

Use of Vocal Signatures for the Inventory of Free-flying Neotropical Bats¹

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ABSTRACT

An ongoing study is being conducted to test the efficacy of the Anabat II detector and analysis system in obtaining reliable vocal signatures for the identification of non-phylostomid species of bats. We sampled a wide range of elevations and associated habitat types throughout Belize. Anabat provides an instantaneous output of echolocation call structure with a laptop computer. Select sequences can be saved directly to the hard drive, avoiding extraneous noise and sound distortion commonly associated with tape recorders. To date, 18 of the 37 species known or expected to occur in the study region were identified by recognizable differences in the time–frequency characteristics of echolocation calls. In general, each family is recognizable by call structure patterns and species readily separated by frequency range parameters. Species that commute or forage at high altitudes are not susceptible to capture but are conspicuous by acoustic sampling. Further work is needed to determine limitations of the equipment, establish better sampling procedures, and develop a comprehensive library of vocal signatures incorporating the range of variation inherent in each species. As this work progresses, we predict the addition of hitherto unknown species occurring within the study region.

Key words: acoustic identification; Anabat; bats; Chiroptera; diversity assessment; inventory; Neotropics.

BATS ARE CRITICAL CONTRIBUTORS TO MAMMALIAN BIODIVERSITY, particularly in the Neotropics. The order Chiroptera is second only to rodents in diversity: 17 families, *ca* 174 genera, and 913 species (Koopman 1994). Nine families live in the New World, six of which only occur in the Neotropics. *ca* 28 percent of all bat species appear in the Neotropics. In Belize, 83 species are known or suspected to exist. The sheer number of individuals and the myriad of food habits represented further support the significant contribution by this group to Neotropical systems.

Because Neotropical rain forest bat communities are very diverse and include many elusive species, major commitments of time and effort are necessary to obtain asymptotic species lists (Voss & Emmons 1996). Historically, the study of bats away from roosts, has relied primarily on the use of nets and traps (Kunz & Kurta 1988). Not all bat species and not all individuals within a species are equally susceptible to capture. The relatively small size of collecting surfaces and the ability of bats to detect these collection devices further limit the effectiveness of these techniques and require

that inventory efforts be limited to roosts, water holes, or along foraging and commuting flyways. To compound the sampling problem, a given location may not be used every night by the same species assemblage. Standard capture techniques require relatively expensive equipment and constant tending, limiting the number of localities that can be sampled simultaneously. In the Neotropics, mist netting has been particularly effective for leaf-nosed bats (family Phyllostomidae), but traps are more effective for other families (Tuttle 1976, LaVal & Fitch 1977). Inasmuch as most surveys for bats in the Neotropics have used mist nets, more is known of the phyllostomids than other families of bats. Such ground-level nets sample < 10 percent of the airspace under a typical rain forest canopy and seldom capture molossid or other high flying taxa (Voss & Emmons 1996) that may be detected using acoustical techniques.

Electronic acoustic devices (bat detectors) have been developed to allow investigators to hear and/or visualize the ultrasonic echolocation calls of bats (Fenton 1988). Echolocation calls of many bat species appear to be distinctive (Simmons *et al.* 1979). Some insectivorous bats in the western United States have been characterized by the frequency-time structure of search and feeding calls, providing

¹ Received 17 April 1997; revision accepted 12 April 1998.

a basis for species recognition of free-flying individuals (Fenton & Bell 1981, O'Farrell 1997). In Sweden, a similar attempt provided an acoustic guide to the identification of European bats (Ahlén 1990). Echolocation calls of some Neotropical members of the family Emballonuridae have been described (Barclay 1983, Kalko 1995, O'Farrell & Miller 1997).

Although there is an increasing demand for biological surveys to assist in conserving biodiversity, there is little chance of major funding increases to carry them out (Burbidge 1991). Voss and Emons (1996) reviewed ten Neotropical rain forest mammal inventories and found that species accumulation curves were not asymptotic for any fauna sampled, suggesting that essential field methods were omitted in every case.

Parker (1991) suggested that avian surveys in the Neotropics without the use of field tape recorders provide incomplete results because many secretive species are rarely seen or netted but often are heard. We suggest that bat detectors hold the promise of not only increasing the effectiveness of surveys for many species but are a cost-effective means of rapidly sampling a given fauna.

A standardized system, using easily obtained field equipment and a reference library of vocalizations containing the range of variation that may be encountered in each species' vocal repertoire, has not yet been achieved. Until recently, the detailed study of bat echolocation calls required the use of ultrasonic detectors, tape recorders, period meters, oscilloscopes, and a range of analytic procedures (Fenton 1988). Major problems with many devices involved cost, availability, and ease in analyzing recordings. Technological advances within the past few years generally have resolved analysis concerns, but cost and availability still present problems.

Recently, a relatively inexpensive bat detector and analysis system (Anabat II) has become available. The equipment uses a zero-crossings method of analysis and allows for a direct interface between the detector and a laptop computer. Detailed aspects of the time-frequency structure of vocalizations can be observed while they are being generated and the observer can select which sequences to save directly to the computer hard drive. A recent study in the southwestern United States (O'Farrell 1997) showed an unprecedented ability to distinguish among most species. The notable exception was the inability of the equipment to detect phyllostomids. Anabat was used to reexamine several Neotropical species of the families Mormoopidae and Emballonuridae (O'Farrell & Miller

1997), revealing previously undescribed structural details of echolocation calls.

This paper presents a progress report on the efficacy of the Anabat II system and establishes baseline data on species-specific echolocation calls for non-phylostomid bats in Belize.

STUDY AREA AND METHODS

Nine major locations throughout all districts of Belize, representing seven broad habitat types, were sampled from February 1995 to the present. An attempt was made to sample the range of elevations and associated habitats found within the region. Depending on the vegetation classification used (Wright *et al.* 1959, Iremonger & Brokaw 1995), the number of finer categories of habitat types sampled ranged from 32 to 34. Sampling sites and habitat types by district were as follows: **Corozal District**—Shipstern Reserve (marshes, broadleaf forest, and agricultural lands); **Orange Walk District**—Greater Gallon Jug area (tropical broadleaf forest, agricultural lands, marsh forest, riparian corridors); Rio Hondo near Blue Creek (agricultural and river edge); Rio Bravo Conservation and Management Area, Irish Creek (riparian corridor); La Milpa Field Station (pond surrounded by clearing); **Cayo District**—Mountain Pine Ridge (broadleaf forested foothills, selected caves, pine forest, agricultural clearing, and riparian corridor); Belmopan (urban areas); **Belize District**—Western Highway at and near Sibun River (pine-oak savannas, river edge, urban); Sibun River at Churchyard (river edge); **Stann Creek District**—Dangriga (urban areas); Cockscomb Wildlife Preserve (riparian corridors, broadleaf forest, open areas near headquarters); Five Blues Lake National Park (caves, broadleaf forest, agricultural areas); **Toledo District**—Blue Creek, Toledo (riparian corridor along Blue Creek River, rice fields); Punta Gorda (urban areas); **Other areas**—Halfmoon Caye (coconut and zircote forest).

Each site selected for acoustic sampling was monitored using an Anabat II bat detector (Titley Electronics, Ballina, Australia) linked to an IBM-compatible laptop computer. Simultaneously with acoustic sampling, voucher samples of bats were collected. Sites were sampled with mist nets and/or double-frame harp traps (Austbat Research Equipment, Victoria, Australia). The intensity of collecting effort was directly influenced by the physical characteristics of each location.

Acoustic sampling entailed monitoring forest trails, habitat edges, streams, ponds, roosts, and

other areas suspected of concentrated bat activity. During such sampling, the computer was monitored to maximize the quality of incoming calls. Sensitivity adjustments minimize or eliminate echoes. Likewise, following the path of a target bat with the detector, and many times, moving the detector closer to points of activity, provided greater numbers of useful call sequences. Concomitant decisions were made to save the best representative samples of vocal sequences that reflected various behaviors (*e.g.*, search, pursuit, capture).

Identifying the source of specific vocalizations was achieved in several ways (O'Farrell *et al.* 1999). Visual recognition was occasionally possible by illuminating free-flying, individual animals with a handheld spotlight while they were being monitored acoustically. Some vocalizing individuals were followed into a net or trap and identification was obtained immediately. When possible, acoustic sampling was conducted near known roost sites in order to follow target species immediately upon the evening dispersal. Captured animals were held for later release under controlled conditions. For species that were abundant, individuals were released near the point of capture at times when bat activity was absent. Some released bats circled the area and provided a series of vocalizations that appeared to be representative of normal flight. Some individuals of abundant species and all individuals of less common species were released in a solid-ceiling, lathesided enclosure (12.5 × 6.75 m). Recordings were obtained for known individuals in unrestrained flight within the enclosure. Occasionally, individuals were recorded after affixing a chemical light-emitting tag (Mini-light Sticks, Chemical Light Inc., Wheeling, Illinois) to the fur, either dorsally or ventrally.

Calls from each species were identified subjectively using the protocol of O'Farrell *et al.* (1999). Calls verified by capture were designated as known species and were cataloged. All saved files were compared visually with cataloged known calls. Basic aspects of call structure, including approximate maximum and minimum frequency, duration, and shape, were used for reference but no attempt at quantification was made. At the resolution used in our study, qualitative assessment was more effective for identification purposes than quantification (O'Farrell *et al.* 1999). It is important to recognize that not all calls or sequences of calls can be used for identification purposes. O'Farrell *et al.* (1999) found that on average, 21.8 percent of the calls within usable sequences were fragmentary and not indicative of the respective species, but only 9.9

percent of the *Saccopteryx bilineata* calls, 9.1 percent of the *Noctilio leporinus* calls, and 14.6 percent of the combined species of *Molossus* calls were unusable. We examined all calls obtained but only used those sequences that contained frequency range and structural characteristics known to be exhibited by a particular species. Of 1749 files examined for this study, only 14 were unusable because of the fragmentary and incomplete nature of the sequences contained. We suspect these were from phyllostomids and may be of future use as more information is collected. If there was doubt or overlap with other species, sequences were disregarded but maintained in the archive for potential future use.

RESULTS

Examination of the frequency-time characteristics of echolocation calls reveals patterns in shape. The frequency range and duration of calls vary within species, depending on behavioral mode (*e.g.*, orientation, foraging; Griffin *et al.* 1960), and among species, depending on foraging strategy (*e.g.*, gleaning, aerial hawking; Faure & Barclay 1994). Either case can be affected physically by distance and angle of the individual bat to the detector. Both cases were observed throughout our study and comprise the range of variation inherent for each species. Basically, we observed that calls are narrowest in frequency range, longest in duration, and have the greatest time between calls during search, orientation, and commuting activities. Calls progressively increase in frequency range, and decrease in duration and time between calls during pursuit of prey. Toward the end of pursuit and at the point of capture, frequency range decreases and duration and time between calls reach their lowest values. Through this range of variation, the differences among species remain distinguishable.

The following figures, from the Anabat5 software display, depict the frequency-time structure for the species found during this study and are suitable for gross generalization and comparison. No attempt was made to perform a quantitative examination of call structure features. The figures simply provide visual evidence for the capability of separating species by call structure. The call sequences presented have been carefully selected to incorporate the clearest and most definitive group of individual calls representative of each species. It is critical to stress that these illustrations are for general comparison and not to be used as a definitive reference base. More detailed studies are re-

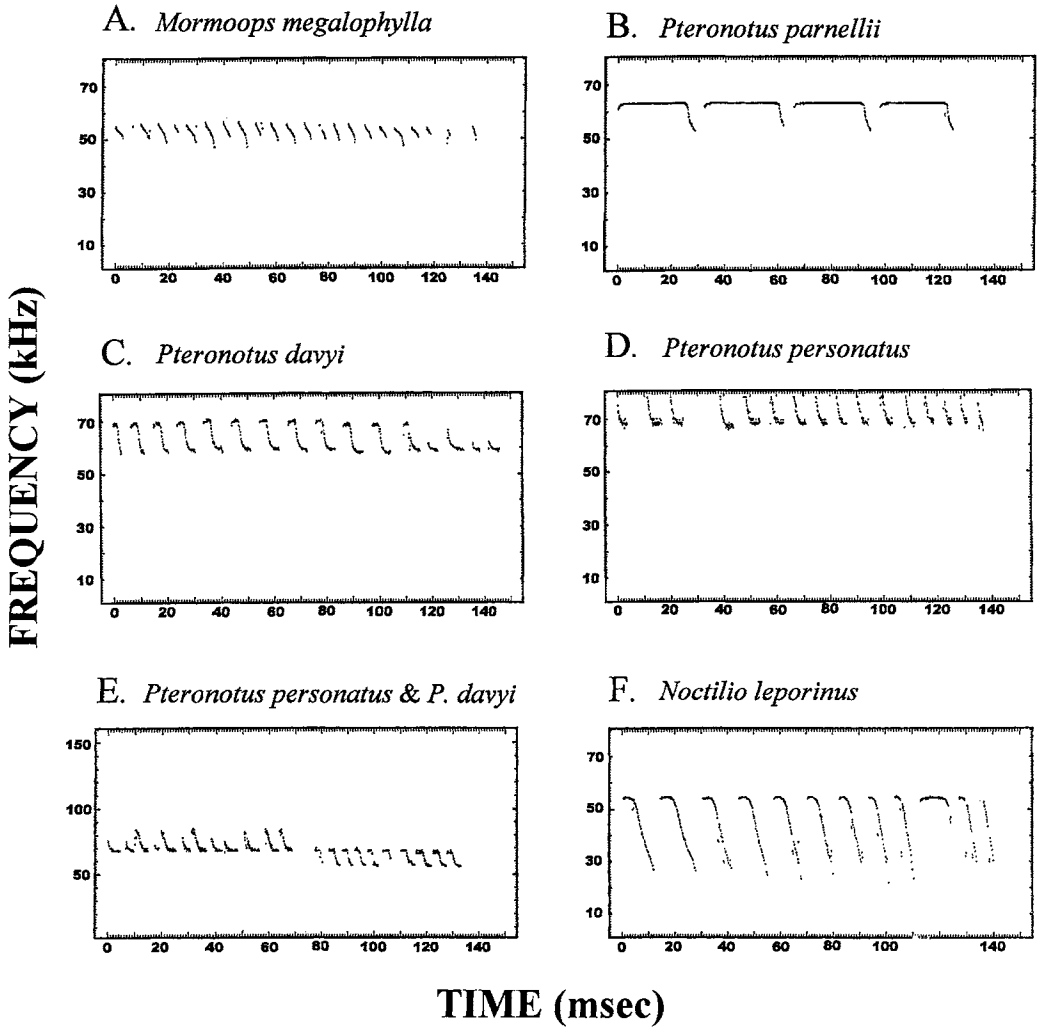


FIGURE 1. Frequency-time display of vocal sequences produced by some bats of the family Mormoopidae (A-E) and family Noctilionidae (F) from Belize. The time between calls on both screens is compressed to allow more calls per screen.

quired to establish the range of variation in call structure within each species.

Bats of the family Mormoopidae have distinct and readily recognizable call structure patterns (Fig. 1). *Pteronotus davyi* (Fig. 1C; number of sequences examined containing the species $N = 133$) and *P. personatus* (Fig. 1D; $N = 289$) have very similar patterns, characterized as a "lazy z," best seen at a scale resolution of 0 to 160 kHz (Fig. 1E). The patterns are composed of an initial short-constant frequency (CF), a steep frequency-modulated (FM) middle portion, and a short-CF end. The frequency range of each species is 10–12 kHz, but they

are offset. The minimum frequency (F_{MIN}) of *P. personatus* is equal to the maximum frequency (F_{MAX}) of *P. davyi*. The presence of a long-CF component in calls of *Pteronotus parnellii* (Fig. 1B; $N = 277$) is unique among New World bats. However, it appears to be an extreme variation of the pattern shown by the preceding two species. For the family, *Mormoops megalophylla* is different by the notable lack of CF components (Fig. 1A; $N = 135$).

A single member of the family Noctilionidae (*Noctilio leporinus*) was recorded (Fig. 1F; $N = 18$). This fishing bat uses echolocation calls with an ini-

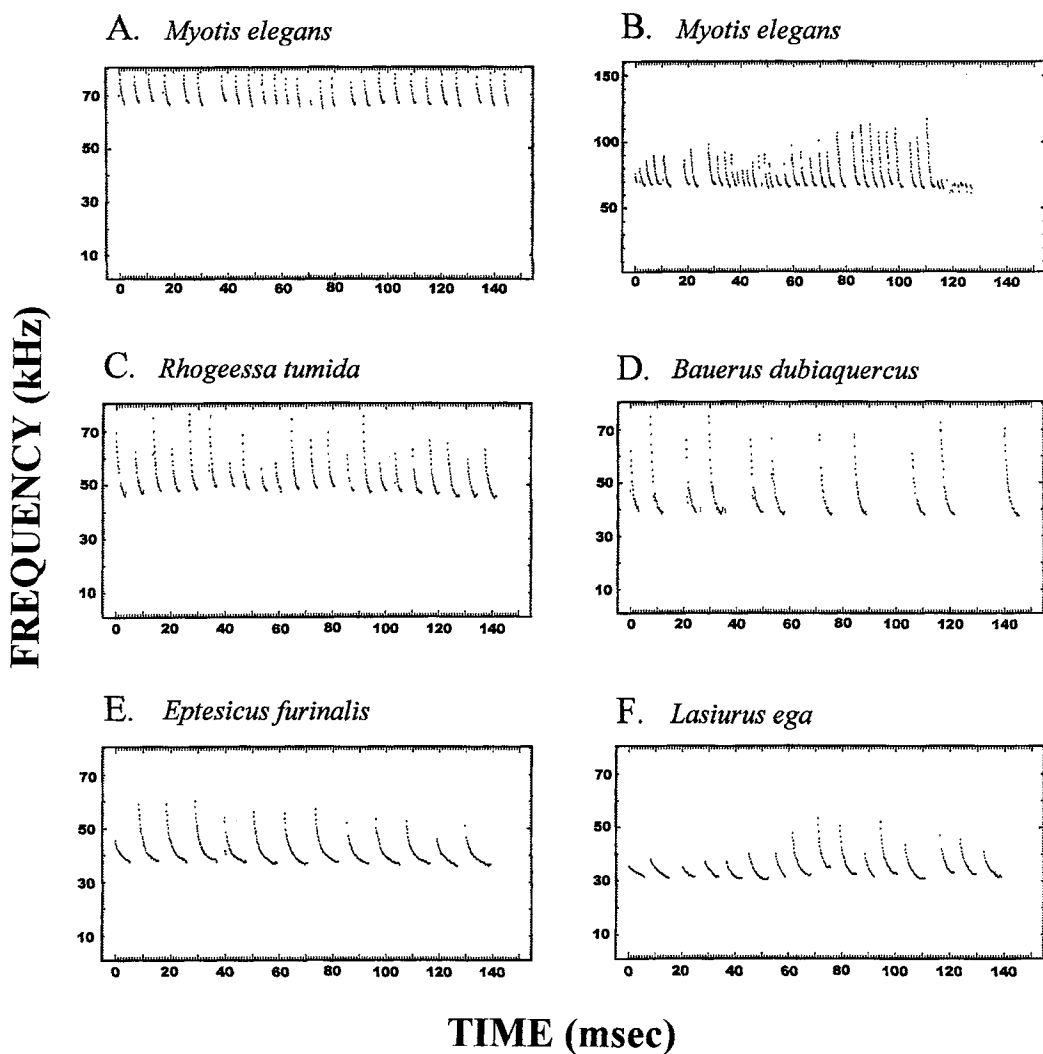


FIGURE 2. Frequency-time display of vocal sequences produced by some bats of the family Vespertilionidae from Belize. The time between calls on both screens is compressed to allow more calls per screen.

tial short-CF component with a long-FM terminal element. The sequence depicted begins with search calls grading into pursuit calls characterized by increasingly shorter CF components.

Bats of the family Vespertilionidae characteristically use FM echolocation calls of short duration (Fig. 2). Duration does differ among some species. As duration increases, the terminal portion of the call becomes flatter. *Myotis elegans*, like all members of this genus, has calls of short duration (Fig. 2A; $N = 275$). The variability within a given sequence is not apparent at the commonly used scale resolution of 0 to 80 KHz, but is evident by expanding

the scale (Fig. 2B). As with most bats that employ FM calls, the most important structural component is F_{MIN} . For example, *Rhogeessa aeneus* and *Bauerus dubiaquercus* have similarly shaped calls but F_{MIN} is offset by *ca* 10 kHz (Figs. C and D; $N = 127$ and 111, respectively). Likewise, bats with longer duration calls (*e.g.*, *Eptesicus furinalis* and *Lasiurus ega*) may be distinguished by differences in F_{MIN} (Figs. 2E and F; $N = 228$ and 48, respectively). The overall shape and pattern of these longer duration calls, however, provide further criteria for distinguishing among species. The *Eptesicus* calls are bilinear, with a distinct break in slope

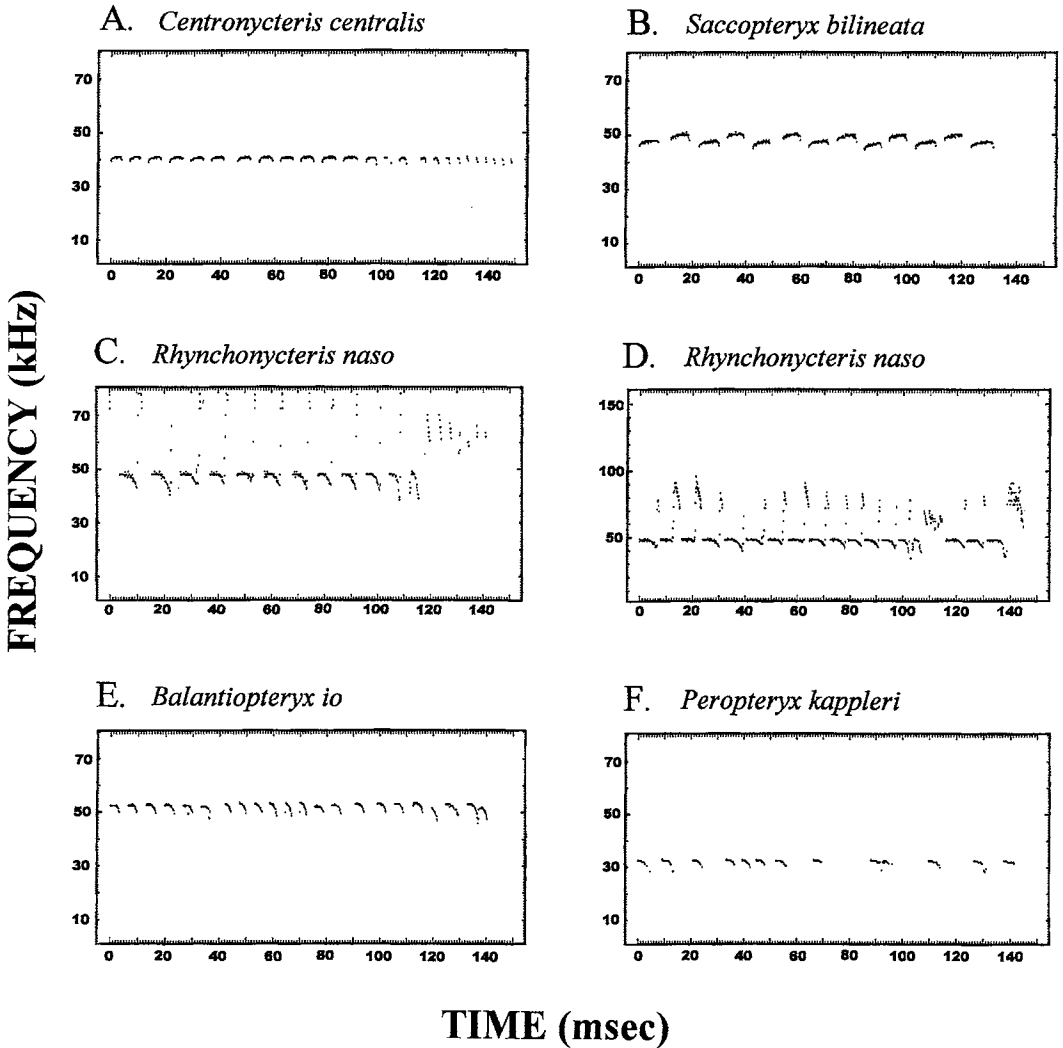


FIGURE 3. Frequency-time display of vocal sequences produced by some bats of the family Emballonuridae from Belize. The time between calls on both screens is compressed to allow more calls per screen.

preceding the flat portion of the call. *Lasiurus* calls are more curvilinear.

Bats of the family Emballonuridae exhibit two variations of a base pattern with a middle short-CF element (Fig. 3). Contrary to the vespertilionid pattern, the most important structural character for distinguishing among species is F_{MAX} . *Centronycteris maximiliani* (Fig. 3A; $N = 388$) and *Saccopteryx bilineata* (Fig. 3B; $N = 1189$) have short, relatively equal, initial ascending and terminal descending components. The middle element is a quasi-CF (Kalko & Schnitzler 1993) with a tendency to increase through time. *Centronycteris max-*

imiliani calls are notable for the uniformity of F_{MAX} ; the reduction in duration in the sequence presented, demonstrates pursuit and terminal "feeding buzz". *S. bilineata* calls are recognizable by an alternating step pattern. The second variation of the basic pattern is a short-CF followed by an arcing terminal FM element (Figs. 3C-F; $N = 78, 102, \text{ and } 8$, respectively). An occasional ascending initial element is present. An interesting and useful aspect of *Rhynchonycteris naso* calls is the presence of a second harmonic. The zero-crossings analysis used by Anabat eliminates the ability to display harmonic components, only the harmonic with the

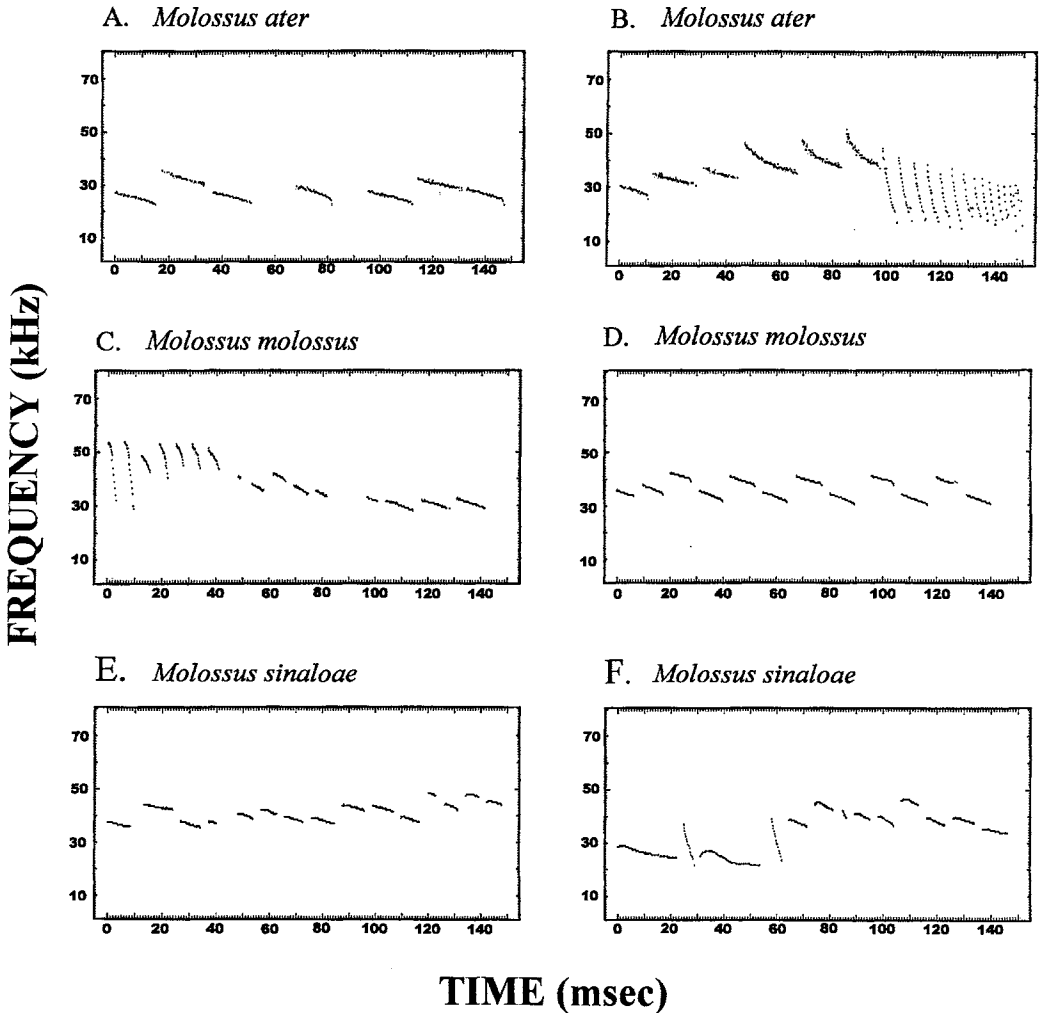


FIGURE 4. Frequency-time display of vocal sequences produced by some bats of the family Molossidae from Belize. The time between calls on both screens is compressed to allow more calls per screen.

greatest intensity. In the case of *R. naso*, it appears that the second harmonic is stronger but the higher frequencies are attenuated more rapidly. Thus with Anabat, the fundamental frequency, particularly at the higher frequencies of a call, is the only (thus strongest) harmonic reaching the detector and is displayed most often. The lower frequencies of the second harmonic are detected if the bat is close enough and in time is displayed at the end of a call (Fig. 3D). A complete call would incorporate the respective portions of each harmonic. Therefore, the frequency range for *R. naso* is 50–35 kHz for the fundamental or 100–70 kHz for the second harmonic.

Bats of the family Molossidae demonstrate a greater range in variability of calls than other groups examined (Fig. 4; $N = 195, 137,$ and 180 , respectively). Within the genus *Molossus*, there is a characteristic stepped pattern of relatively flat calls during the search phase. The overall frequency range ($F_{MAX}-F_{MIN}$) of the stepped calls is important in distinguishing among the species. Duration and general shape of the calls also are useful characteristics. It is important to note the changes that occur during pursuit and capture of prey (Fig. 4B). Care should be taken at roost sites because the vocalizations emitted are distinctly different than those issued by a free-flying individual (Fig. 4C).

Other types of vocalizations, generally referred to as social or communication calls, are occasionally detected. These are encountered most frequently in molossids (Fig. 4F). When encountered, they appear to be different for each species but insufficient data exist for a more thorough comparison. Social calls appear to differ for a species depending on the context (*e.g.*, at a roost, free-flying individuals).

We have recorded a number of other bats that are readily recognizable as distinctly different species but their identities have not been established yet. These species are mainly emballonurids and molossids that were flying at high altitudes. Capture is required to match species with vocal signature.

DISCUSSION

The ability to acoustically distinguish species of free-flying bats has been well-documented (Fenton & Bell 1979, 1981; Bell 1980; Barclay 1983; Ahlén 1990; Kalko 1995; O'Farrell 1997). The equipment available, however, has evolved dramatically only in the past 15 years, becoming less expensive and more accessible to field investigators. Ultrasonic detectors have been used to determine bat presence and sometimes identify species. The range of approaches and limitations have been discussed in detail by Fenton (1988). The Anabat system we used was relatively inexpensive and had the advantage of providing instantaneous displays of call structure with high resolution and detail (O'Farrell *et al.* 1999).

In general, echolocation data have been available in two forms: (1) vocalizations presented as a representative vocal pulse; and (2) verbal descriptions of certain characteristics (*e.g.*, maximum and minimum frequency). Photographs of sound spectrograms (Fenton & Bell 1979, Kalko 1995) or apparently hand-drawn sound spectrograms (Fenton & Bell 1981, Barclay 1983) at varying scales make comparisons difficult. A comparison of Anabat displays with other equipment (O'Farrell & Miller 1997) has demonstrated the increased resolution of structural aspects of specific calls. Instantaneous display of the structural features of calls allows field identification and selection of representative sequences to save; the use of a laptop computer and saving to the hard drive avoids tape distortion and machine noise (O'Farrell *et al.* 1999). Passive data collection to tape must be reviewed in real time; 8 h of tape recordings will require a minimum of 8 h to review. The ability to save select

sequences in the field eliminates collecting calls of unknown quality, thereby reducing analysis time.

Few visual representations have been published that demonstrate the variability inherent in calls of the species studied. A single pulse is not adequate to furnish reliable identification (O'Farrell *et al.* 1999). Although it has been recognized that signal shape changes from search through detection of a target and pursuit of a prey item (*e.g.*, Griffin *et al.* 1960, Simmons *et al.* 1979, Schnitzler & Henson 1980), the range in variation exhibited by individual species has seldom been described. A recent study (Kalko & Schnitzler 1993) described the variation in signal characteristics for three species of European pipistrelles in relation to habitat and specific foraging behavior, providing critical information for discriminating species under varied circumstances. O'Farrell and Miller (1997) have given descriptive sequences for a few Neotropical species of the families Mormoopidae and Emballonuridae.

The database gathered during this study represents a start toward a comprehensive library of vocal signatures. Further determination of diagnostic signal characteristics, however, will be required. The maximum and minimum frequency of a vocal sequence needs to be examined, recognizing that both are subject to variation. Duration of a signal varies with activity but the average duration for a behavioral sequence may be important. Changes in shape, which incorporate both bandwidth and duration, may be a valuable tool, particularly as defined by Kalko and Schnitzler (1993). The components of signal characteristics must be subjected to critical statistical analyses, permitting a more rigorous examination of geographic and temporal differences. Currently, there is no standard agreement as to what calls should be included or excluded from measurement, which measures are important, and how to obtain those measures. We found that a qualitative evaluation of F_{MIN} , F_{MAX} , duration, and shape provides sufficient information to identify many free-flying species.

Quantification of specific features will be meaningful but only when performed under stringent, controlled conditions. Time intensive studies following individuals marked by light tags or radio transmitters will guarantee that all incoming calls are from the same source and will provide a context in which to interpret the sounds. Knowledge of how the animal is oriented with respect to the detector will approximate distance and type of behavior. Some standardized procedure will be required to choose the individual calls on which to perform measurements. Not all incoming calls,

even within the same sequence, are of the same quality. It is important to be selective and eliminate call fragments. Measures on fragments will definitely overlap with those of other species and introduce confounding error. Other factors (e.g., echoes, presence of multiple bats) also need to be addressed prior to subjecting a series of calls to measurement.

To amass a comprehensive library of vocal signatures, it will be necessary to target a species and follow that species through a variety of seasons and during the range of behaviors exhibited by that taxon. Individual variation must be described. This will require the ability to follow a known individual through a variety of behaviors. Under any condition, the amassing of a comprehensive library for a given species, let alone an entire bat community, is not a trivial exercise. One may envision that such a process will be a continual one.

Geographic range data provide an essential alternative source of diversity estimates. Comparisons of inventory results with geographic expectations suggest that all existing Neotropical mammal inventories are incomplete (Voss & Emmons 1996). Within the limits of the equipment, acoustic sam-

pling provides a powerful tool for performing rapid inventories and demonstrates great promise for inventories as well as behavioral and ecological studies of free-flying bats.

As with any tool, certain limitations exist. Bats with low intensity calls (e.g., Phyllostomidae) are not detected. Other techniques are necessary for these species. In the case of phyllostomid bats, mist netting is effective. Thus for a comprehensive inventory, multiple techniques are required. During development of a reference library of vocal signatures, unknown species will outnumber those with established identities. This is still of value. First, there will be a more accurate determination of species richness. Second, as further work clarifies a species' vocal signature, an archive of cataloged unknowns will suddenly reveal a wealth of information.

ACKNOWLEDGMENTS

We wish to thank C. M. Miller for field and editorial assistance. M. B. Fenton, W. L. Gannon, and E. K. V. Kalko reviewed an earlier draft of the manuscript. This study was supported by the Wildlife Conservation Society, the Terra Foundation, and Bowen & Bowen, Ltd.

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