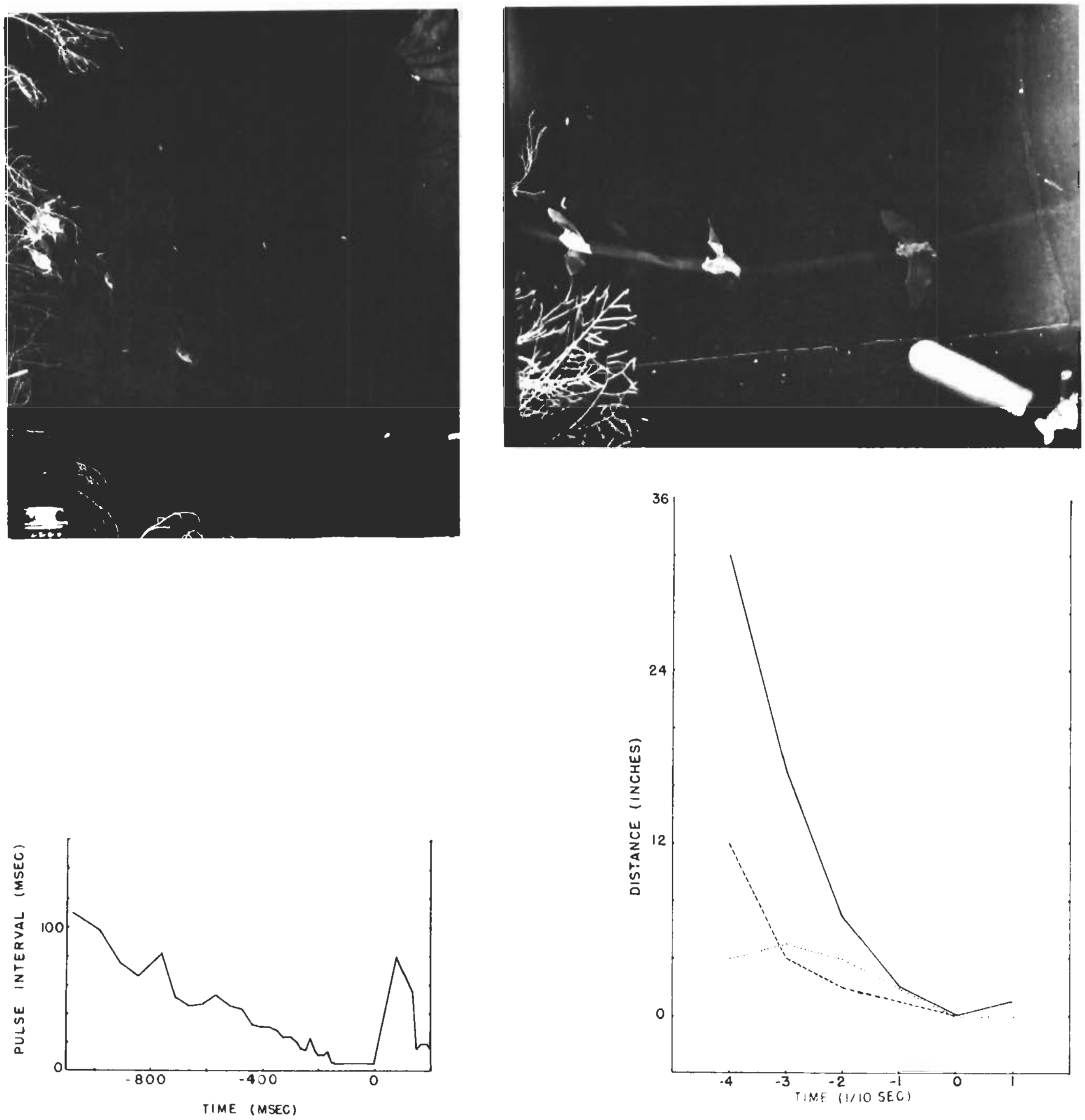

FIGURE 30. Example of catch just inside edge of hemlock twigs. The bat had to deflect the twigs to make the catch.

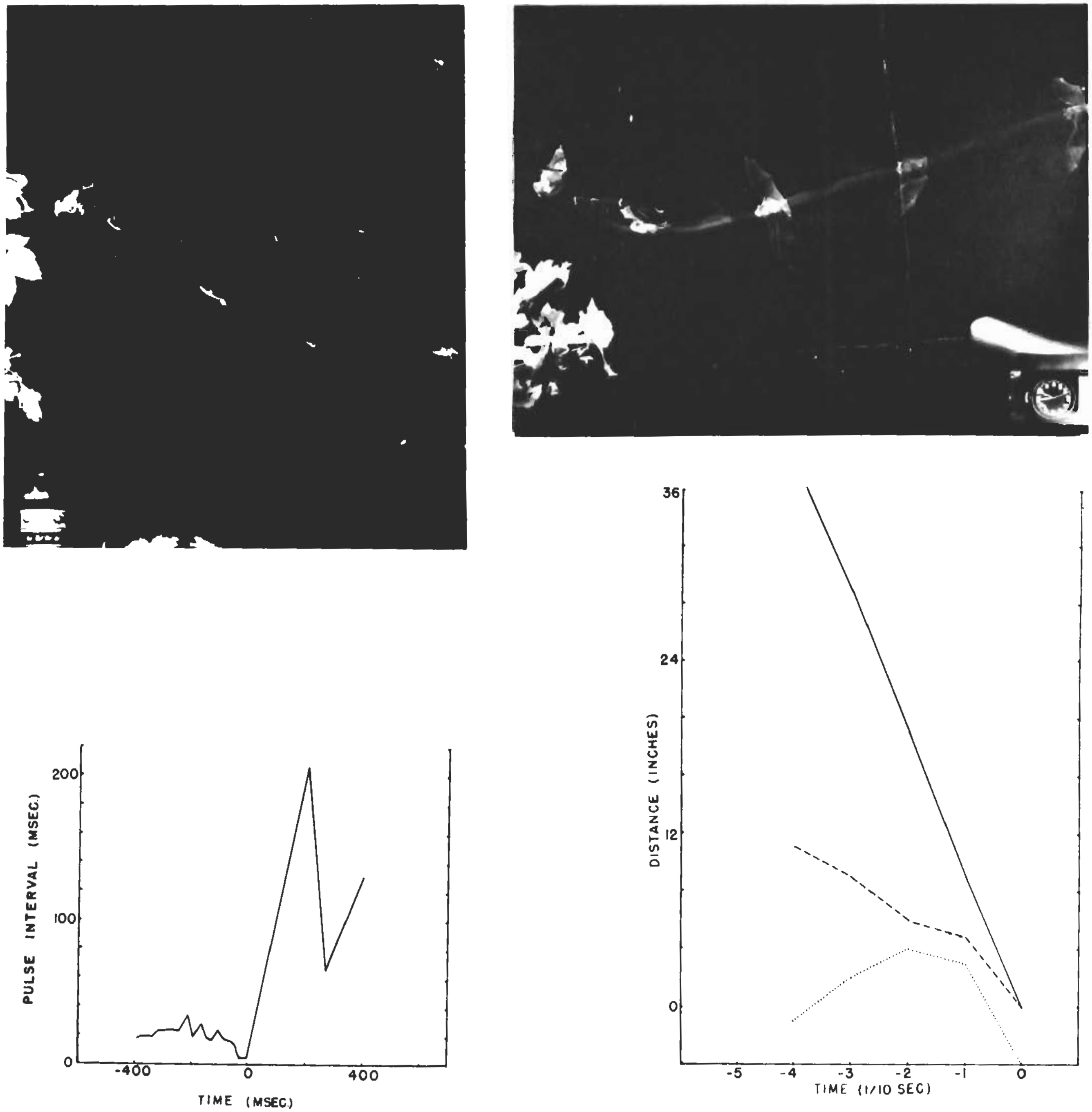

FIGURE 31. Example of catch close to maple leaves. Note shorter-than-usual terminal segment (high repetition rate "buzz" just before catch).in the plot of the emitted signal.

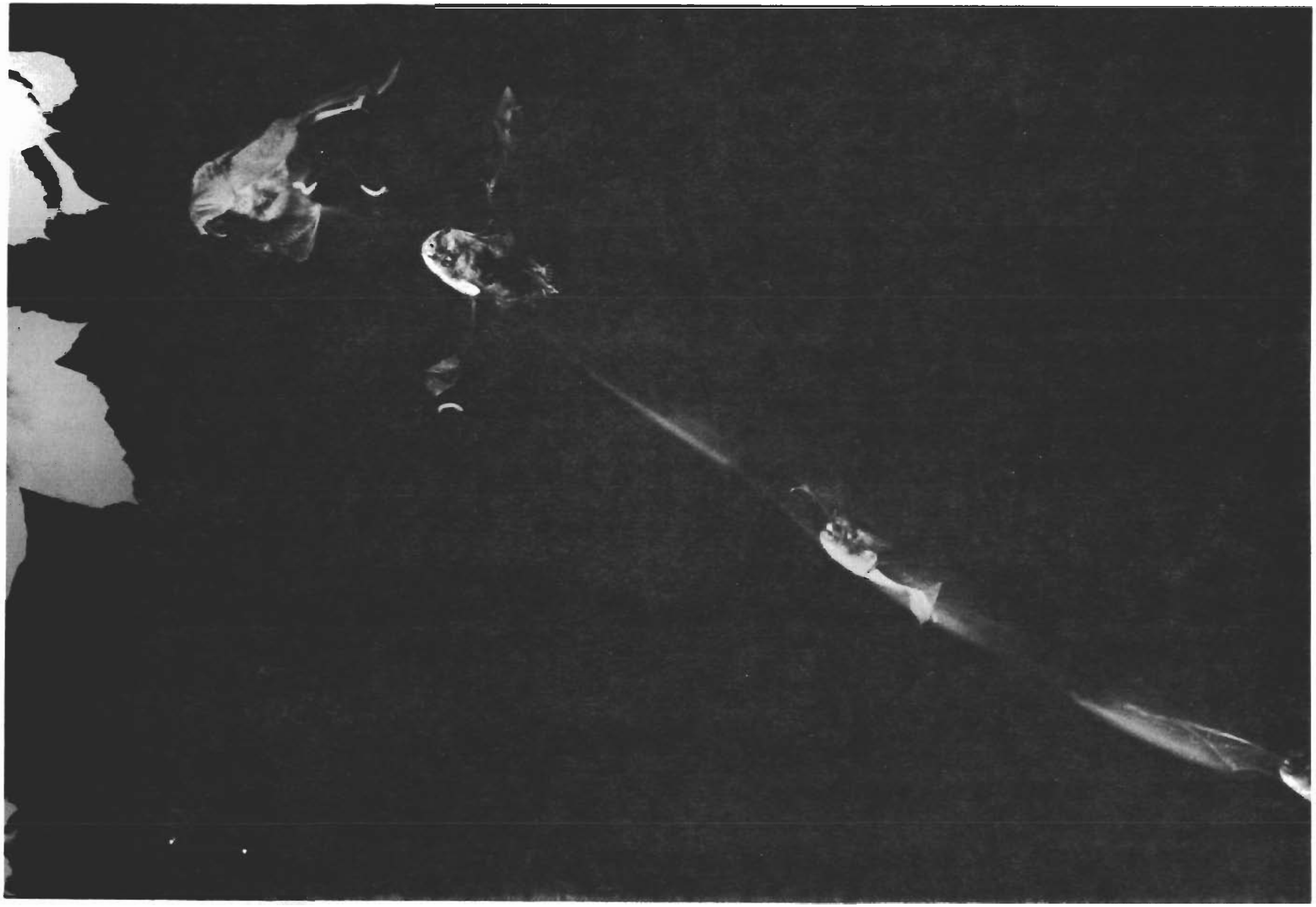

FIGURE 31a. Details of approach.

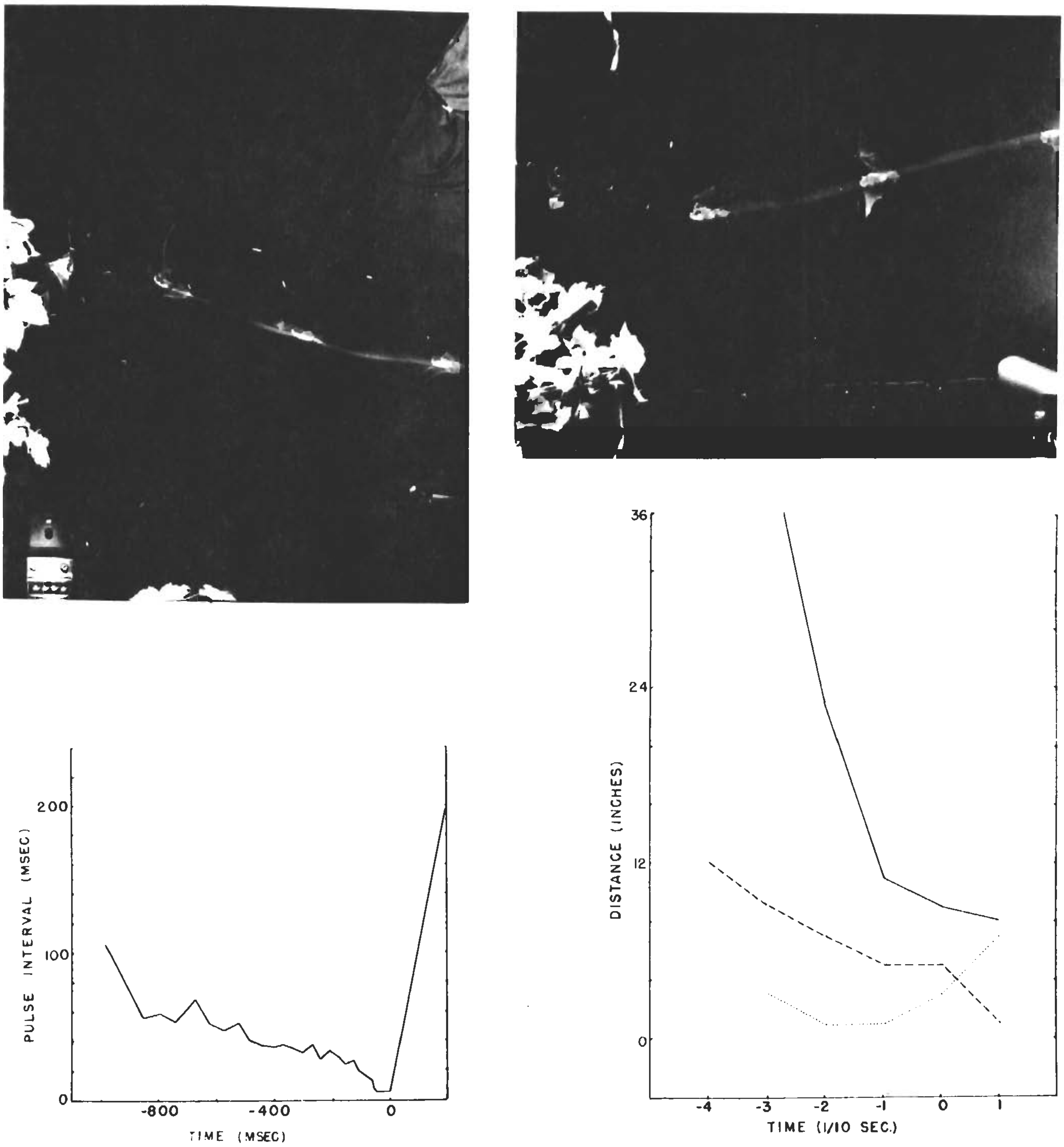

FIGURE 32. Example of hit close to maple leaves. The hit occurred just after the picture sequence.

FIGURE 32a. Details of approach.

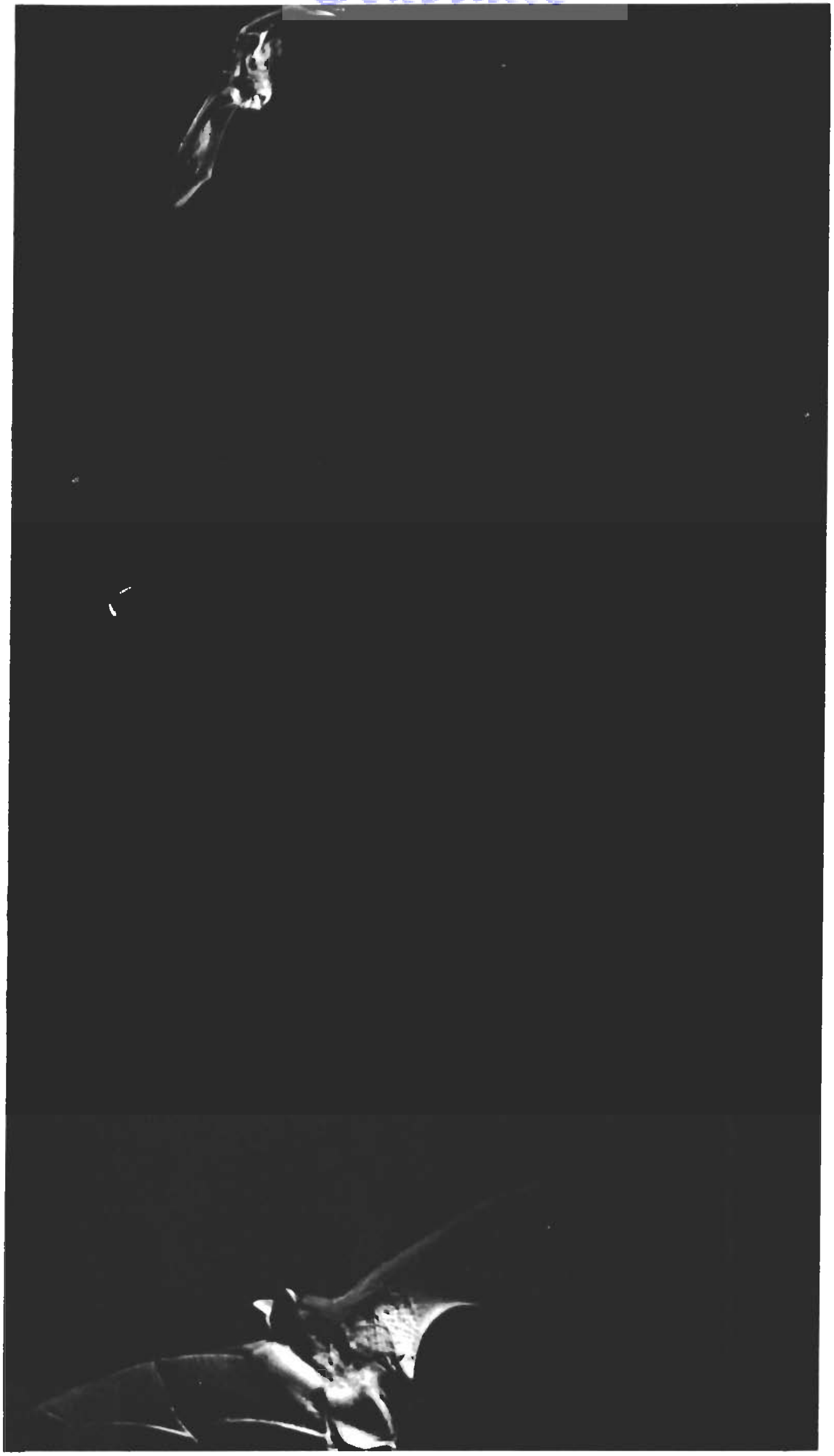

FIGURE 33. Simultaneous approach to a single target by two bats. In this instance the bat at the right seized the target just before the other bat reached it.

FIGURE 34. Collision at the target by two bats approaching from opposite directions. See text for discussion.

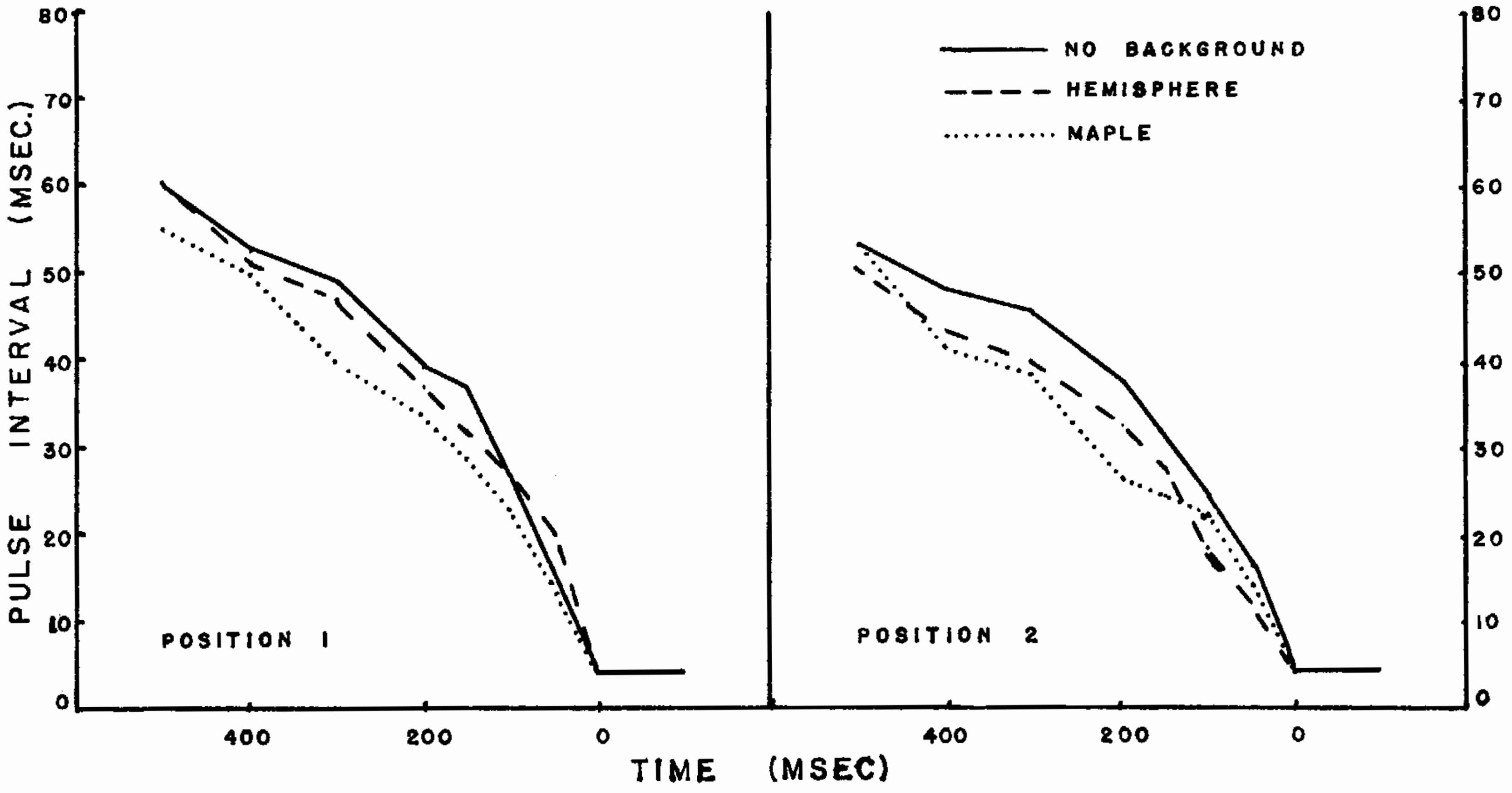

FIGURE 35. Graphs of average pulse patterns (for flights resulting in catches) illustrating pulse response during tests representing three clutter conditions and two trajectories. The point of synchronization (zero reference) for these plots was the start of the terminal buzz rather than the end of the buzz as in Figures 2 and 3.

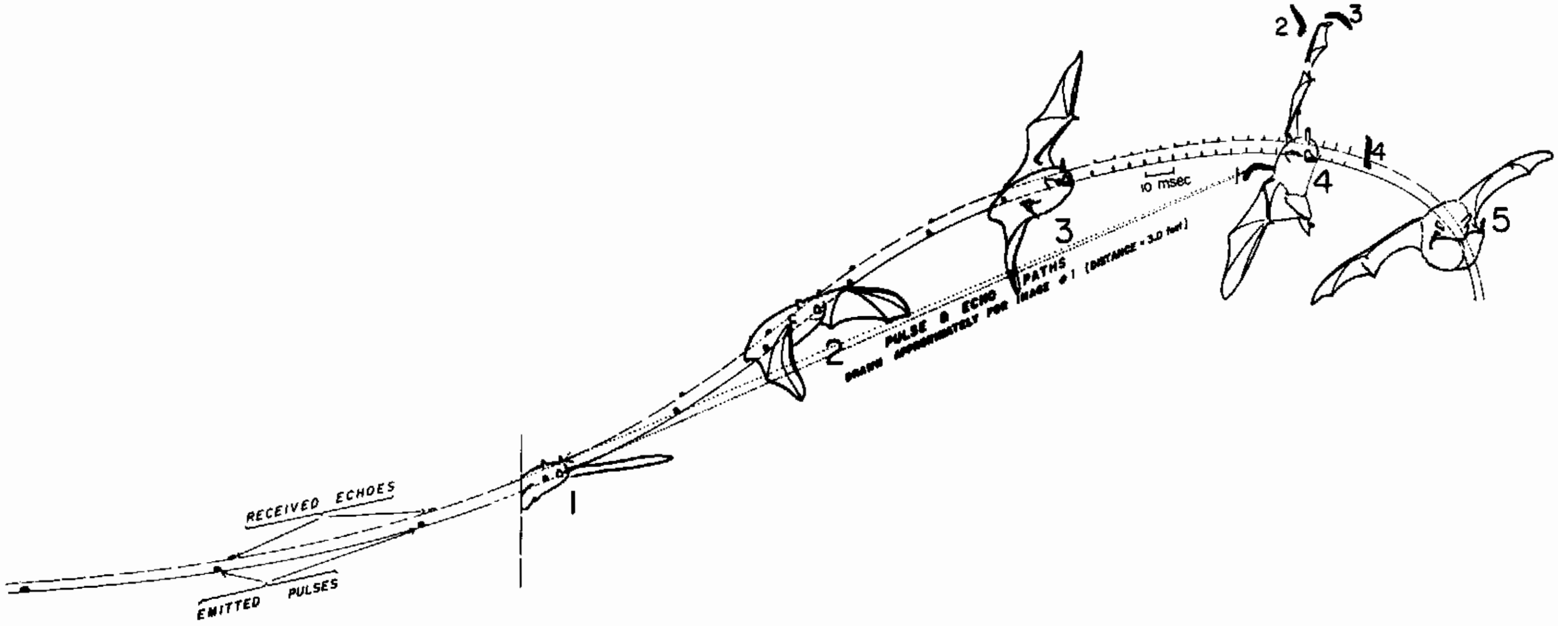

FIGURE 36. Example of relation between approach path and emitted pulses for Myotis lucifugus. Bat's action is traced from a multi-flash sequence, distances between bat and target being triangulated with the use of a second camera. At image #1 the bat-to-target distance was 3 feet, producing an echo time of approximately 5 milliseconds. The line drawn through successive positions of the bat's mouth carries blips which represent the points at which pursuit pulses were emitted (the width of these blips approximating pulse durations). Just above, is a line drawn through successive positions of the bat's ears. The blips on this line represent the received echoes. Note that the terminal buzz (at about 185 pulses per second) occupies roughly the last foot of approach prior to the catch.

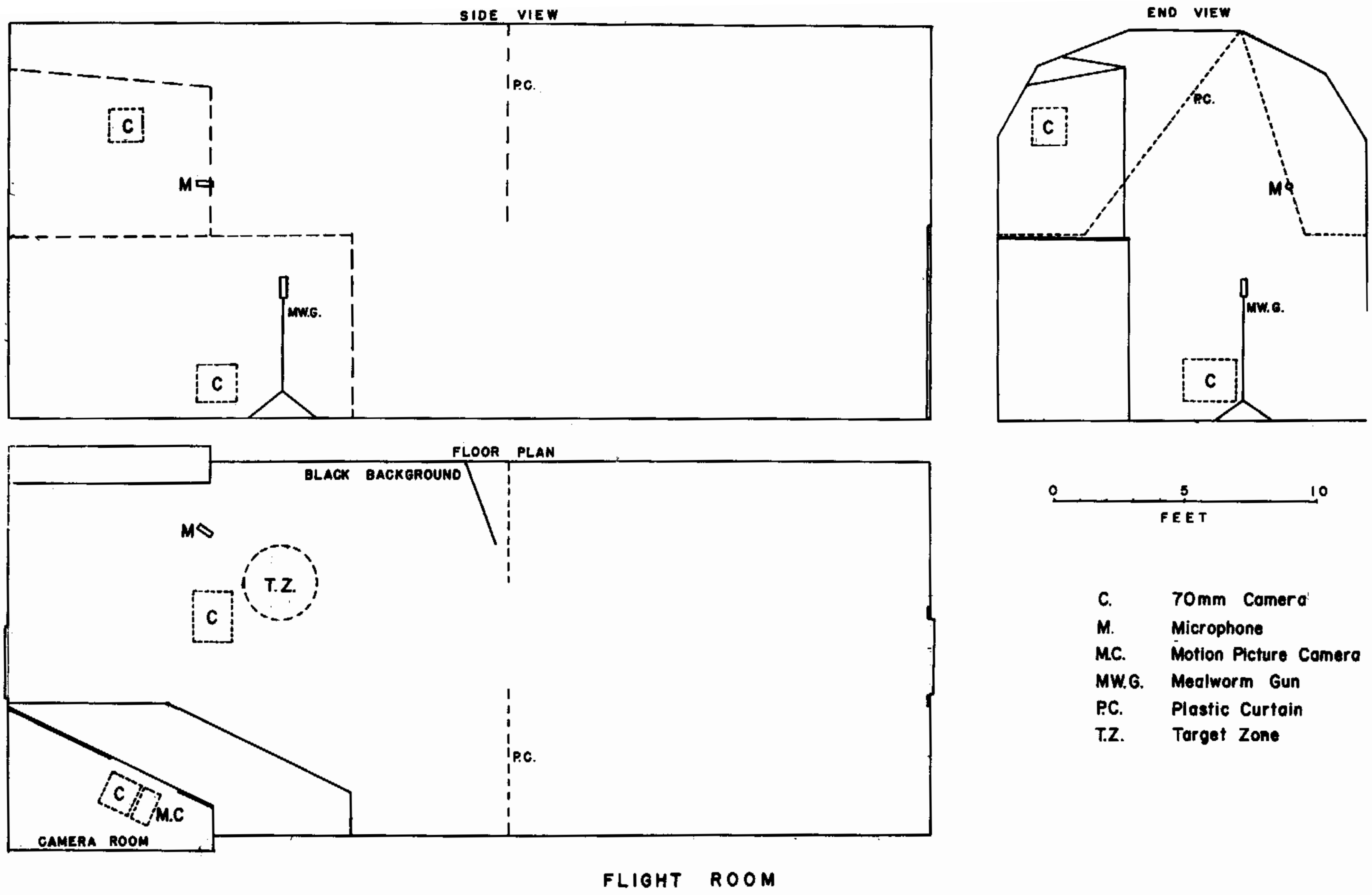

FIGURE I-1. Plan of flight room.

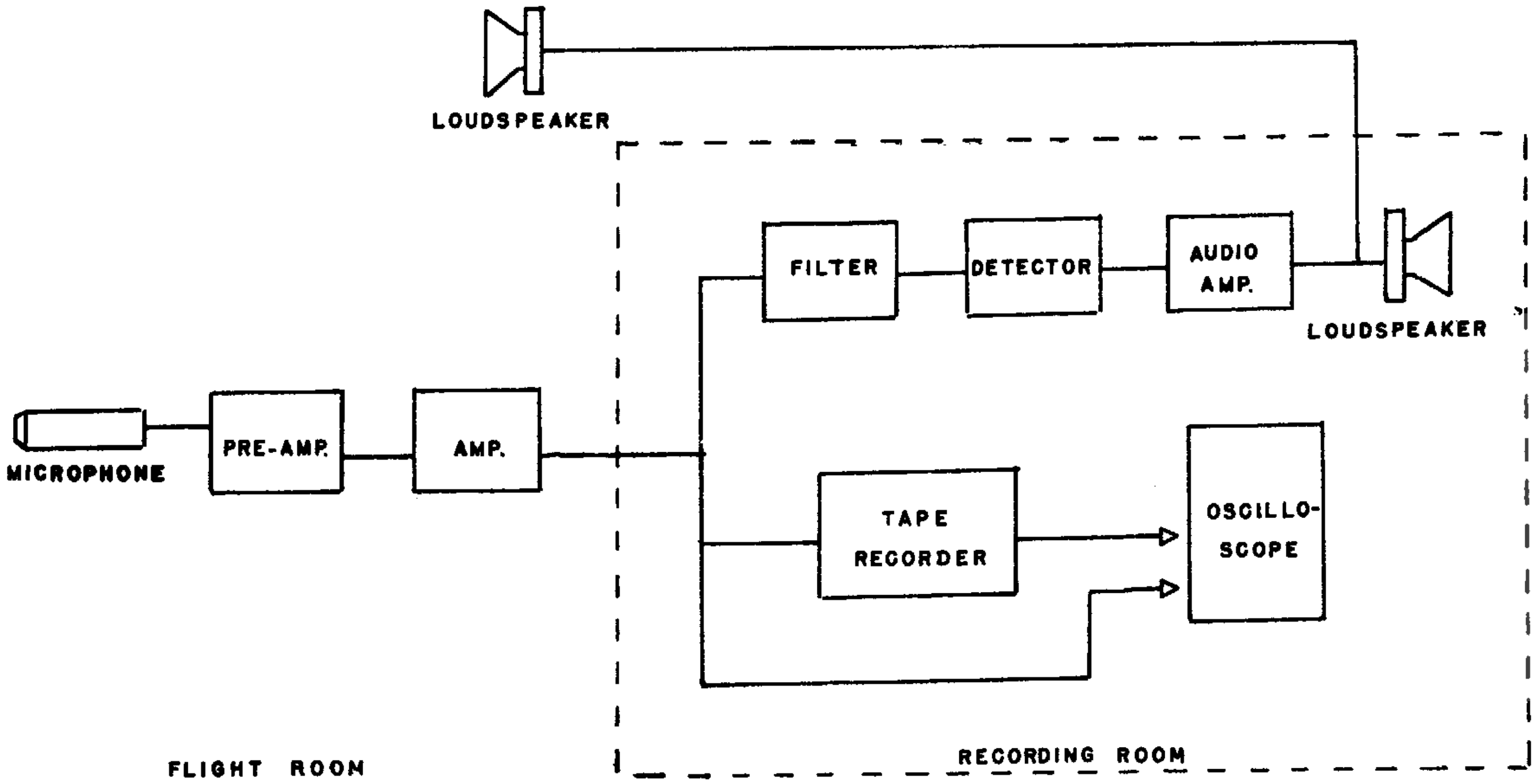

FIGURE I-2. Block diagram of recording and monitoring system.

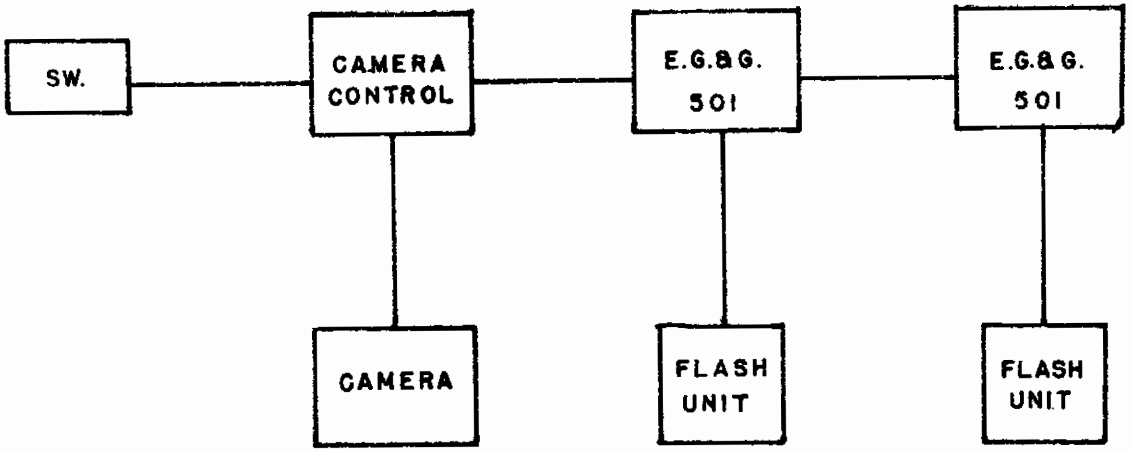

FIGURE I-3. Block diagram of Fastax high speed movie camera system.

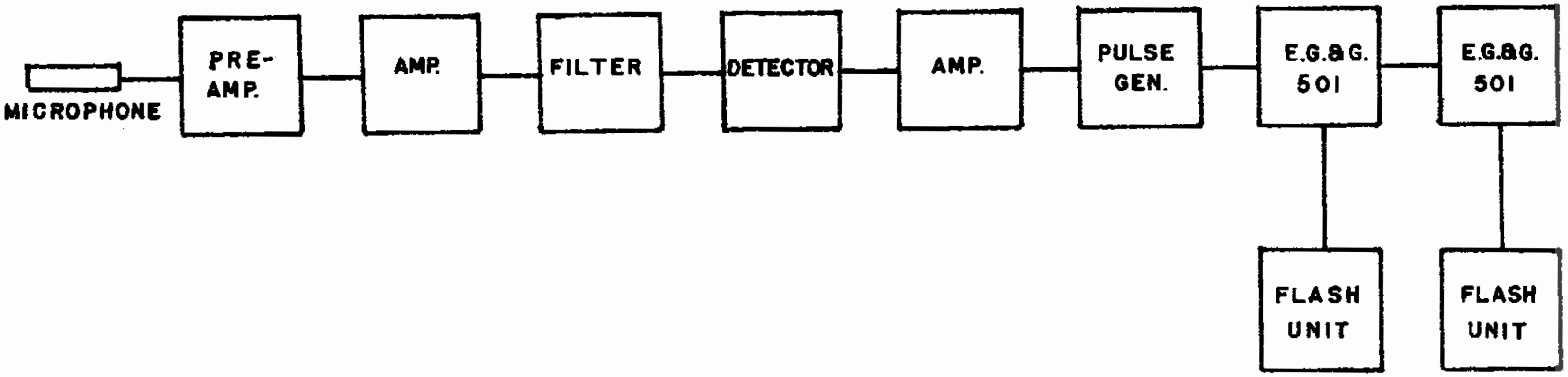

FIGURE I-4. Block diagram of circuit for pulsed-strobe photography.

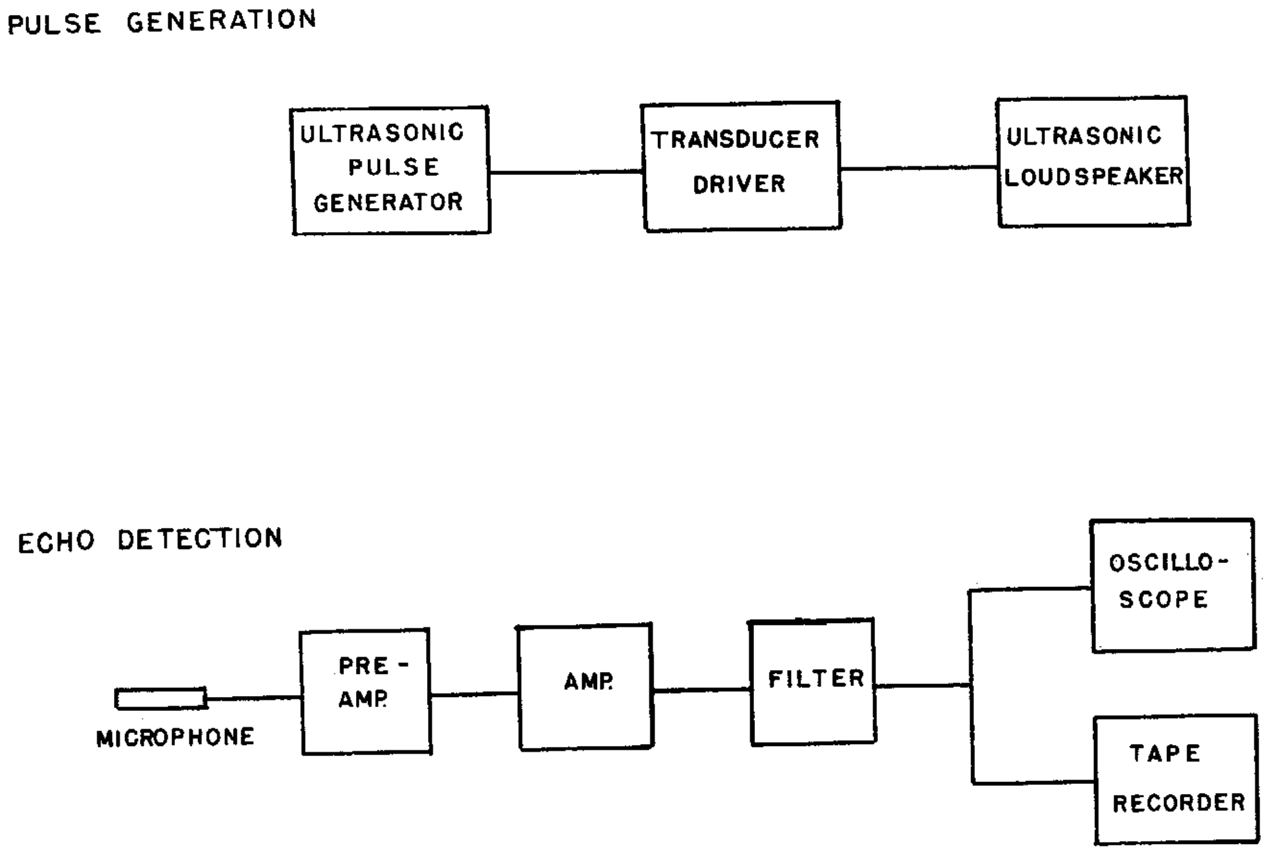

FIGURE II-1. Block diagram of echo measuring equipment.

FIGURE II-2. Mounting arrangement for microphone (above) and ultrasonic loudspeaker (below) with example of yew clutter at left.

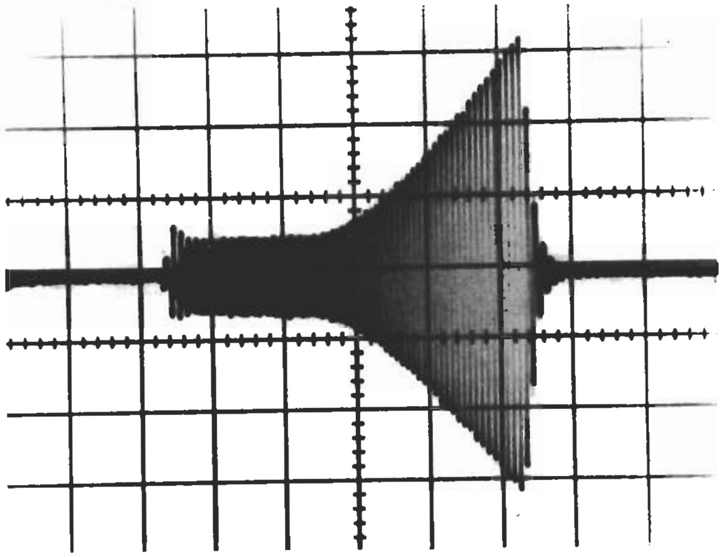

FIGURE II-3. An example of resonance in the echo measuring system. The echo is from a steel plate mounted perpendicular to the microphone and loudspeaker. The pulse used was 1 millisecond in duration and swept from 100-50 kc.

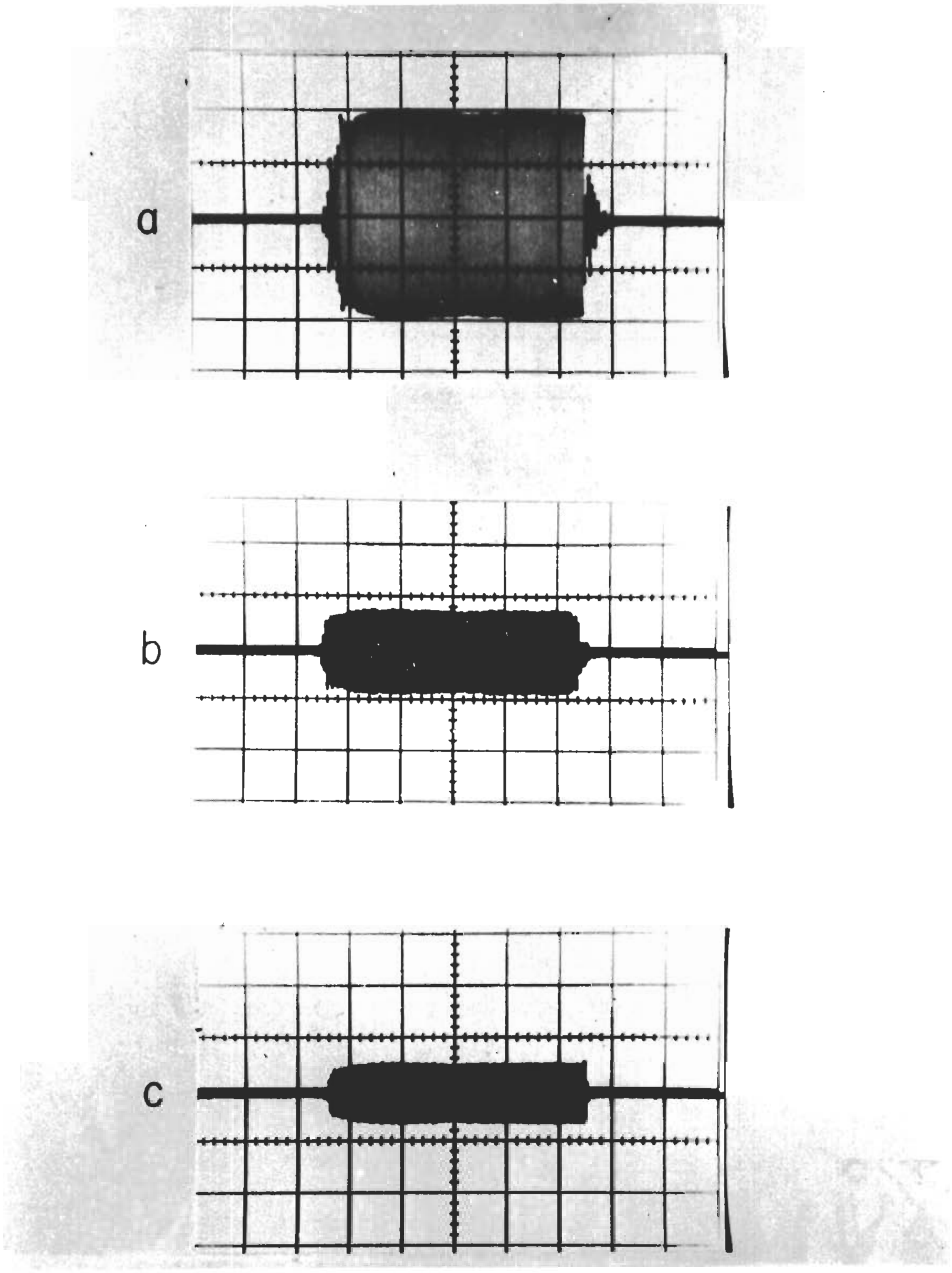

FIGURE II-4. Examples of echoes from a mealworm and a fruit fly at a distance of 1 foot. A 1 millisecond constant frequency pulse of 100 kc was used.
a) Curved mealworm. b) Straight mealworm. c) Fruit fly.

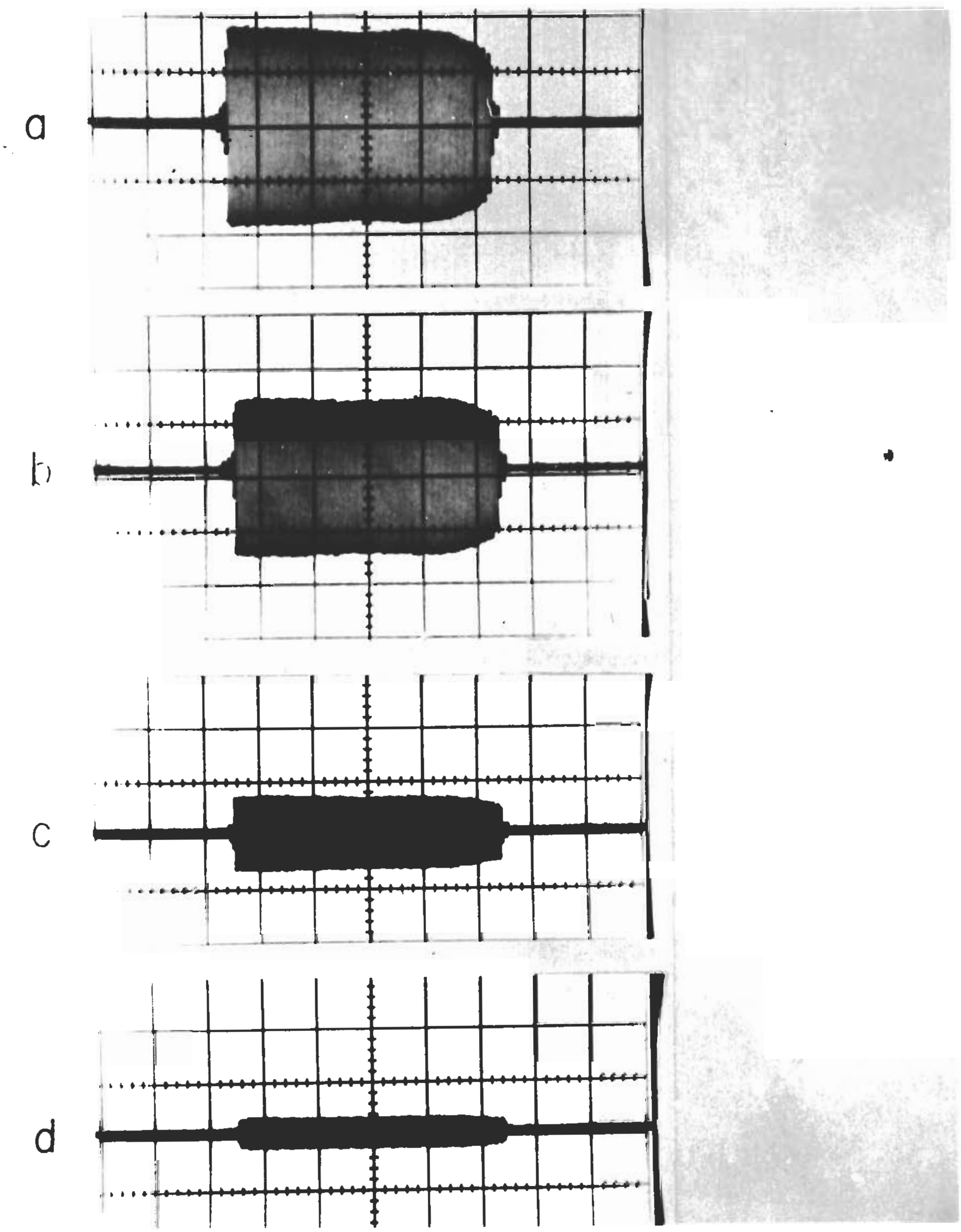

FIGURE II-5. Examples of echoes from four sizes of nylon spheres at a distance of 1 foot. A 1 millisecond constant frequency pulse of 100 kc was used.
a) 8mm sphere. b) 6.4mm sphere. c) 3.2mm sphere. d) 1.6mm sphere.

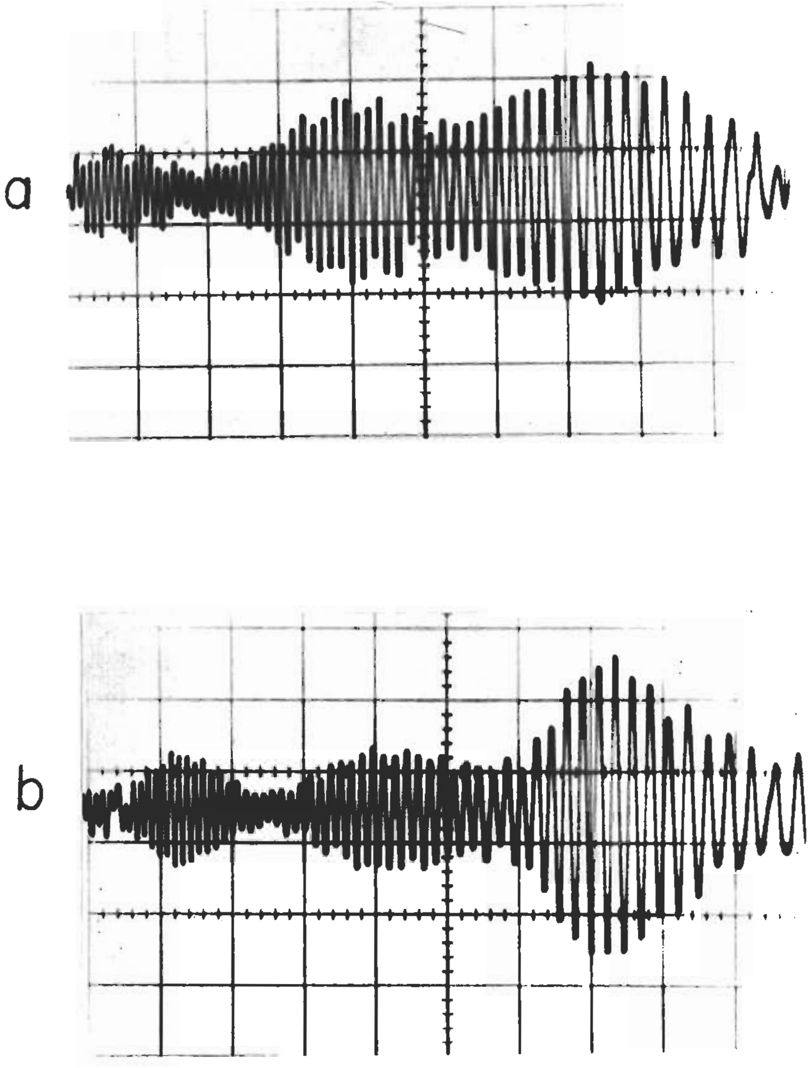

FIGURE II-6. Examples of echoes from a mealworm at a distance of 1 foot. A 1 millisecond pulse, swept from 100-20 kc, was used. a) S-shaped mealworm. b) C-shaped mealworm.

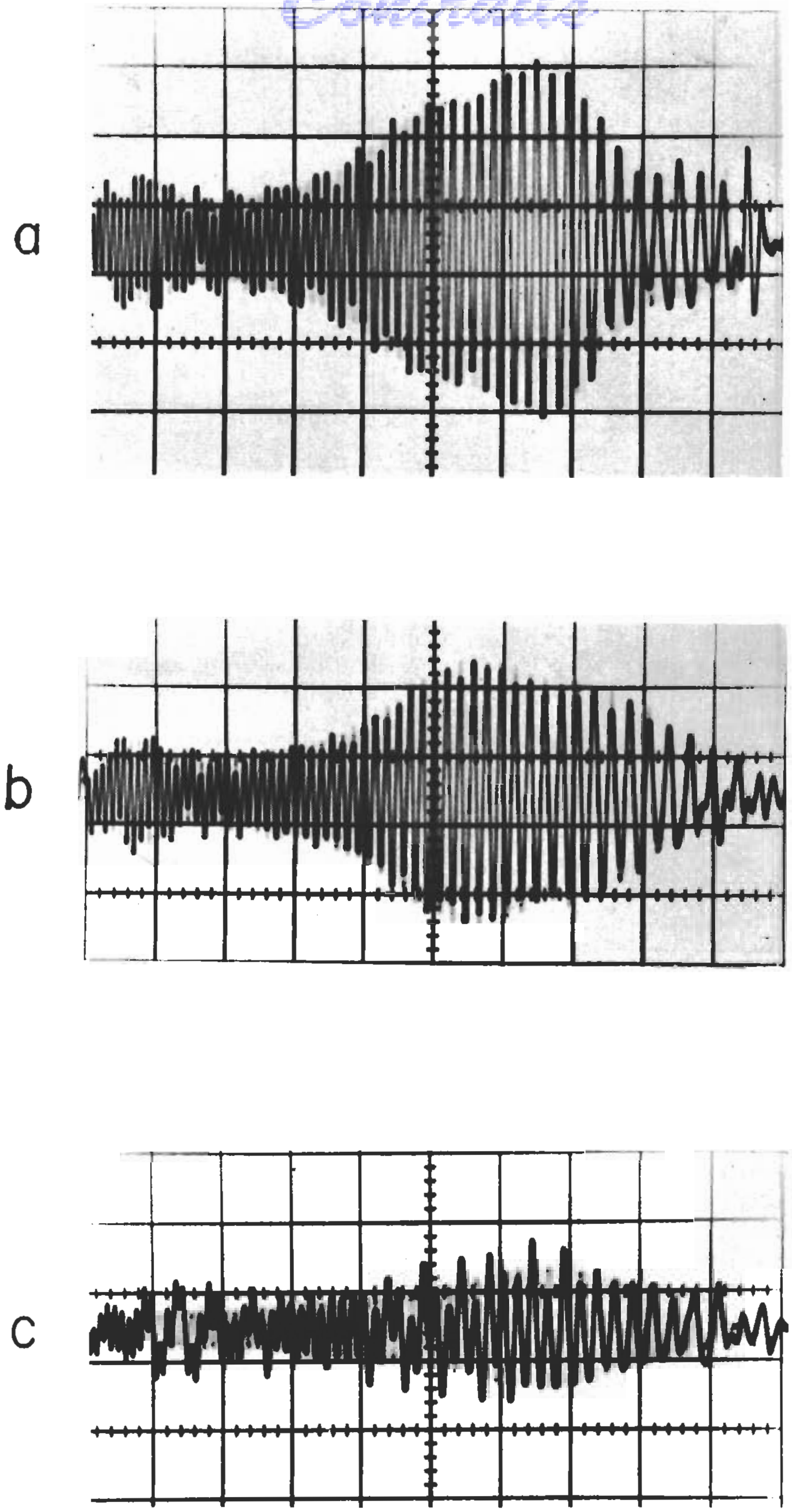

FIGURE II-7. Examples of echoes from three sizes of nylon spheres at a distance of 1 foot. A 1 millisecond pulse, swept from 100-20 kc was used.
a) 8mm sphere. b) 6.4mm sphere. c) 3.2mm sphere.

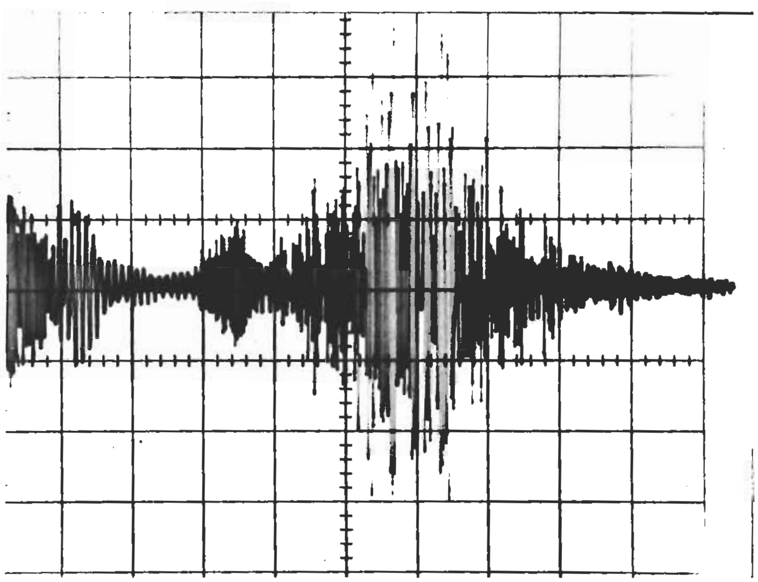

FIGURE II-8. Example of the echo from a mealworm suspended a few inches from a yew branch. The mealworm echo occupies the second horizontal space to the left of the center line. The disturbance to the right of it represents the echo from the yew branch, while the disturbance on the extreme left edge represents direct pick-up from the microphone. A 1 millisecond pulse swept from 100-20 kc was used.

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13. ABSTRACT

The echolocation techniques of bats provide functioning models with useful attributes: versatility of application, ultraminiaturization of components, and processing methods capable of dealing rapidly and reliably with complex echo indications despite the inherent slowness of unit neutral components. Present experiments, carried out on captive bats trained to catch natural and artificial targets projected into their flight paths, have quantified certain basic measures of performance. Spheres as small as 1/16 in. diameter were detected and localized at two or more feet, with resulting interceptions being accomplished in 1/4 second. Final localization accuracies of 1 cc were sometimes achieved, even when resolution of up to 16 nearby targets was required. Massive or complex clutter backgrounds tended to reduce interception performance at short target-to-clutter distances, but some interceptions were accurately completed during actual contact with natural twigs or foliage; or when pursuit paths had to be radically adapted to background configurations. Interception scores for food targets sometimes exceeded 99% while like-sized negative targets of a different shape could be correctly discriminated roughly 95% of the time. Failure to make proper evaluation of trajectories tended to produce extensions of the terminal pursuit signal; but such modifications were not significantly increased in most clutter situations.

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