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ACOUSTIC ORIENTATION OF NEOTROPICAL BATS

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ELEVEN FIGURES

Previous investigations of the acoustic orientation of bats have been confined for the most part to North American and European members of the family Vespertilionidae. These bats feed almost exclusively upon flying insects which they pursue and capture on the wing. They detect obstacles, and probably also their insect prey, by the process known as echolocation, that is, by hearing echoes of the intense pulses of high frequency sound which they emit at rates of 10 to 200 per second. The frequency of the sound making up these pulses ranges from 20 to 120 kilocycles per second, and it usually drops by about an octave between the beginning and end of each pulse, even though the pulse duration is only one to 5 milliseconds. But under some circumstances these bats emit somewhat longer pulses with a nearly constant frequency, and during the pursuit of flying insects marked changes occur, both in the frequency pattern and the pulse repetition rate (Griffin, '53a).

In the tropics, however, there are bats which feed on fruit, the nectar and pollen of flowers, fish, or the blood of larger animals. In seeking such a variety of foods, these bats must face problems of orientation quite different from those confronting insectivorous bats in temperate latitudes. We have, therefore, analyzed the high frequency sounds of 16 species of bats from Panama, and the resulting data reveal pronounced differences between certain families and genera, together with a significant correlation between the type of

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sound used for orientation and the habits of the bats, in particular, their methods of obtaining food. The families studied were: (1) the Emballonuridae, or sac-winged bats, which are insectivorous, (2) the Noctilionidae, which feed on insects or fish, (3) the very abundant leaf-nosed bats of the family Phyllostomidae, most of which feed on fruit or flowers, and (4) the Desmodontidae or vampire bats which feed on blood. A few species were studied in the field, and the rest in the laboratory in Panama. Eight species lived sufficiently well in captivity that healthy individuals could be brought back to the United States for more detailed study.

This work would not have been possible without the generous cooperation of the Office of Naval Research, both through research contracts with Cornell and Harvard Universities, and in arranging laboratory facilities and transportation in the Republic of Panama and the Canal Zone. We wish to express our gratitude to many of the personnel of the Fifteenth Naval District, and in particular the late Dr. Herbert Mundt, Director of the Canal Zone Corrosion Laboratory, where the first phase of the work was performed by Griffin during 1953. We are equally indebted to the Gorgas Memorial Laboratory, and most especially to Dr. Harold Trapido, for the use of laboratory and field station facilities, and for guidance in locating colonies of the less abundant species of bats. Mr. Prentice Bloedel assisted in the work in Panama during 1953 and will report elsewhere his collateral studies of the fish eating bat *Noctilio leporinus* and the life histories of other Panama bats. Finally, we wish to acknowledge the cooperation of the Woods Hole Oceanographic Institution and the Woods Hole Laboratory of the U. S. Fish and Wildlife Service, both of which provided facilities essential for studying the underwater sounds of captive *Noctilio* during their fishing activities.

METHODS

Most of the bats used for these studies were caught at their roosts in buildings, caves, trees, culverts, or under bridges.

While some were also taken in 1953 in trammel nets, we used only those removed from the nets quickly before they could injure themselves. Like Van Tyne ('33), we caught frugivorous bats more often, but we also captured a few insectivorous *Myotis* and *Rhynchiscus,* although these became less firmly entangled and often escaped before they could be removed from the net. Not all species survived for long in captivity, but records of the sounds emitted by the less hardy species were obtained within a few hours of capture. Measurements made in the laboratory in Cambridge necessarily involved bats that had been in captivity for some time, but only those in good health were used. Some species such as *Carollia, Artibeus, Glossophaga,* and *Lonchophylla* lived for many weeks on a diet of bananas, cantaloupes, melons, and mangoes; the semi-carnivorous *Phyllostomus* was fed both fruit and meat, while the vampire bat *Desmodus* thrives indefinitely on defibrinated mammalian blood from a slaughter house.

Specimens of all bats collected in 1953 were identified by P. Bloedel and S. Benson, Museum of Vertebrate Zoology, University of California. General descriptions of the various species, together with brief notes regarding their habits, may be found in papers by Goldman ('20) and Goodwin ('46). While Simpson ('45) has suggested many changes in the scientific names of these bats there does not appear to be unanimity regarding the changes among mammalian systematists. Since there are no common names in sufficiently general use to guide one through the shifting scientific nomenclature we have followed Goodwin's terminology.

The apparatus employed in Panama by Griffin during 1953, and for most of the laboratory measurements described below, consisted of Western Electric 640AA condenser microphones, cathode followers, voltage amplifiers, variable electronic filters, cathode ray oscillographs, and camera similar to those described previously (Griffin, '50, '53a). For field studies of *Noctilio* and *Dirias* a parabolic horn with a mouth diameter of 21 cm was used, but no horn was involved in any of the other records obtained with the condenser microphone. Power was supplied in the field by a portable 1200 watt a.c. generator driven by a gasoline engine; the noise was reduced to tolerable levels by using an automobile type muffler and by keeping the generator 200 feet or more from the microphone. Time and intensity calibrations were less accurate in the field than in the laboratory, but, in all cases, frequency and duration measurements were accurate to within 5% or at the very most 10%. Most of the records presented below are continuous ones — the camera shutter remained open and the 35 mm film moved at constant speed so that the motion of the sweep from left to right produced a sloping baseline. In some of the more recent records a dual beam oscilloscope was used in order to photograph simultaneously both unexpanded and expanded versions of the same pulse. The expanded version shows only a part of the pulse, but has a high enough sweep speed so that frequencies well above 100 kc can be resolved. One to 5 variable electronic filters were used, usually set at 15 or 20 kc high pass and 120 to 200 kc low pass. The sensitivity of the 640AA microphone declines at approximately 12 db per octave above 10 kc, and hence when a bat's sound contains two frequencies at equal intensities the lower of the two appears at higher amplitude in the records.

In some recent studies Rochelle salt crystal microphones have also been used with the same electrical system; in this case the frequency response does not show the progressive decline by a factor of 4 per octave, but the crystals are subject to uncontrolled variations in sensitivity. We ordinarily found it best to use the condenser microphone for all intense sounds and for faint sounds below 60–70 kc, while the crystal was preferable for low intensity sounds in which most of the energy appeared to be above 70 kc. Whenever possible condenser microphone records were also obtained of the higher frequencies to permit at least a rough intensity measurement based on the manufacturer's calibration of the 640AA microphone.

A simpler, easily portable apparatus was used by Novick in Panama from May to July, 1954. It consisted of a Rochelle salt crystal microphone ((45° X cut slab 1.5″ × 0.75″ × 0.25″), a parabolic horn with 21 cm mouth diameter, and a compact, battery operated amplifier and pulse detecting circuit which produced in earphones an audible click corresponding roughly to the envelope of the bat's high frequency pulse. An estimate of frequency was possible by tuning for a maximum audible click in the earphones, although this was often impracticable because of the varying amplitude of the pulses. Most of the frequency determinations with this apparatus were therefore obtained by displaying the amplifier output (before the detecting stage) on a cathode ray oscillograph and photographing these traces with a conventional 16 mm motion picture camera. This portable pulse detector, which was similar in purpose to some of the instruments used by G. W. Pierce (Noyes and Pierce, '37; Pierce, '48), was designed and constructed by Dr. S. Arnow, Department of Biophysics, Massachusetts General Hospital, expressly for use with bat sounds. The pulse detector responds to sounds containing frequencies from 10 to 100 kc and generates an audible frequency or click if the ultrasonic sound is amplitude modulated or pulsed. It thus "translates" into the range of human hearing all known bat sounds, which are either pulses or have enough amplitude modulation to activate the detector.

The portable pulse detector with its crystal microphone proved to be more sensitive to frequencies above about 45 kc than the condenser microphone, so that Novick was able to discover many types of low intensity pulses from species of bats that had appeared to be virtually silent when studied with the condenser microphone the year before. Although the pulse detector could not be calibrated, a direct comparison of the two microphones showed that at frequencies from 45 to 95 kc the Rochelle salt crystal itself is two to three times more sensitive than the condenser microphone, and that the parabolic horn increases the sensitivity of either microphone by roughly a factor of 4. The pulse detector also contains an amplifier that can be tuned to fairly narrow frequency bands, giving it an additional advantage. Nevertheless, all species that could be adequately compared in the laboratory showed virtually the same sound output whichever instrument was used, except that the condenser microphone had to be brought to within a few centimeters of the bat's mouth before some of the fainter sounds with frequencies above 70 kc could be detected. For certain species which did not survive in captivity we can report only the results obtained in Panama in 1954 with the pulse detector.

The general nature of the high frequency sounds of neotropical bats

Before describing the sounds emitted by each of the 16 species studied it is helpful to consider certain of their general properties, as well as some of the problems encountered in their analysis. Like all bats we have studied to date, these neotropical species emit both audible cries of relatively long duration, and very short pulses (generally inaudible) which appear to be used for orientation. The audible cries have a wide spectrum of frequencies including some in the range of human hearing, but many other strong components are above 20 kc. Since their properties are variable and since they do not seem to be used for orientation, these audible cries will not be considered further here. The pulses, like those described from other families of bats, have variable envelope patterns, the amplitude of high frequency sound varying in an irregular fashion. But the significant and characteristic properties which we have analyzed are: (1) the pulse duration, (2) the intensity or sound pressure, (3) the frequency and the manner in which it changes from pulse to pulse or during a single pulse. Other important properties concerning which we can offer only limited evidence are the pulse repetition rates under various conditions, and directional intensity patterns.

The species we have studied fall into two groups with regard to the pattern of frequency changes in their pulses, the family Noctilionidae on the one hand, and the families Emballonuridae, Phyllostomidae, and Desmodontidae on the other. The first group, discussed in Part I of this paper, emit sounds rather similar to those of the Vespertilionidae, while those of the second group are distinguished by complex and changing patterns of frequencies described in Part II. There are also striking differences in intensity, the insectivorous species emitting much louder sounds.

Part I.

The family Noctilionidae (including a fish catching bat)

Early observations of the fish eating bat *Noctilio leporinus mexicanus* have been summarized by Gudger ('45); and Bloedel will describe elsewhere their feeding habits as revealed by high speed photography. For present purposes, it is sufficient to state that small fish are caught on the darkest nights — sometimes in mist and fog — by *Noctilio* which fly for some distance just above the surface of the water and occasionally dip their hind feet beneath the surface. These bats weigh 30–40 gm and take fish one to three inches in length. Since many *Noctilio* stomachs have been found to be filled with fish, their fishing efforts must be successful a reasonable proportion of the time. On some occasions, however, insect remains have been found in their stomachs.

Records were obtained from *Noctilio* fishing on the Chagres River and also from captive bats which Bloedel had induced to fish from a shallow tank of water. The wild *Noctilio* were found to be emitting pulses of high frequency sound whenever they were within range of the microphone. These pulses varied considerably in duration and may be divided for convenience into three types: (A) relatively short pulses with a continuously dropping frequency much like those of the insectivorous bats of temperate latitudes. (B) longer pulses without any obvious amplitude peak and with rather less than an octave of frequency drop, and (C) a combination of A and B into a single long pulse consisting of an initial part with relatively low and constant amplitude and a terminal peak during which the frequency dropped more rapidly. A few pulses were intermediate between these three types. Duration and frequency measurements from a large number of records are summarized in table 1, and typical oscillograph records are shown in figures 2 to 5. The frequency drops during all records, but the rate of frequency change varies from about 1 kc/msec in type B pulses to 3 kc/msec or more in some of the short pulses and in the terminal peaks of type C.

Three *Noctilio* which had been in captivity for some weeks were brought to Woods Hole in August, 1953 and induced to catch fish from a shallow wooden tank located in a room 4 m wide, 3 m high, and 10 m in length. They tended to emit more of the shorter type A pulses than did wild bats studied on the Chagres River. Often, as one of these bats would approach the tank, it would emit type A pulses at a rate of about 60 per second (fig. 3). At other times, however, even these captive *Noctilio* emitted type B and C pulses. Intensity measurements were also made at Woods Hole with a calibrated 640AA condenser microphone, and at 50 cm from the bat's mouth typical *Noctilio* pulses had peak-to-peak sound pressures of 30 to 60 dynes/cm^2, compared to 60 dynes/cm^2 at 10 cm (or about 12 dynes/cm^2 at 50 cm) in *Myotis* (Griffin, '50).

It is of interest to inquire how these bats locate the fish which they catch by flying just above the water and dipping their hind feet beneath the surface only a small fraction of the time. Often, the water was perfectly calm when we observed this activity with the aid of powerful flashlight, and from a distance of 25 to 50 feet no ripples or disturbance of the water could be seen at a spot where, a moment later, one of these bats would dip its feet into the water. It is possible, as Bloedel is inclined to believe, that the fishing is a

TABLE 1

Duration and frequency measurements of pulses emitted by the fish-catching bat Noctilio leporinus mexicanus. Average values are listed, followed by extremes of the series in brackets; for definitions of the types of pulses see text

TYPE OF PULSE		DURATION		FREQUENCY					
				Start		Middle		End	
		no.	msec.	no.	kc	no.	kc	no.	kc
A		47	5.2 (2.8– 8.3)	8	38 (34–44)	4	31 (28–38)	11	28 (23–31)
B		5	10.1 (7.8–14.0)	1	44	7	46 (27–49)	2	34 (26–43)
C	first part	7	11.3 (8.1–15.0)	7	55 (50–64)	17	51 (44–58)	2	43 (41–45)
	last part			6	39 (37–41)	7	32 (24–36)	8	30 (24–37)

purely random process, the bat dragging its gaff-like claws just below the surface while flying over areas where it has learned to expect good fishing. This method seems likely to be rather inefficient, however, and since vision is of little use on dark nights we should consider the possibility that *Noctilio* detects fish by echolocation, as some insectivorous bats appear to locate flying insects (Griffin, '53a).

This hypothesis encounters a formidable difficulty in the very inefficient transfer of sound energy from air to water or vice versa. As clearly set forth, for example, by Olsen ('47, p. 119), the energy of a sound wave penetrating from air into water, at right angles to the surface, is reduced to approximately 0.0012 of the incident energy. Oblique incidence would cause even greater loss by reflection. Any echoes of *Noctilio* pulses from a submerged fish would thus be reduced in energy by a factor of roughly 10^6 merely in passing twice through the air-water interface, quite aside from the further losses due to the small proportion of the underwater sound atcually reflected from the fish. A rough determination of the sound energy present in the water under a *Noctilio* fishing from the tank at Woods Hole was made with a type AX-58 crystal hydrophone kindly loaned by Dr. B. Hersey of the Woods Hole Oceanographic Institution. While not itself calibrated, this hydrophone and its associated cathode follower unit were very similar in construction to units for which accurate calibrations were available over the frequency range of *Noctilio* sounds. With this hydrophone wholly sumerged in a wooden tank 60 cm wide and 180 cm long in water 28 cm deep, the sounds of *Noctilio* were readily observed either as the bat flew low over the water or when it actually immersed its feet to capture small fish. The maximum underwater sound pressure registered under these conditions was 15–20 dynes/cm^2 (corresponding to about 6×10^{-10} watt/cm^2). This was rather less than the theoretical expectations based on the known sound pressure in the air and the reduction to 0.0012 of the incident energy on passing vertically through the surface. There is thus no evidence that *Noctilio* have any efficient method of generating underwater sound.

Yet *Noctilio* do manage to catch fish even on dark nights, emitting pulses of high frequency sound as they do so. These pulses might merely be used for orientation with respect to the water or other objects in the air; or fish may be detected through slight disturbances of the surface which the bat could detect acoustically although we could not see them while watching the tank from which fish were taken by the captive *Noctilio*. If, on the other hand, acoustic detection of submerged fish does indeed occur, the distance from bat to fish may be quite short, possibly as little as 20 cm. When other bats detect flying insects in the air, both their outgoing sound and the returning echoes probably obey the inverse square law over most of the distance separating the bat from its prey, and there is evidence that small targets are detected at about two m (Griffin, '53a). Let us thus compare two hypothetical cases: a *Noctilio* attempting to locate a submerged fish at 20 cm and an *Eptesicus* attempting to locate a flying insect at 200 cm. Other factors being equal, this difference in distance would cause the echo from the nearer object to contain 10^4 times more sound energy. The insertion of an air-water interface between the bat and its target causes a reduction by a factor of 10^6, which leaves a factor of 100 in favor of the insectivorous bat. A further problem encountered by *Noctilio* would be the overlap in time between outgoing pulse and any echoes from a fish as close as 20 cm. Yet the insectivorous horseshoe bats discussed below (page 286) seem able to overcome this difficulty in their acoustic orientation based on 100 msec pulses (Möhres, '53a). Another consideration which may narrow this gap is the somewhat greater intensity emitted by the fishing bat. While the evidence at hand is neither conclusive, nor encouraging for the hypothesis of echolocation of submerged fish by *Noctilio*, further investigation of the matter is in order.

Another member of the family Noctilionidae is the strictly insectivorous *Dirias albiventer minor* which weighs 15–22 gm. Of 21 pulses recorded as these bats flew over the Chagres River in pursuit of numerous small insects, the average duration was 8.0 msec (4.1–13.0). In the laboratory, *Dirias* tended to emit shorter pulses, although we did not observe any differences in duration as great as in *Eptesicus fuscus* and *Lasiurus borealis* (Griffin, '53a). There is a considerable frequency drop in *Dirias* pulses, as in those of the Vespertilionidae. With the condenser microphone used in 1953, the average of 4 measurements near the start was 51 kc (44–59), 7 in the middle of *Dirias* pulses averaged 48 kc (31–58), and two measured near the end were 31 and 33 kc. This small series includes both field and laboratory records, but there was no apparent difference between the two. In 1954 with the pulse detector, the average of 16 measurements near the beginning was 62 kc (46–69), 77 in the middle averaged 56 kc (37–72), and 21 at the end averaged 41 kc (33–49). While these measurements show clearly that the frequency tended to drop, the change was very slight or absent in many individual records, a few even showing a slight rise in frequency during a part of a pulse. But whenever an appreciable rate of change of frequency was apparent the direction of the change was downward. The peak-to-peak sound pressures from a *Dirias* which had been in captivity for some weeks were 20–40 dynes/cm^2 at 50 cm from the bat's mouth. No significant harmonics were noted with either the condenser or crystal microphone. In short, *Dirias* pulses can be distinguished only with difficulty from those of bats belonging to the Vespertilionidae.

Part II

The families Emballonuridae, Phyllostomidae, and Desmodontidae

The bats of these three families emit pulses of sound which almost never show the progressive drop in frequency that is so characteristic of both the Vespertilionidae of temperate latitudes and the family Noctilionidae considered above. In some pulses the frequency is essentially constant; in others there are two or more component frequencies which may all be present at high amplitudes or may change rapidly in their relative intensities. Often some of the major components are multiples of the lowest frequency present, and it is therefore convenient to describe such a mixture as a fundamental frequency plus 2nd, 3rd or higher harmonics. Interpretation of these sounds is complicated, however, by the fact that the higher of two component frequencies is often much greater in amplitude than the lower. What will be called the "fundamental" may thus be weaker than some of its "harmonics", or it may even become so faint as to be lost in the noise level of the apparatus.

Sounds of this degree of complexity are best described in terms of their frequency spectrum, the list or graphic representation of the several component frequencies together with the relative amplitude of each. In many of the cases described below an oscillograph record does not clearly reveal all of the major components of the frequency spectrum that are present at significant amplitudes. This difficulty is most clearly demonstrated by figure 11 which shows a series of reasonably pure waves of about 100 kc that are varying in amplitude at a rate of approximately 20 kc, that is, the amplitude is maximal about once every five of the 100 kc waves. Such a series of waves is similar to the amplitude modulated radio waves of a standard broadcast transmitter; and borrowing terminology from this well-known case, we could call the 100 kc of figure 11 the "carrier frequency", C, and 20 kc could be called the modulation frequency, M. As explained in textbooks of radio engineering, the frequency spectrum in such a case contains the frequencies C, C + M, and C − M, *but not the modulation frequency,* M, *itself.* If, as is the case in many bat pulses, the waveform of the modulation frequency is other than sinusoidal, or if it is changing, still other frequencies will be prominent in the spectrum.

The example of amplitude modulated waves shown in figure 11 thus warns us that all important components need not be represented by obvious peaks at regular intervals across the oscillograph record. In many cases it was not feasible to obtain records as clear as figure 11; and with a lower sweep speed only the highest peaks may be clearly visible above the noise level. Such a record of the same pulse shown in figure 11 might easily be interpreted as 20 kc mixed with some of its harmonics, whereas 20 kc may not have been present in the frequency spectrum at all! In other words, many of our records cannot be resolved in sufficient detail to distinguish with certainty between two possible interpretations: (1) that a particular frequency, F, is mixed with one of its harmonics, for example 3F, or (2) that frequency 3F is undergoing amplitude modulation at frequency F, in which case the frequency spectrum would contain 2F and 4F at greater amplitudes than F itself.

In view of these complications, and others introduced by shifting phase relationships between the several components, we shall call attention only to the more prominent components, those having the highest amplitude, and those which the records show clearly to have been actual components of the frequency spectrum. But it should be born in mind that other less obvious components may also have been present at significant amplitudes, especially when there were sudden shifts in the predominant frequency, as for example in figure 8.

Family Emballonuridae, the sac-winged bats

The Emballonuridae are considered by Miller ('07) to be relatively primitive, having a shoulder joint less highly specialized for flight than many other families of the suborder Microchiroptera. The distinguishing features of the family are glandular sacs in the wing membranes (most prominent in the males) and a tail which protrudes through the dorsal surface of the interfemoral membrane. There is no nose leaf. The two species we studied both roost during the day in relatively better lighted retreats than other bats, and they are more alert and difficult to approach. Both are insectivorous and could only be fed in captivity with great difficulty, so that all records discussed below were obtained within a few hours of capture from bats which still gave every evidence of good health.

Rhynchiscus naso. These very small bats (weight 3.5–4 gm) emitted high frequency sounds that were easily detected by the condenser microphone and associated apparatus used in Panama in 1953. Although intensity calibration of the apparatus was not attempted in Panama, the sound pressure levels were evidently much closer to those in pulses emitted by the Vespertilionidae than to the low levels emitted by the leaf-nosed bats discussed below. Aside from the audible cries of relatively long duration that these bats emitted when disturbed or excited, we detected two distinct types of pulses when *Rhynchiscus* were crawling about in small cages or when they were held gently in the hand in the same manner that serves to elicit pulses from the Vespertilionidae. These two types differed most obviously in duration, but the shorter type also contained higher frequencies. Filter settings of 20 kc high pass, at 36 db per octave slope, were used for all the records obtained in 1953, so that the declining sensitivity of the condenser microphone reduced the relative amplitude of the higher frequency components visible in the photographs.

A typical group of the short pulses of Rhynchiscus is illustrated in figure 6, and it was characteristic of these short pulses that they were emitted in bursts of 5 to 12 within 80 to 150 msec. Nine typical pulses averaged 5.0 msec in duration, the extremes being 4.0 and 6.8. The fundamental frequency in 8 typical short pulses averaged 45 kc (41–47), and there was no apparent change in fundamental frequency during the pulse; measurements at the end did not differ from those at the beginning of the pulse or in the middle. A second harmonic, however, is a predominant feature of many of these pulses, such as those included in figure 6. The appearance of the pulses shown in figures 6 and 7 results from the horizontal compression of a series of waves of the type shown in figure 1. This is unavoidable in records such as figure 7 in order to show a substantial part of the pulse in one picture and only the crests of the waves remain clearly distinguishable. Or, at still lower sweep speeds, as in figure 6, the individual crests fuse to give a series of lines.

Correcting for the declining sensitivity of the condenser microphone, the true amplitude of the second harmonic is 4 times that shown in photographs such as figures 6 and 7. As can be seen in figure 7, the amplitude ratio of harmonic to fundamental varies from pulse to pulse, and within single pulses, from no discernible harmonic to cases such as figure 7 where the corrected amplitude of the harmonic is many times that of the fundamental. Indeed the fundamental almost disappears in some cases so that isolated parts of such pulses show only one component of about 90 kc.

Fig. 1 The same artificially generated waves having a strong second harmonic, photographed at three different sweep speeds to show the origin of oscillograph patterns such as those seen in figures 6 and 7. Note how the peaks and inflections form bright spots (owing to the lower velocity of the cathode ray trace), and how at the slowest sweep speed (shown on the right) these spots fuse into continuous lines.

Pulses were also detected without difficulty from the *Rhynchiscus* studied in 1954 with the portable pulse detector tuned to approximately 100 kc. The duration ranged from 4 to 7 msec, and the frequencies of 18 pulses were 84 to 103 kc. These pulses picked up by the crystal microphone did not show the combination of fundamental and second harmonic so striking in figure 7, but appeared instead to be nearly pure and constant frequencies averaging 94 kc. This difference may be due either to the different apparatus used, or to a difference in the type of sound emitted by the particular bats studied in 1953 and 1954. Whichever explanation is correct it is clear that strong components in the neighborhood of 90 kc are commonly emitted in the short pulses of this species.

The *Rhynchiscus* studied in 1953 sometimes emitted much longer pulses which were definitely lower in frequency than the short pulses. The average duration of 11 long pulses was 90 msec (66–108), and the average of 13 frequency measurements in various parts of such pulses was 26 kc (21–30). Again there was no consistent shift in frequency within a single pulse, the frequency at the beginning and at the end being the same within the accuracy of our measurements. There were no appreciable harmonics. The long pulses were observed far less often under laboratory conditions in 1953 than the short pulses, and they were not observed at all in 1954, perhaps in part because of the type of camera used to photograph the cathode ray traces. It may be significant that the average frequencies of the long pulses and of the two components of the short pulses are separated by intervals of roughly an octave (26, 45, and 90 kc). Further investigation would be required to determine which type predominates under natural conditions, or whether the two are used during different types of flight as are the short and long pulses of *Eptesicus* (Griffin, '53a). While the durations of the long pulses emitted by *Rhynchiscus* are similar to those described by Möhres ('53a) as typical for the European horseshoe bats, the short duration pulses seem to predominate, so that it seems unlikely that *Rhynchiscus* normally employs a type of acoustic orientation similar to that of the horseshoe bats.

Saccopteryx bilineata. These bats, slightly larger than *Rhynchiscus*, appear to be similar in their general habits; but neither in 1953 nor in 1954 did we obtain as satisfactory records of their sounds. Most of those detected in 1953 (under the same conditions prevailing for our observations of

Rhynchiscus except that filters were set at 15 kc high pass) were relatively long in duration or consisted of long trains of pulses, each lasting one or two msec and separated from the next by about the same interval. Occasional parts of such sounds show frequencies as high as 40, 46, or 58 kc, but most of the frequencies measured were much lower — for example one series of 7 measurements averaged 19 kc (14–25). Harmonics were sometimes present, but not in so regular a pattern as in *Rhynchiscus*. The records obtained in 1954 with the pulse detector showed definite pulses with durations of not less than 3.5 nor more than 15 msec (this uncertainty resulting from the film and shutter speeds employed with the 16 mm camera). No shift in frequency during a single *Saccopteryx* pulse was observed, and the highest frequencies measurable in these pulses ranged from 20 to 33 kc. Many were nearly pure frequencies of 22 to 32 kc, while others appeared to be frequencies of about 27 kc amplitude modulated at 9 kc. Still others showed a fundamental frequency of 12 to 16 kc. plus a strong second harmonic.

It is of interest to note that under natural conditions *Saccopteryx* was the only bat which produced readily audible clicks during flight. These sounds were reminiscent of those produced by a rachet type noise maker heard at some distance. The nature of this audible component is not evident, nor have we obtained oscillograph records from flying *Saccopteryx*. In view of the cases described below in which our first attempts to study certain species did not disclose the pulses used for orientation during flight, we suspect that we may not have an adequate sample of the sounds emitted by *Saccopteryx*.

Family Phyllostomidae, the leaf-nosed bats

This is by far the most abundant group of bats in the American tropics, and, indeed, the bats of this family appear to outnumber all other native mammals. The family is characterized by a fleshy projection extending upwards from the tip of the snout, just posterior to the external nares. The nose leaf varies widely in size and shape, as can be clearly seen in the illustrations in Goodwin's paper ('46). This structure resembles the "horseshoe" surrounding the external nares of the Rhinolophidae studies by Möhres ('53a), and similar structures surrounding the nostrils of two other Old World families of bats, the Hipposideridae and the Megadermidae. The nose leaf of the Phyllostomidae, however, is the simplest of these structures. Furthermore it is lacking altogether in one subfamily, the Chilonycterinae, which also show such characteristic differences in their high frequency sounds that they will be discussed in a separate section.

Sub-family Chilonycterinae

The best known member of this subfamily is *Chilonycteris r. rubiginosa,* a species of which hundreds were present in certain caves in or near the Canal Zone. Bats of this species weigh 18–22 gm and are insectivorous. While they lived for a few days in captivity, they did not eat and were studied only in Panama. Pulsed sounds were as readily elicited from *Chilonycteris rubiginosa* as from the Vespertilionidae. While no sound pressure measurements are available, *Chilonycteris* pulses are not greatly different in intensity from those of the Vespertilionidae. The records obtained in 1953 with the condenser microphone showed widely varying pulse durations. Two records showed peaks lasting 2.9 and 3.8 msec rising above a background of more continuous sound, and another record shows a pulse lasting 130 msec. But the great majority of the pulses lasted 10–30 msec, the average of the 10 most satisfactory duration measurements from the standpoint of intensity resolution being 21 msec (13–29). Records were obtained by Novick in 1954 with the portable pulse detector from one bat of this species and they showed durations of 8 msec and greater.

The frequencies measured in 15 condenser microphone records of this species averaged 26 kc (21–30) with filters set at 20 kc high pass; and the pulse detector indicated frequencies from 22 to 28 kc. There was little if any change in frequency during the pulses except for the intermittent presence of very intense second harmonics. Interestingly enough, three records show pairs of pulses separated by only 10–15 msec in which the first member of the pair contained little or no second harmonic while the second pulse showed a second harmonic exceeding the fundamental in amplitude, when corrected for the declining sensitivity of the microphone. Certain records obtained with the pulse detector show frequencies of approximately 46 kc with no trace of the usual 22–25 kc component. There are frequent examples, in addition, of transitions from a clear fundamental of 23 kc, with a second harmonic, to an apparently pure frequency of 46 kc. In many respects the pulses of *Chilonycteris rubiginosa* are similar to the short pulses of *Rhynchiscus*, except that the frequencies are lower. While no progressive frequency modulation occurs during the pulse, the strong second harmonic, when present, would provide another frequency an octave above the fundamental.

Chilonycteris personata. This species is the smallest of the Chilonycterinae studied, being about one half the size of *Eptesicus fuscus*. A large colony was found in 1954 sharing a small cave in the vicinity of Penonemé, Panama with *Chilonycteris rubiginosa, Pteronotus suapurensis,* and *Carollia perspicillata azteca. Chilonycteris personata,* a vividly colored bat believed to be insectivorous, failed to survive in captivity, and hence was studied only with the pulse detector in Panama. Its pulses are typically short in duration, 12 measurements averaging 2.4 msec (1.5–4.5) with occasional trains of three or four short pulses in almost continuous succession. Analysis of 36 pulses shows that they contain a fundamental frequency averaging 33 kc (30–36) invariably accompanied by a second harmonic and, rarely, by a third harmonic as well. The relative amplitudes of the harmonics may shift gradually or abruptly, and the third harmonic often drops out during the pulse. These pulses never contained the fundamental alone or the second harmonic alone, as occurs in *Chilonycteris rubiginosa*. The amplitudes of the pulses of these two species are approximately the same.

Pteronotus suapurensis. This bat, remarkable for having its wings attached along the middle of its back, is insectivorous and very closely related to *Chilonycteris*. In size, it falls between the two species of *Chilonycteris* studied. It, too, failed to eat in captivity and so was studied only in Panama with the pulse detector. The pulses proved to be uniformly short as in *Chilonycteris personata*, 8 averaging 2.2 msec (1.9–2.7) in duration. In frequency, 31 pulses contained a fundamental of about 22 kc (20–25) invariably accompanied by a second, sometimes by a third, and occasionally a 4th or even a 5th harmonic of significant amplitude. The highest frequency noted was 125 kc in two pulses which also showed components at 25, 50, 75, and 100 kc. There was no indication of progressive frequency modulation, but the highest component sometimes dropped out, resulting, for example, in shifts of the predominant frequency from 65 to 45 kc, 70 to 50 kc, and 70 to 43 kc. This species thus produces sounds spanning more than two octaves, with the strongest components tending to be separated by harmonic intervals. The sound pressures are roughly the same as those of *Chilonycteris*.

Sub-family Carolliinae, Carollia perspicillata azteca

These medium-sized leaf-nosed bats, which are perhaps the most abundant wild mammals in Panama, were easily maintained in captivity on a diet of bananas and other fruit. Although they weigh 14–20 gm, they are clearly more adept at flying in small spaces than 6–8 gm bats of the family Vespertilionidae such as *Myotis lucifugus*. *Carollia*, for instance, can turn and fly back and forth in a cage 1 × 0.5 × 0.5 m in size without touching the walls. Since the sounds and acoustic orientation of these bats were studied more thoroughly than those of any other leaf-nosed bats, *Carollia* will be discussed first, and other species briefly compared with it in later sections.

Our first impression, on attempting to detect their sounds with the condenser microphone, was that *Carollia* were remarkably silent. An amount of time and effort which would easily have induced any of the Vespertilionidae to make dozens of pulses easily detectible with the condenser microphone yielded nothing but a few low frequency noises of relatively long duration. To be sure, an occasional one to two msec pulse was elicited, and such pulses ranged in frequency from 18 to 31 kc (Griffin, '53b). A few of these pulses showed a gradually declining frequency similar to the pattern characteristic of the Vespertilionidae (for example 29 kc at the start and 18 kc at the end of a 2.2 msec pulse). But most of the time no sound whatsoever could be detected, whether the bats were allowed to fly about in a large cage or laboratory room or were gently held in the hand in a manner known to elicit pulses from other species.

Yet blinding did not affect the ability of 4 *Carollia* to fly normally or avoid obstacles, and like other bats they became quite helpless and disoriented when their ears were plugged. Clearly they were dependent upon some type of sound for their orientation, but this was very seldom detectible either by the unaided human ear or by the condenser microphone and associated apparatus used in Panama during 1953. During the spring of 1953–54 a few live *Carollia* were shipped to Cambridge. On studying these in an improved flight chamber we first noted faint, but clear, audible clicks as a bat flew past our ears at a distance of a foot or two in a quiet room. These audible sounds could be detected by the 640AA microphone, which has its maximum sensitivity at frequencies below 12 kc. Their frequency was 1600–2100 c.p.s., corresponding to wave lengths in air of about 20 cm. Yet these bats avoided fine wires with such great skill that these long wavelengths could scarcely have been the basis of their orientation (see table 2). Hence a more intensive search was made for high frequencies, and, indeed, when the condenser microphone was within two or three inches of a flying *Carollia*, short pulses of 50–100 kc sound were at last detected. The audible clicks are presumably comparable with the low frequency, low amplitude components which seem to accompany the high frequency pulses of other bats (Griffin, '51).

The high frequency pulses of *Carollia* had been overlooked previously not because of their frequency but because of their intensity, which is very much lower than the levels to which we had become accustomed in the Vespertilionidae and other bats. This experience demonstrates how easily we might have been misled if our attempts to explain the orientation of these bats had terminated earlier. For example, it seemed quite possible that *Carollia* was orienting itself visually, until we blinded one individual and plugged the ears of another. Later it seemed as though the few pulses we detected at 18 to 31 kc were typical of the vocal repertoire of *Carollia,* but more thorough study showed that these were exceptional and probably more analogous to the occasional low frequency pulses of the Vespertilionidae. Once we knew what to look for, it has always been possible to detect pulses from *Carollia,* but only with the condenser microphone very close to the bat's mouth, either during flight, before and during takeoff, or with the bat loosely held in the hand. It seems likely, though not certain, that the sound is concentrated into the forward direction, but we have not seen evidence of so narrow a beam as Möhres describes in the Rhinolophidae. Accurate measurement of directional pattern must await further investigations.

Since a microphone more sensitive above 50 kc than the 640AA was clearly necessary, we turned to Rochelle salt crystals of the type used by Pierce in his original apparatus for the study of high frequency sounds in air. While far from the ideal microphone for analyzing bat sounds (which would be highly and uniformly sensitive to all frequencies from 10 to 200 kc), these Rochelle salt crystals make it possible to pick up the faint high frequency sounds of *Carollia* and similar bats at somewhat greater distances. It was largely because of this experience with *Carollia* that the portable pulse detector described above was developed for Novick's 1954 trip to Panama.

Several long series of records were obtained from captive *Carollia* that were in excellent condition, using both the condenser and crystal microphones with filter settings of 20 kc high pass; and we feel confident that these represent the typical pulses used for orientation during flight. The average duration of a series of 24 such pulses was 1.4 msec (0.9–2.3). The sound pressure, measured with a calibrated 640AA microphone in 45 pulses from flying *Carollia,* averaged 3.6 dynes/cm^2 (1.0–11.7). These records were obtained by having the bats fly past the microphone, the distance from bat to microphone varying widely. When the condenser microphone was held as much as 30 cm from a *Carollia* the pulses were only barely visible above the noise level of the apparatus. Since the photographs with the best signal-to-noise ratio were selected for the measurements, these values represent sound pressure levels at a few centimeters from the bat's mouth.

The frequencies varied considerably in the pulses emitted by *Carollia.* Out of a series of 40 satisfactory photographs of short pulses detected by the condenser microphone from *Carollia* that were in full flight, or taking off, the measured frequencies ranged from 15 to 101 kc. Frequencies below 60 kc were exceptional, however, and, in the typical pulses, frequencies near the beginning ranged from 76 to 92 kc, those in the middle from 63 to 101, and those near the end from 70 to 92 kc. When the crystal microphone was used with the same amplifiers and filters, somewhat higher frequencies were recorded. Nine satisfactory records with the crystal microphone included frequencies of 86–128 kc near the beginning, 114–119 kc in the middle, and 71–114 kc at the end. Since the condenser microphone favors lower frequencies, and, since only a few pulses could be detected with either microphone at high enough signal-to-noise ratios to permit satisfactory measurements, it is not surprising that those achieving this status with the crystal microphone should range somewhat higher in frequency.

These measurements show that there is no clear trend for the frequency to rise or fall during the pulse, and, hence, there is no frequency modulation comparable to that of the Vespertilionidae. While individual bats show some differences in frequency, there is at least as much variation among the pulses emitted by a single bat within a fraction of a second. Even within an individual pulse there are often striking changes of frequency, in either direction. Sometimes a reasonably pure frequency suddenly acquires a second or higher harmonic which increases rapidly in amplitude until it appears to be the only frequency present. In other records sudden shifts by less than an octave can be seen. An exceptional, but not unique, case of frequency shift within a single pulse is shown in figure 8. The expanded portion of this record lasted about 0.7 msec out of a total pulse duration of approximately 1.8 msec. The first 4 waves in the expanded portion have a frequency of 23 kc, but the distorted wave form shows that harmonics are present, and it should be recalled that their true amplitudes were several times greater than indicated in the figure because of the declining sensitivity of the microphone. There is then an abrupt shift to a frequency of 75 kc for about 15 waves, followed by an interval with irregular inflections in these waves. Finally a frequency of 96 kc appear for the balance of the record.

In certain records of *Carollia* pulses there is thus an interval of fairly low frequency (20–30 kc) preceded or followed in a very short time by multiples of this frequency. More often, only the higher frequencies are apparent, but these often show shifts by 20–25 kc. For example, in one record there was a sudden shift from 77 to 98 kc, and, in another, from 80 to 100. Other records show more gradual changes such as 79 to 92 kc and 93 to 85 kc in about ½ msec. Still other records of *Carollia* pulses show amplitude modulation at ½ or occasionally ¼ the predominant frequency, but

TABLE 2

Success of three species of leaf-nosed bats in avoiding a row of vertical wires spread across the center of a 4 × 10 m room. The wires were 60 cm apart for Artibeus, 30 cm for Carollia, and 30 cm for Glossophaga (except that for some of the tests of Glossophaga with 0.175 mm wire one space was 60 cm). Wire diameter listed at the top of each column. Maximum wingspreads: Artibeus 45 cm, Carollia 30 cm, and Glossophaga 25 cm.

WIRE DIAMETER		1.05 mm		0.60 mm		0.275 mm		0.175 mm	
SPECIES		No. of trials	% misses	No. of trials	% misses	No. of trials	% misses	No. of trials	% misses
Carollia	No. 1	—	—	—	—	—	—	270	72%
Carollia	No. 2	—	—	—	—	—	—	122	46%
Carollia	No. 3	—	—	—	—	—	—	101	36%
Carollia	No. 4	—	—	—	—	—	—	82	66%
Carollia	No. 5	—	—	—	—	—	—	112	46%
Carollia	No. 6	—	—	—	—	—	—	70	60%
Carollia	No. 7	—	—	—	—	112	70%	59	39%
Carollia	No. 8	—	—	—	—	55	56%	—	—
Carollia	No. 9	—	—	—	—	33	67%	—	—
Carollia	No. 10	—	—	—	—	43	61%	—	—
Average						243	65%	816	56%
Glossophaga	No. 1	34	80%	—	—	—	—	—	—
Glossophaga	No. 2	—	—	54	63%	—	—	—	—
Glossophaga	No. 3	—	—	37	76%	—	—	—	—
Glossophaga	No. 4	—	—	—	—	181	84%	—	—
Glossophaga	No. 5	—	—	—	—	133	70%	—	—
Glossophaga	No. 6	—	—	—	—	—	—	104	79%
Glossophaga	No. 7	—	—	—	—	—	—	279	90%
Glossophaga	No. 8	—	—	—	—	—	—	177	94%
Average		34	80%	91	68%	314	75%	560	89%
Artibeus	No. 1	25	76%	35	94%	—	—	—	—
Artibeus	No. 2	39	67%	47	85%	68	85%	54	72%

such amplitude modulation appears to be less common than the mixture of a fundamental of 20–30 kc with one or more of its harmonics.

The avoidance of fine wires by Carollia. In view of the rather different type of sound used for orientation by *Carollia,* the ability of these bats to avoid small obstacles was compared with that of the Vespertilionidae studied some years ago (Griffin and Galambos, '41). The *Carollia* were allowed to fly back and forth in a room 4 × 10 m in size, divided into two 4 × 5 m areas by a row of vertical wires extending from floor to ceiling (2.5 m). The spacing of the wires (30 cm) as well as the method of scoring hits and misses was the same as in the earlier experiments with *Myotis.* Because the actual wingspread and the angle of approach varies widely, it is not possible to calculate the precise percentage of misses to be expected if the bat were avoiding wires by chance alone. With *Myotis lucifugus,* having a maximum wingspread of about 25 cm, the actual chance score for wires 30 cm apart was close to 35% misses. Since *Carollia* have a maximum wingspread of about 30 cm, the chance score might be somewhat lower. The results of these tests are shown in table 2, together with the data for two other species of leaf-nosed bats to be discussed below. It is clear that some of the *Carollia* avoided even the smallest wire used (diameter 0.175 mm) far more often than could be explained by chance alone. A comparison with the performance of *Myotis* shows that *Carollia* avoided small wires even better than this small member of the family Vespertilionidae. The average scores in several hundred trials with *Myotis lucifugus* were: 72% misses for wire 0.35 mm in diameter, 52% for 0.26 mm, 39% for 0.12 mm, and 36% for 0.07 mm (Curtis, '52).

The superior performance of *Carollia,* despite the low intensity of their pulses, may be associated with their habit of flying more slowly and often hovering in front of the barrier before flying between the wires. This mode of flight may also be related to their normal diet of fruit, rather than flying insects. Yet under natural conditions *Carollia* are more often caught in trammel nets constructed of fine linen thread than are the insectivorous bats or *Noctilio*. Perhaps *Carollia* and other fruit eating bats are accustomed to brushing against vegetation and fail to distinguish the nets from harmless natural obstacles. But it reamins a puzzling paradox that under natural conditions *Carollia* failed to avoid these nets far more often than Myotis, while the opposite was true of the small wires used in our laboratory tests.

Experiments with mouth, nostrils, and nose leaf of Carollia

Carollia and most other members of the family Phyllostomidae resemble the horseshoe bats of the Old World in having a nose leaf, although there are many differences between the structure of the simple spear-shaped nose leaf of the Phyllostomidae and the complicated "horseshoe" surrounding the nostrils of the Rhinolophidae. Möhres ('53a) has recently shown that the "horseshoe" serves as a small horn concentrating the emitted sound into the forward direction, but as far as we can determine the feeble pulses emitted by the Phyllostomidae are not nearly so strongly concentrated into a narrow beam as Möhres reports for the very intense pulses of the horseshoe bats. When the nose leaf of one *Carollia* was amputated (a virtually bloodless procedure) the bat showed no appreciable impairment of flying skill or ability to avoid obstacles. Four other *Carollia* were used to study the relative importance of the mouth and nostrils in the emission of the high frequency pulses. When the mouths of three of these bats were tightly sealed the pulses were either quite normal or were slightly reduced in intensity. When their nostrils were sealed two of the bats emitted pulses that could not be distinguished from normal, and the other two emitted a series of pulses that included the whole range of frequencies usually present, but an abnormally large proportion contained frequencies from 20 to 60 kc rather than frequencies above 80 kc.

Carollia (and presumably other Phyllostomidae) thus resemble the horseshoe bats in being able to emit sound through the nostrils. Another similarity involves the habit of frequently and rapidly turning the external ears from side to side while investigating their surroundings. It is tempting to conclude that these movements represent a form of scanning, and that the nose leaf of the Phyllostomidae serves either to render the outgoing sound more directional, or to aid in auditory localization of sounds reaching the bat's ears — including perhaps echoes of its own pulses. But the low intensity of the pulses emitted by the Phyllostomidae places formidable obstacles in the way of a detailed analysis of the directional intensity pattern of the emitted pulse, so that testing of such hypotheses as these must await further improvements in our technical facilities.

Sub-family Phyllostominae

Lonchorhina aurita. These bats are slightly smaller than *Carollia* (10–16 gm), and they have a long, narrow nose leaf. They did not survive for long in captivity even though provided with a variety of fruit. The records obtained in 1953 with the condenser microphone showed many short duration pulses of relatively low frequency. In 28 measurements, the average duration was 2.7 msec (1.0–5.4), and the average of 15 measurements of the fundamental frequency was 12 kc (11–13). There were no signs of frequency modulation within the pulses, but both second and third harmonics were very prominent, so that strong components as high as 39 kc were present in almost all pulses recorded from this species. Indeed some records show the 12 kc. component dwindling to an insignificant amplitude, so that virtually pure waves of 22–39 kc were left. Records obtained with the pulse detector in 1954 showed similar values for pulse duration; and the highest frequency components ranged from 24 to 46 kc, the average of 43 measurements being 36 kc. Other apparent components of 11–14 kc were also present in many records, and in each case these were one third or one half of the highest frequency discernible. Some of these lower frequencies may have been frequencies of amplitude modulation.

Macrophyllum macrophyllum. These bats are among the smallest leaf-nosed bats studied, weighing 6 to 9 gm. They did not eat fruit in captivity, and hence survived only a few days. They resembled *Lonchorhina* in emitting short pulses containing a fairly low frequency fundamental plus strong harmonics. The condenser microphone records obtained in 1953 showed durations ranging from 0.9 to 1.9 msec (average of 19 values 1.2 msec) and frequencies ranging from 21 to 30 kc, with no frequency modulation. No records of *Macrophyllum* were obtained with the pulse detector in 1954.

Phyllostomus hastatus panamensis. This is the largest bat we have studied; it weighs approximately 100 gm, and its food includes not only fruits but insects, smaller bats, and small birds (Dunn, '33). It emits short pulses which are much more easily detected with the condenser microphone than those of *Carollia.* The sound pressures at 50 cm are about 1 dyne/cm^2 in contrast with *Carollia* which produces this order of sound pressure only at 10 cm or less. The average duration of 30 *Phyllostomus* pulses was 1.6 msec (1.0–3.1), and the frequencies measured with the condenser microphone average 37 kc (30–45) with no signs of frequency modulation like that of the Vespertilionidae. Nor do our records show the sudden shifts of frequency that are common in *Carollia* pulses. The crystal microphone tended, as usual, to pick up somewhat higher frequencies; 22 records ranging from 42 to 55 kc averaged 48 kc. Some records show frequencies of 45–50 kc plus a component at 90–100 kc, and others show amplitude modulation at about one third the principal frequency. Still other records, some of which are longer duration pulses, contained waves of 10–15 kc plus second or third harmonics.

Sub-family Stenoderminae

Uroderma bilobatum. These medium sized, leaf-nosed bats (weight 13–21 gms) have the unusual habit of constructing their own roost by cutting partly through the middle portion of large, broad palm leaves, so that the leaves bend down into a tent-like shelter in which the bats roost by day (Allen, '39). In 1953, when the condenser microphone was used, very few pulses were detected from *Uroderma*, but in 1954 the pulse detector registered many pulses of 1 to 2 msec duration having frequencies ranging from 69 to 88 kc. These were apparently of the same low level of intensity as those of *Carollia*, and there was an equally pronounced tendency for the frequencies to be multiples of some frequency in the vicinity of 20–25 kc. The frequency also commonly changed within a single pulse by relatively small amounts, for example, during 1.5 msec of one record the frequency fell from 78 to 69, and then rose to 87 kc.

Artibeus jamaicensis palmarum. These moderately large leaf-nosed bats weighing 55–70 gm are commonly found roosting in unoccupied buildings. They survived for long periods in captivity on a diet of fruit. As with *Carollia*, the condenser microphone used in 1953 revealed only a few pulses with frequencies in the neighborhood of 20 kc, but use of the pulse detector in 1954 showed that short pulses of higher frequency were common. Pulses recorded in Panama with the pulse detector ranged from 0.9 to 1.8 msec in duration, and from 68 to 77 kc in frequency. All contained at least traces of a fundamental frequency of about 24 kc plus a second and third harmonic. A more thorough analysis of the pulses emitted by captive *Artibeus* that had been shipped to Cambridge (but were still in excellent health) showed acoustic properties rather similar to those described above for *Carollia*. It was difficult to detect *Artibeus* pulses with the condenser microphone, but occasionally an intensity as high as 10 dynes/cm² at 80 kc could be registered as the bat took off within a few centimeters of the microphone. The average of 24 duration measurements was 2.2 msec (1.4–3.9). Eleven records with the condenser microphone (filters set at 20 kc high pass) showed frequencies from 64 to 86 kc, with an average of 72 kc. There was no indication of any difference between the beginning, middle and end of the pulse. The crystal microphone indicated a slightly higher range of frequencies, the average of 21 measurements being 81 kc (49–94), and there was again no sign of a progressive shift in frequency from beginning to end.

As with *Carollia* some records showed pulses having a fundamental frequency considerably lower than the figures listed above, together with strong harmonics. Indeed a wide variety of conditions appeared in individual records, ranging from 14–15 kc with only traces of harmonics through instances where a fundamental of about 20 kc showed very prominent second and third harmonics, to cases in which the record seemed to be a nearly pure frequency of 70–90 kc. Other records showed frequencies of 75–90 kc undergoing amplitude modulation at $\frac{1}{3}$ of the predominant frequency. *Artibeus* thus has at its disposal a wide range of frequencies with a strong tendency for these to occur as multiples of 15–25 kc.

Experimental impairment of the hearing of *Artibeus* gave results similar to those described above for *Carollia*. One *Artibeus* with its ears plugged collided with all obstacles it encountered and appeared completely disoriented as any other deafened bat. The ability of two healthy Artibeus to avoid small wires was tested in the same manner as described above for *Carollia* except that the wires were spaced 60 cm apart, and the resulting data are included in table 2. To our surprise there was no significant difference in their success at avoiding wires ranging in diameter from 0.175 to 1.05 mm, and even at the smallest wire size these large bats were remarkably skillful.

Sub-family Glossophaginae

These small leaf-nosed bats have an elongated rostrum and long tongues used to obtain pollen and nectar from flowers, some of which bloom at night apparently to facilitate cross pollination by these bats (Porsch, '32; Allen, '39; Wille, '54). The two species studied were apparently typical of the sub-family, although other genera have a more extreme lengthening of the rostrum and may depend more heavily on flowers rather than fruit and insects for their food supply. Both species discussed below were maintained in captivity on a diet of fruit, *Lonchophylla* for a few weeks and *Glossophaga* for several months.

Glossophaga soricina leachii. This species seemed even more nearly silent than *Carollia* when studied in Panama with the condenser microphone. Some pulses ranging up to 58 kc in frequency were detected, but it remained for the pulse detector to show that short duration, high frequency pulses were as characteristic of this species as the others studied. These bats are smaller than *Carollia* (weight about 10 gm), and the frequencies are characteristically higher. When healthy captive *Glossophaga* were studied in the laboratory with the 640AA microphone it was necessary to use filter settings of 50 or 70 kc high pass in order to obtain satisfactory records. The pulse durations were 0.3 to 0.6 msec (average of 7, 0.46 msec), and the frequencies ranged from 73 to 126 kc, the average of 18 measurements being 98 kc. The 8 highest amplitude pulses averaged 2.6 dynes/cm^2 at about 5 cm from the bat's mouth, the maximum pressure in the series being 6 dynes/cm^2 at 121 kc. This value is based on an extrapolation beyond 100 kc of the manufacturer's calibration curve of the 640AA microphone, and it should be recalled that this microphone was not designed for use above about 20 kc. Hence the actual sound pressures may be higher or lower than 6 dynes/cm^2, but these measurements show that *Glossophaga* emits much of the energy in its pulses at wavelengths of 2.5 to 4 mm.

With the crystal microphone better signal-to-noise ratios were obtained, and it was practicable to use filter settings of 20 kc high pass. With this setting 21 frequency measurements averaged 102 kc (75–115), and, when the crystal microphone was used with filter settings of 80 kc high pass, the average of 26 measurements was 106 kc (91–128). As with *Carollia* there were often shifts in frequency within a single pulse, and two pulses emitted within 1/10th second sometimes contained quite different frequencies. But there was no sign of the progressive shift of frequency characteristic of the Vespertilionidae. A typical shift within a single pulse is illustrated in figure 10, obtained with the condenser microphone, and this figure also shows the very short duration characteristic of *Glossophaga* pulses. The frequency of the first 10 waves clearly visible in the expanded sweep is 79 kc; that in the next 14 waves is 109 kc; and the higher frequency can be seen to commence as a small inflection on the lower frequency waves.

One *Glossophaga* set free with its ears plugged was completely disoriented and collided with all obstacles in its path. Tests of the skill of this species at avoiding small wires are included in table 2, and it is clear that these bats avoided the 0.175 mm wire without difficulty, even though the wave length of the highest frequency detected in *Glossophaga* pulses was 2.7 mm, or 15 times the diameter of the wire.

Lonchophylla robusta. This species is quite similar to *Glossophaga* in size and probably in its feeding habits. It was not taken in 1953, but in 1954 one of these bats was brought to Cambridge in apparent good health and a few records were obtained with both the condenser and crystal microphones. The pulses were low in intensity, like those of *Glossophaga,* a typical sound pressure measurement being 2.7 dynes/cm^2 at 80 kc. The durations were short (0.5 to 2.7 msec, the average of 14 being 1.2 msec). With filters at 20 kc high pass the condenser microphone picked up a few pulses with frequencies from 25 to 45 kc together with obvious harmonics. When the filters were set at 80 kc high pass ten records showed frequencies ranging from 65 to 91 kc (average 82 kc), with the same type of shift in frequency that has been described above for *Glossophaga* and *Carollia.* A typical example of such pulses is shown in figure 11. The crystal microphone gave a better signal-to-noise ratio in records of *Lonchophylla* pulses, and the average of 16 measurements was 108 kc (98–119). There was no consistent tendency for the frequency to rise or fall from beginning to end of the pulse. The *Lonchophylla* pulses tended to show amplitude modulation more conspicuously than those of the other species studied, many records being similar to figure 11 in this respect. The modulation frequency may be ⅕ of the predominant frequency, as in figure 11, or in other records ¼ or ⅓. In such cases a considerable part of the sound energy was presumably present in the "side bands" and little or none at the modulation frequencies of 20 to 25 kc.

Family Desmodontidae, Desmodus rotundus murinus, the vampire bat

These bats, which feed exclusively on the blood of living animals, are confined to the American tropics. General descriptions of their habits and the manner in which they attack sleeping men and domestic animals such as horses and goats are given by Ditmars and Greenhall ('35). It has recently been reported by Malaga-Alba ('54) that vampire bats seldom bite dogs because the dogs are awakened at the bat's approach. This is of interest inasmuch as dogs seem able to hear higher frequencies than larger mammals (see for example Bekesy and Rosenblith, '51). Several vampire bats were studied in Panama in 1953, and, while they often emitted fairly long duration audible cries when handled or otherwise excited, pulsed sounds were as rare in our records as in those of leaf-nosed bats, and apparently for the same reason. With the condenser microphone, with filters set at 20 kc high pass, short pulses have now been detected with frequencies ranging from 15 to 92 kc and two typical pulses are shown in figure 9. Out of this 10 fold range in frequency the most common type of pulse contained frequencies from 60–75 kc, or less commonly, from 50 to 90 kc. When frequencies below 50 kc were recorded they were always accompanied by prominent harmonics, and in many records the frequency shifted by roughly 20–25 kc or multiples thereof, as in *Carollia.* In many records having a fundamental of 60–65 kc there was also a significant component at twice this frequency, so that appreciable energy is emitted by the vampire bat above 100 kc. One record shows 138 kc at an indicated sound pressure of 2 dynes/cm^2, based on an extrapolation of the manufacturer's calibration of the 640AA microphone. The crystal and condenser microphones did not show any pronounced differences in frequencies recorded from *Desmodus,* and frequency changes during the individual pulses were less common than with *Carollia.* The average of 67 *Desmodus* pulses recorded with both microphones was 73 kc and the average of 12 duration measurements was 2.2 msec (0.64–4.0).

DISCUSSION

The original demonstration that bats use sound to detect obstacles, as well as most of the subsequent investigations of acoustic orientation in bats, have involved a single family — the insectivorous Vespertilionidae. But enough of the other families have now been studied so that we can begin to judge the validity for other kinds of bats of the concept of echolocation originally derived from studies of the Vespertilionidae. A species of *Myotis* studied in Panama showed no differences in its sound from the *Myotis* of temperate latitudes. A second insectivorous family, the Molossidae or free-tailed bats, appear from our laboratory experience with the genus *Tadarida* to emit pulses of sound very similar to those of the *Vespertilionidae,* and Part I of this paper presents data demonstrating that the Noctilionidae, which feed on insects or fish, employ sounds which are very similar to those of the Vespertilionidae in intensity, duration, and frequency pattern. Still another insectivorous family, the horseshoe bats (family Rhinolophidae) produce sounds which Möhres ('53a) has shown to differ from those of the Vespertilionidae in two important respects: the frequency is constant at about

80 to 100 kc instead of dropping an octave or more during each pulse, and the pulses are longer in duration — about 100 msec instead of one to 15 msec. Möhres also presents evidence that the sound is much more concentrated into the forward direction, in part because the "horseshoe" acts as a small horn. Dijkgraaf ('46) had demonstrated that *Rhinolophus* emit sound only through the nostrils, in contrast to the Vespertilionidae, most of which emit through the mouth (Griffin, '46). The horseshoe bats thus employ acoustic procedures in their echolocation which differ from those used by the other three insectivorous families discussed above. Objects closer than about 15 m must return echoes which overlap the outgoing pulse in time, and Möhres believes that the more concentrated beam, together with specializations of the external ear, enable the horseshoe bats to discriminate between sound returned from objects lying in different directions. Further discussion of these intriguing problems is beyond the scope of this paper, however, and the important point for the present discussion is that three widespread and successful families of insectivorous bats, together with the Noctilionidae which catch either insects or fish, all emit intense pulses of sound for purposes of echolocation.

Of the bats which feed on fruit, the sub-order Megachiroptera (the "flying foxes" and other Old World fruit bats) has not yet been studied adequately, although Möhres ('53b) has reported briefly that *Rousettus* employs echolocation, but that *Pteropus* relies on vision for its orientation. The other major group of bats that feed on fruit are the leaf-nosed bats of the family Phyllostomidae discussed in Part II of this paper. We have presented evidence that the pulses employed by these bats share with the families Emballonuridae and Desmodontidae a basic design which distinguishes them from the other families discussed above. The pulses emitted by the members of these three families contain one or more predominant frequencies which appear to be either simultaneously or successively drawn from a harmonic series. There are often sudden changes in the frequency spectrum, either during a single pulse or from one pulse to the next, but such shifts bear little resemblance to the progressive frequency modulation characteristic of the Vespertilionidae, Molossidae, and Noctilionidae, in which each pulse begins at its highest frequency and gradually drops to its lowest frequency at the end. The pulses emitted by these three neotropical families can be divided into three sub-groups which appear to be correlated with the feeding habits of the bats.

The first group includes the family Emballonuridae and the sub-family Chilonycterinae. The pulses of these bats have high sound pressures, comparable to those of the Vespertilionidae, and their frequency spectra are relatively simple. They usually contain a fundamental frequency plus one or more harmonics of large amplitude. Variety in this group appears limited to the addition or subtraction of one or more harmonics. This may occur within a pulse as well as from one pulse to the next, but it does not occur repeatedly within a single pulse. Some members of this group also emit pulses of relatively long duration.

The second group, the leaf-nosed bats of the sub-family Phyllostominae, is represented here by three species all of which produce short pulses of relatively uniform design. These pulses usually contain only one frequency, but components of one half or one third of this frequency are found in other pulses, so that the higher frequency may be a second or third harmonic of a "fundamental" which only occasionally appears at high amplitudes. Amplitude modulation at a submultiple of the predominant frequency sometimes occurs. Shifts of frequency within a pulse are rare, while shifts from one pulse to the next are of limited scope and not striking. The sound pressure of the pulses of this group are clearly intermediate between those of the Emballonuridae and Chilonycterinae and the third group defined below.

The third distinguishable group consists of *Carollia*, the Glossophaginae, the Stenoderminae, and *Desmodus*. These 6 species are characterized by the lowest sound pressures together with great variety and sudden changes in the frequencies emitted. At any one instant during these short pulses there may be a single frequency, a fundamental frequency plus distinct harmonics, or a frequency undergoing amplitude modulation at a small submultiple of itself. The frequencies present, whether pure, accompanied by harmonics, amplitude modulated, or complicated in still other ways, usually seem to be members of a harmonic family in which the fundamental or any harmonic from second to 6th may predominate. The bats of this group share with the Phyllostominae the trait of changing the relative amplitude of harmonics so as to to produce any one of several nearly pure frequencies. But they have also developed, to a higher degree than the first or second groups, the feature of abruptly shifting frequencies within a single pulse or from one pulse to the next. These shifts appear in most pulses of this group and occur repeatedly within very short periods of time, as illustrated in figure 8. The pulse durations are short, as in the second group. The low sound pressures which distinguish the third group may be of considerable significance. With every species we experienced great difficulty in detecting and recording these sounds, although we rarely had such difficulty with any of the first and second groups. Many pulses emitted by this third group contain fundamentals as well as harmonics above 100 kc, and it is quite possible that still higher frequencies would be disclosed by a microphone which was sensitive to frequencies above 150 kc.

While complexity is thus a striking attribute of the sounds of these bats, especially the third group, it should be pointed out that we have no evidence concerning their ability to discriminate between the several component frequencies in these pulses. While it is clear that *Carollia* uses its pulses for echolocation, we can only speculate that perhaps the higher components are useful for detecting small objects. It is also of interest to point out that the bats of the first group have no nose leaf, while all those of the second and third groups have this structure, with the exception of the vampire bat. It is thus pertinent to inquire whether the feeding habits of these bats show any correlation with the types of sound employed for echolocation.

Little direct evidence is available concerning the food of most of these species of bats, but specializations of the teeth and mouth provide some indication of the customary diet, together with observations of the types of food eaten in captivity. Of the first group defined above the Emballonuridae are known to be insectivorous, and the Chilonycterinae are thought to be. Of the second group *Phyllostomus* is omnivorous, and the third group are all frugivorous or feed on nectar or pollen, except for *Desmodus* which feeds on blood. Bats of our third group fly through the jungle and have a constant need to navigate through an environment thick with closely spaced obstacles. The slow, deliberate, and hovering type of flight of the Glossophaginae and *Carollia* correlates well with this mode of life — as does the skill of these bats and *Artibeus* in avoiding small wires. Such habits of flight may be served adequately by short pulses with low sound pressures and a wide variety of frequencies. The Emballonuridae, on the other hand, were frequently observed flying in rather open places, as do most of the insectivorous bats of temperate latitudes. Unfortunately not enough is known of the habits of the Chilonycterinae or Phyllostominae to permit any decision concerning the role of their pulses which have an intermediate intensity.

It is thus clear that the bats which are known to pursue flying insects in the open employ sound pressures of the order of 100 dynes/cm^2 at about 10 cm from the mouth, while those that seek relatively large and motionless food in dense vegetation (such as fruit or large sleeping animals) employ pressures of roughly one to three dynes/cm^2. In terms of sound energy this represents a difference of 1000 to 10,000 fold. These differences in intensity, and in pattern of frequencies making up the pulses, may well represent adaptations for two distinct types of orientation — the detection of relatively large and stationary objects and the tracking of small moving targets on the wing. It may also be significant that *Noctilio* employs the high intensity type of pulse, with progressive frequency modulation, while catching fish.

SUMMARY

1. The high frequency sounds of sixteen species of neotropical bats of the families Noctilionidae, Emballonuridae, Phyllostomidae, and Desmodontidae were analyzed, and the results compared with available information concerning their habits. All emit short pulses, lasting only 0.4 to 25 msec.
2. The Noctilionidae closely resemble the insectivorous Vespertilionidae of temperate latitudes in the short pulses they emit for orientation. The sound pressures at 10 cm from the mouth are about 100 dynes/cm^2, and the frequency drops progressively from beginning to end of the pulse, a typical range being 50 to 30 kc. *Noctilio* also employs longer and somewhat more complex frequency modulated pulses while catching fish. Consideration is given to the hypothesis that submerged fish may be detected by echolocation, despite the severe loss in energy that would occur during two passages through the air-water interface.
3. The insectivorous bats of the family Emballonuridae, and the probably insectivorous sub-family Chilonycterinae, emit relatively intense pulses which lack the progressive frequency modulation characteristic of the families Vespertilionidae, Molossidae, and Noctilionidae. Instead these bats emit a mixture of frequencies, usually at harmonic intervals. The predominant frequencies range from 20 to 100 kc. The relative amplitude of the various components may vary continuously over a wide range, and in any particular record the fundamental or one of the harmonics may fall below the noise level of the apparatus. Such changes may occur within a single pulse or from one pulse to the next.
4. The leaf-nosed bats of the sub-family Phyllostominae emit short pulses of intermediate intensity and relatively

simple frequency spectrum, consisting of a predominant frequency of 12 to 50 kc in the species studied, together with harmonics of variable amplitude. Some pulses show amplitude modulation at a frequency of one third the predominant frequency. The pulses are quite uniform in content, changes within a pulse being rare. The best known member of this group, *Phyllostomus hastatus panamensis* is omnivorous.

5. The primarily frugivorous leaf-nosed bats of the subfamilies Carolliinae, Stenoderminae, and Glossophaginae, as well as the vampire bat *Desmodus*, emit very low intensity pulses with sound pressures of about 1 to 3 dynes/cm^2 at a few centimeters from the bat's mouth, in contrast to the sound pressures of over 100 dynes/cm^2 found at this distance from bats of the family Vespertilionidae. Single frequencies or a spectrum of components at harmonic intervals occur, and the relative amplitudes of these components vary widely and often abruptly, so that quite different frequency spectra may be found a fraction of a millisecond apart. These changes may be in either direction. There are also cases in which a given frequency undergoes amplitude modulation at a small submultiple of itself, and in these cases the frequency spectrum presumably contains frequencies other than the modulation frequency. The predominant frequency may be very high in certain species, for example it averages about 100 kc in *Glossophaga*, and may sometimes be as high as 120 kc in *Carollia*, *Lonchophylla* and *Desmodus*. The high frequency limits of our measurements may well be set by the microphones used, rather than by the bat sounds themselves.

6. The leaf-nosed bats *Carollia*, *Artibeus*, and *Glossophaga* can avoid fine wires better than *Myotis lucifugus*, but their superiority is at least partly due to their slower and more cautious manner of flight. Their low intensity pulses allow them to detect wires as small as 0.175 mm in diameter. When their ears are plugged they become completely disoriented, but blinding has no noticeable effect on their flight or skill at avoiding obstacles. Removal of the nose leaf is also without apparent effect.

7. *Carollia* are able to emit essentially normal pulses of high frequency sound either through the mouth or through the nostrils.

8. There seems to be a clear correlation between high sound intensity and habits that require the capture of flying insects in the open. On the other hand the bats that are known to feed on fruit, together with the vampire bat that attacks large animals while they are asleep, emit pulses having only about 1/1000 of the sound energy that characterizes bats which feed on insects or fish.

LITERATURE CITED

Allen, G. M. 1939 Bats. Cambridge, Massachusetts, Harvard University Press.

Bekesy, G. von, and W. A. Rosenblith 1951 The mechanical properties of the ear. Ch. 27 of Handbook of experimental psychology (S. S. Stevens, ed.). New York, Wiley.

Bloedel, P. 1953 Fishing habits of noctilionid bats. Anat. Rec., *117:* 566–567.

——— 1955a Observations on the life histories of Panama bats. J. Mammalogy, *36:* 232–235.

——— 1955b The hunting methods of fish-eating bats, particularly *Noctilio leporinus.* J. Mammalogy, *36:* 390–399.

Curtis, W. E. 1952 Quantitative studies of echolocation in bats *(Myotis l. lucifugus);* studies of vision in bats *(Myotis l. lucifugus* and *Eptesicus f. fuscus);* and quantitative studies of vision of owls *(Tyto alba pratincola).* Thesis deposited in library of Cornell University, Ithaca, New York.

Dijkgraaf, S. 1946 Die Sinneswelt der Fledermäuse. Experientia, *2:* 438–448.

Ditmars, R. L., and A. M. Greenhall, 1935 The vampire bat. Zoologica, *19:* 53–76.

Dunn, L. H. 1933 Observations on the carnivorous habits of the spear-nosed bat, *Phyllostomus hastatus panamensis* Allen, in Panama. J. Mammalogy, *14:* 188–199.

Goldman, E. A. 1920 Mammals of Panama. Smithsonian Inst. Misc. Collections *69(5):* 1–309.

Goodwin, G. G. 1946 Mammals of Costa Rica. Bull. Am. Mus. Nat. Hist., *87:* 271–474.

Griffin, D. R. 1946 Supersonic cries of bats. Nature, *158:* 46–48.

——— 1950 Measurements of the ultrasonic cries of bats. J. Acoustical Soc. Am., *22:* 247–255.

——— 1951 Audible and ultrasonic sounds of bats. Experientia, *7:* 448–453.

——— 1953a Bat sounds under natural conditions, with evidence for echolocation of insect prey. J. Exp. Zool., *123:* 435–466.

GRIFFIN, D. R. 1953b High frequency sounds of tropical bats. Anat. Rec., *117:* 567.

GRIFFIN, D. R., AND R. GALAMBOS 1941 The sensory basis of obstacle avoidance by flying bats. J. Exp. Zool., *86:* 481–506.

GUDGER, E. W. 1945 Fisherman bats of the Caribbean region. J. Mammalogy, *26:* 1–15

HUND, A. 1942 Frequency modulation. New York, McGraw-Hill.

MÁLANGA-ALBA, A. 1954 Vampire bats as a carrier of rabies. Am. J. Public Health, *44:* 909–918.

MILLER, G. 1907 The families and genera of bats. Bull. U. S. Nat. Mus., *57:* 1–282.

MÖHRES, F. P. 1953a Über die Ultraschallorientierung der Hufeisennasen (Chiroptera-Rhinolophinae). Zeit. f. vergl. Physiol., *34:* 547–588.

——— 1953b Ultraschallorientierung auch bei Flughunden. Naturwiss., *40:* 536–537.

NOYES, A., AND G. W. PIERCE 1938 Apparatus for supersonic research. J. Acoustical Soc. Am., *9:* 205–211.

OLSON, H. F. 1947 Elements of acoustical engineering. 2nd ed. New York, D. Van Nostrand Co.

PIERCE, G. W. 1948 The songs of insects. Cambridge, Mass. Harvard University Press.

PORSCH, O. 1932 Crescentia — eine Fledermausblume. Oesterr. Bot-Zeitschr., Wien, *80:* 31–44.

SIMPSON, G. G. 1945 The principles of classification and a classification of mammals. Bull. Am. Mus. Nat. Hist., *85:* 1–350.

VAN TYNE, J. 1933 The trammel net as a means of collecting bats. J. Mammalogy, *14:* 145–146.

WILLE, A. 1954 Muscular adaptation of the nectar-eating bats (subfamily Glossophaginae). Trans. Kansas Acad. Sci., *57:* 315–325.

PLATE 1

EXPLANATION OF FIGURES

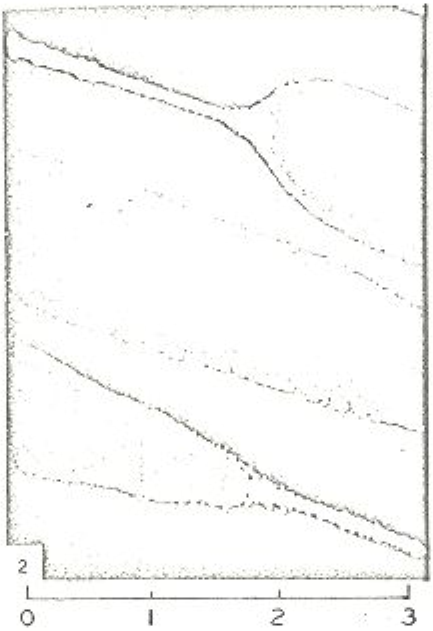
Oscillograph records of the sounds of *Noctilio* obtained with the condenser microphone. All time scales in milliseconds.

2 A pulse of sound emitted by a *Noctilio* while fishing under natural conditions over the Chagres River, Panama. Sweep frequency 200 per second, slightly expanded; electronic filters with 18 db/octave slope set at 20 kc high pass. This is an example of the type B pulses described in the text and in table 1.

3 A series of type A pulses emitted by a captive *Noctilio* while catching small fish from a wooden tank. Sweep frequency 60 per second; filters with 54 db/octave slope set at 25 kc high pass.

4 A type C pulse emitted by a *Noctilio* while fishing under natural conditions. Sweep frequency 200 per second, expanded about twofold; filter settings as for figure 2. Note the marked drop in frequency between the second and third sweep shown in the photograph.

5 A pulse emitted by a captive *Noctilio* held at 50 cm from a calibrated condenser microphone. Filters with 36 db/octave slope set at 25 kc high pass; sweep frequency 200 per second. This pulse is intermediate between types A and C, and its maximum amplitude was 15 dynes/cm^2 peak-to-peak at 31 kc. Other pulses of the same series had sound pressures exceeding 60 dynes/cm^2.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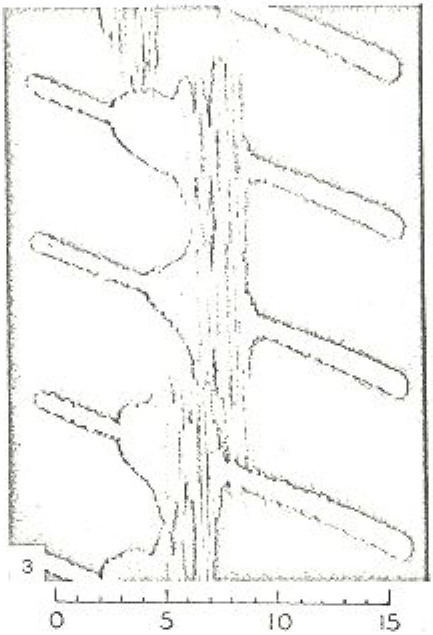
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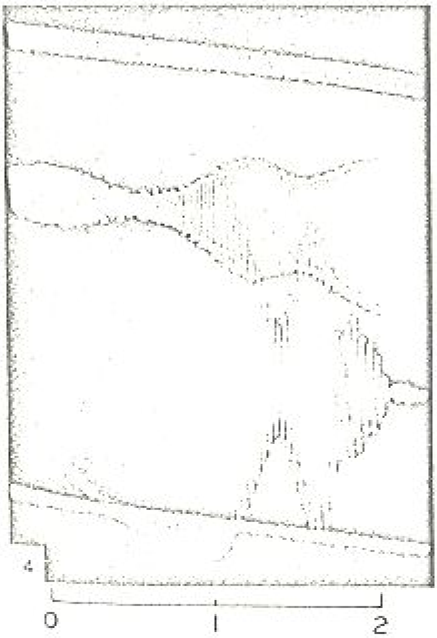
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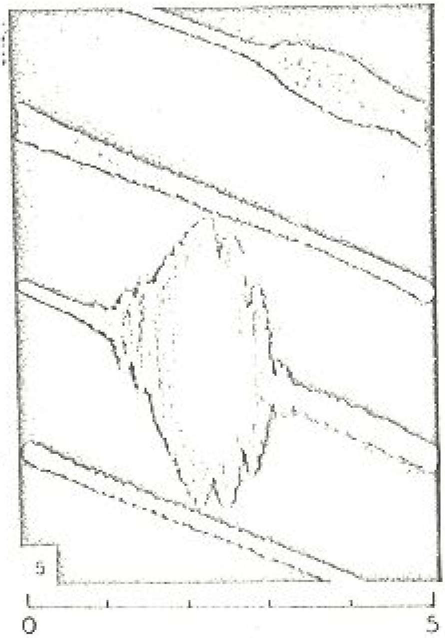
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PLATE 2

EXPLANATION OF FIGURES

Oscillographic records of pulses of sound emitted by bats of the families Emballonuridae, Phyllostomidae and Desmodontidae. All records obtained with a condenser microphone; all time scales in milliseconds.

6 Pulses of a captive *Rhynchiscus;* sweep frequency 60 per second; filters with 36 db/octave slope set at 20 kc high pass. This photograph shows 4 of 6 pulses emitted within 80 msec. Compare with figures 1 and 7.

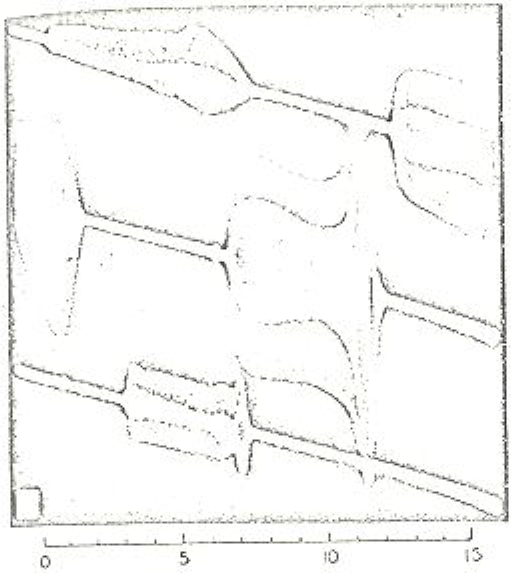
7 Part of a *Rhynchiscus* pulse similar to those shown in figure 6, but photographed with expanded sweep (same filter settings as for figure 6). Note that towards the end of the pulse the second harmonic greatly exceeds the amplitude of the fundamental.

8 Expanded and unexpected records of a pulse emitted by a captive *Carollia.* Filters with 96 db/octave slope set at 20 kc high pass; sweep frequency 200 per second; 80% of each sweep photographed on the right-hand channel, and 15% on the left. About 0.7 msec of the second of the two pulses visible on the right is displayed on the left with sufficient expansion to show actual frequencies: 23 kc at the start of the expanded sweep (0.09 dyne/cm² peak-to-peak), 75 kc at the slight peak near the center (3.2 dynes/cm²), and 96 kc at the end (3.9 dynes/cm²). The abrupt shifts of frequency are present in many other records, but only occasionally were two such shifts observed within one millisecond.

9 Expanded and unexpanded records of pulses from a captive vampire bat, *Desmodus.* Sweep frequency 200 per second, unexpanded on left, expanded about tenfold on right; filters with 60 db/octave slope set at 20 kc high pass. Compare the increasing amplitude of the harmonic in the first pulse with the nearly pure waves in the second.

10 Typical pulse emitted by a captive *Glossophaga.* Filters with 96 db/octave slope set at 70 kc high pass, and similar filters of 24 db/octave slope set at 210 kc low pass; sweep frequency 200 per second. The 79 kc waves at the start of the expanded sweep had an indicated sound pressure of 1 dyne/cm² and the 109 kc waves at the end of the pulse were about 1.7 dyne/cm².

11 Pulse emitted by a captive *Lonchophylla.* Sweep frequency 200 per second; filters of 60 db/octave slope set at 80 kc high pass. The predominant frequency is 101 kc, but note the amplitude modulation at approximately 20 kc.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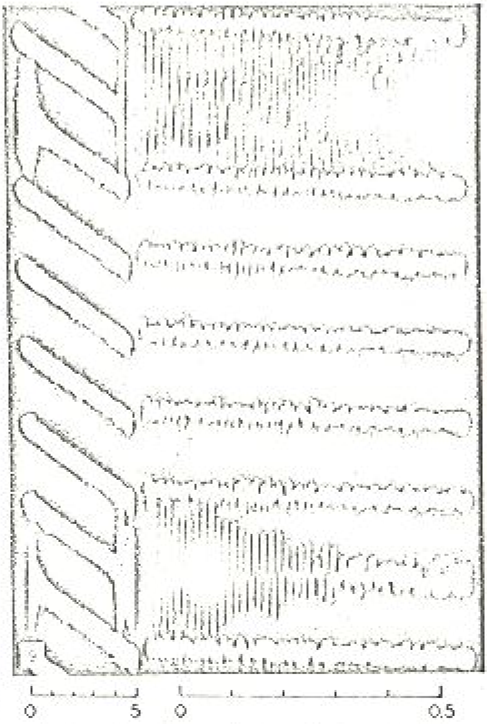
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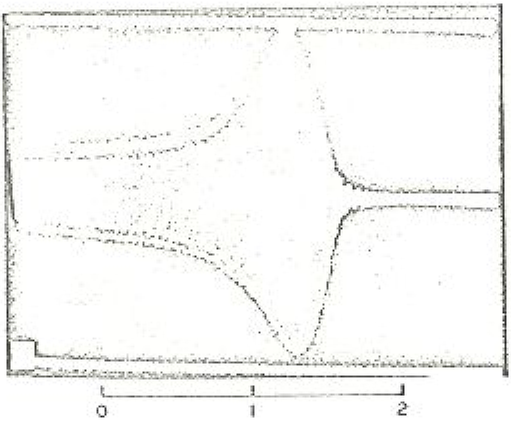
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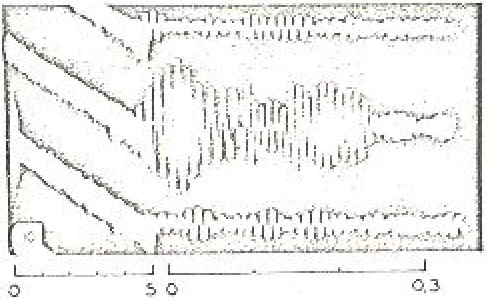
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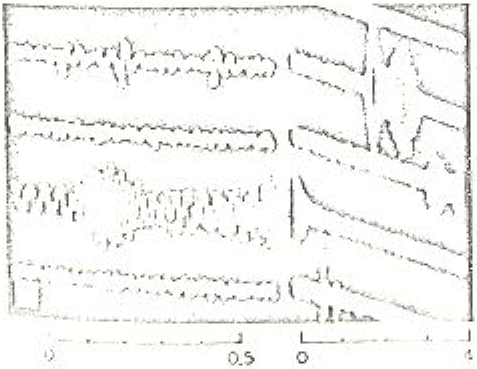
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