Acta Chiropterologica, 2(2): 171–183, 2000
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS

Contribution of acoustic methods to the study of insectivorous bat diversity in protected areas from northern Venezuela

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We present the results of an acoustic survey of aerial insectivorous bats conducted in four protected areas in northern Venezuela. These areas represent localities where the taxonomic composition of the bat communities was relatively well known. We conducted field surveys using the Anabat II detector and analysis system. We compared acoustic inventories with previous lists obtained with conventional sampling methods (principally mist nets). We identified 30 species acoustically (representing 15 genera of the families Emballonuridae, Noctilionidae, Mormoopidae, Vespertilionidae, and Molossidae) on the basis of vocal signatures. Nineteen of these were verified by capture and subsequent recording of released animals; the remainder were identified by comparison with verified vocalizations from other localities. An additional 11 unidentified but distinct taxa were recorded and are referred to here as 'sonotypes' (based on similarities in call structure to known species) representing eight genera of the families Emballonuridae, Vespertilionidae, and Molossidae. The short-term acoustic surveys nearly equaled or exceeded the known species richness at three of the four localities, and added two to nine species to previous lists from all locations; many of these bats correspond to taxa difficult to detect with conventional capture methods.

Key words: insectivorous bats, acoustic survey, Anabat, community inventory, technique comparison, Neotropics, protected areas, Venezuela

INTRODUCTION

Neotropical rainforest bat communities are diverse and include many elusive species, magnifying the problems of studying volant, nocturnal animals. In the past, inventories of bats were restricted to capture at roost sites or with mist nets at locations with concentrated activity. In the Neotropics, mist nets have been effective particularly for collecting bats that use senses other than echolocation for primary orientation and hunting (e.g., Phyllostomidae), whereas harp traps have been more effective for other families (Tuttle, 1976; LaVal and Fitch, 1977). Recently, acoustic methods have added significantly to the knowledge of occurrence and distribution of free-flying insectivorous species (Kalko *et al.*, 1996; O'Farrell and Gannon, 1999; O'Farrell and Miller, 1999).

Among Venezuelan mammals, bats have received major attention in terms of taxonomic inventories (e.g., Handley, 1976; Ochoa, 1985; Soriano *et al.*, 1999). Recent literature reveals the presence of at least

155 species, representing 44.2% of the mammals recorded for this country (Soriano and Ochoa, 1997; Ochoa and Aguilera, In press). Many of these inventories have been performed in protected areas (e.g., Fernández and Ulloa, 1990; Ochoa *et al.*, 1993, 1995; Bisbal, 1998) using standard collection methods (primarily mist nets).

The importance of Neotropical bat communities to biological diversity is evident when species richness approaches half of the total mammal species found in many ecosystems (Voss and Emmons, 1996). Consequently, a detailed inventory of bats constitutes a critical aspect for evaluating ecological conditions of natural areas and the consequences of primary habitat degradation on wildlife composition (Fenton *et al.*, 1992; Brosset *et al.*, 1996; Ochoa, 2000; Schulze *et al.*, 2000; Miller, In press; Soriano and Ochoa, In press).

Detection of bat species using conventional methods (e.g., mist nets and harp traps) represents an important tool for evaluation of biodiversity and the study of functional structure of habitats within a particular region (Simmons and Voss, 1998; Ochoa, 2000). However, it may be a lengthy process to establish the identity of all species, particularly in those ecosystems with high complexity and diversity. The more comprehensive the inventory is, the greater its value will be to ecological assessments and conservation strategies. As a practical matter, most inventories to assess biodiversity rarely allow sufficient time to adequately locate and identify all species present. Generally multiple years of sampling through all seasons is necessary to obtain an exhaustive list of species. Simultaneous diversification of sampling methods should maximize the number of species recorded.

Use of acoustic detection has been shown to be a powerful supplement to standard capture methods to identify many insectivorous bats that are generally underrepresented in field inventories (O'Farrell, 1997; Kuenzi and Morrison, 1998; Murray *et al.*, 1999; O'Farrell and Gannon, 1999). Acoustic methods also provide relevant information on other community and population characteristics (Kalko, 1995; Kalko and Schnitzler, 1998; Kalko *et al.*, 1998), some of which are of particular interest when defining conservation strategies.

In assessing biodiversity, we submit that knowledge of species richness, regardless of the ability to actually give a name to each, is useful for establishing conservation priorities. Precise identity of species can be assigned later as more information becomes available, provided appropriate voucher material is collected during each sampling. In our approach to acoustic sampling, we have attempted to confirm the vocal repertoire of each species encountered (O'Farrell *et al.*, 1999). This is usually a lengthy process for certain bats that are difficult to capture.

Jones and van Parijs (1993) introduced the concept of phonic types by differentiating two distinct forms of pipistrelle bat (*Pipistrellus pipistrellus* sensu lato) using differences in the frequencies of search phase echolocation calls. Vaughan *et al.* (1996) subsequently used these phonic types to investigate the foraging behavior in riparian habitats. We expanded the concept of recognizing unidentified yet unique species by echolocation search phase calls. We define a sonotype as an unidentified species whose calls do not match known vocal signatures but are clearly distinct.

For this study unconfirmed species were distinguished by sonotype, sequences of calls that share similarities in shape and frequency characteristics. Sonotypes were grouped into categories based upon similarity of call patterns and frequency ranges. These categories form the basis for determining the number of distinct species present and suggest a focus of future work on identifying those unknowns. In addition to the sonotype concept, we develop a method for hypothesizing identifications and taxonomic affinities of the echolocation call patterns. We compared the results of short-term acoustic inventories of aerial insectivorous non-phyllostomid bats with existing data collected with conventional capture techniques in three national parks and one wildlife refuge in northern Venezuela. These sites were selected because of the relatively large amount of information recorded over the past three decades on species composition of complex bat communities.

MATERIALS AND METHODS

Study Areas

We conducted acoustic sampling at eight localities within Guatopo, Henri Pittier, and Yacambú national parks, as well as the Cuare Wildlife Refuge (Fig. 1). The locations of these areas correspond to the northern coastal region of Venezuela and the northeast extreme of the Andean mountains (MARNR, 1992). The general characteristics of these localities and those of relevant previous studies are as follows:

Guatopo National Park — This park is situated in the interior mountainous region of the Central Coastal Range in the states of Miranda and Guárico. Three localities were sampled: El Lucero, Agua Blanca, and La Colonia (near Altagracia de Orituco, 600–700 m a.s.l.), which are dominated by primary deciduous and evergreen forests. Some sectors located along the principal roads are associated with secondary forests and herbaceous vegetation, as a consequence of agricultural activities and the construction of infrastructures prior to the creation of the park in 1958. Past studies documented 60 species of bats, 22 of which were aerial insectivores belonging to the families Emballonuridae, Mormoopidae, Vespertilionidae, and Molossidae (Table 1; see also Eisenberg *et al.*, 1979; Salazar, 1984; Ochoa *et al.*, 1995).

Henri Pittier National Park — Two localities were sampled at Rancho Grande, near El Limón, Aragua State: Paso Portachuelo and Biological

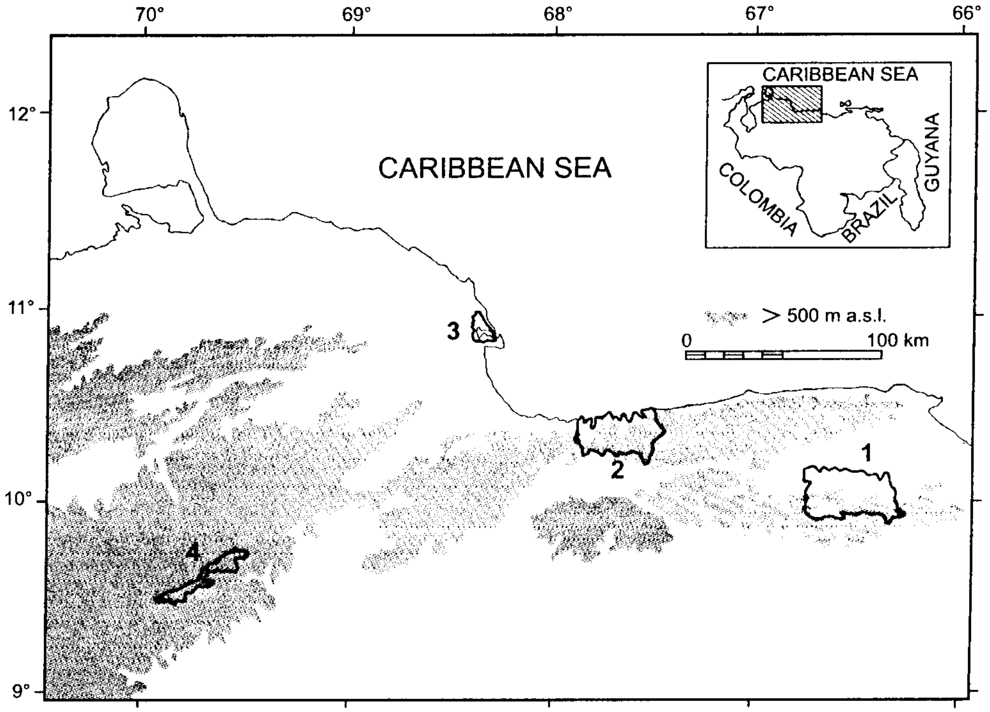

FIG. 1. Geographic locations for acoustic surveys of aerial insectivorous bats in northern Venezuela: 1 — Guatopo National Park (Miranda and Guárico States); 2 — Rancho Grande, Henri Pittier National Park (Aragua State); 3 — Cuare Wildlife Refuge (Falcón State); and 4 — Yacambú National Park (Lara State)

Station (1,000–1,100 m a.s.l.). Abrupt mountainous relief characterizes this part of the highlands of the Central Coastal Range. Dominant vegetation consists of a transition between evergreen and cloud forests, with small patches of second-growth vegetation located in areas associated with the development of park infrastructures. Rancho Grande is one of the localities with the greatest quantity of information regarding bat species inhabiting highland forests in northern Venezuela. Most previous studies were based on irregular and isolated sampling. Fifty-seven species of bats, 24 of which are aerial insectivores of the families Noctilionidae, Mormoopidae, Thyropteridae, Vespertilionidae, and Molossidae were known to occur in the park (Table 1; see also Tate, 1947; Ochoa, 1980; Fernández *et al.*, 1988).

Yacambú National Park — One area was sampled around El Blanquito (1,500–1,600 m a.s.l.), near Sanare, Lara State. This site is located in the mountainous highlands of the northeastern extreme of the Venezuelan Andes. Vegetation is predominately primary cloud forests, with some disturbed sectors for recreation facilities and *Eucalyptus* plantations. Seventeen species of bats, including four aerial insectivorous species of the families Mormoopidae, Vespertilionidae, and Molossidae are known to occur in the park (Table 1; see also ASOVEM, 1986).

Cuare Wildlife Refuge — Sampling occurred in the surroundings of Chichiriviche de la Costa and Casa Vieja (0–10 m a.s.l.), Falcón State. Flat coastal plains and associated lagoons characterize the area. Vegetation is a mosaic of thorn forest, mangrove, pastures, coconut plantation, and secondary stubble. The area also includes a mountainous region of limestone origin (Chichiriviche Hill; 282 m a.s.l.) that is dominated by dry deciduous forests and contains a complex system of caves. The refuge contains 32 documented species, 13 of which are aerial insectivores belonging to the families Emballonuridae, Noctilionidae, Mormoopidae, Vespertilionidae, and Molossidae (Table 1; see also Bisbal and Ribero, 1998).

Sampling Methods

Acoustic sampling was performed between April and July of 1999, using Anabat II bat detectors (Titley Electronics, Ballina, New South Wales, Australia) linked to IBM-compatible laptop computers by means of a Zero-crossings Analysis Interface Module. Bat activity was monitored in real time providing a display of the time-frequency structure of calls. After examination of incoming signals, complete sequences were saved as binary files directly to the computer. Methods for monitoring and establishing identity of species followed those of O'Farrell *et al.* (1999).

In general, sampling occurred at fixed points, which coincided with previous sampling locations. When possible, monitoring was conducted outside known roost sites. Fixed points were sampled for approximately 2.5 hours after sunset. Opportunistic supplemental sampling was conducted by driving routes, 1–2 hrs after sunset, through a gradient of habitats at Cuare (1 hr), Guatopo (0.5 hr), and Yacambú (3 hrs). Acoustic sampling at fixed points totaled 45 hrs of recording: 10 hrs each for Cuare (18–19 April), Guatopo (21–22 April), and Yacambú (26–30 July); and 15 hrs at Henri Pittier (15–17 April). The April sampling occurred at the end of the dry season; the moon ranged from new to half. The July sampling occurred in the middle of the rainy season and the moon was full.

At each locality, acoustic sampling was supplemented by standard capture techniques using mist nets and double-frame harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia). Captured bats were released under controlled conditions to obtain vocalizations from known species. Common species were taken to an open area near the point of capture for release. For bats >3 g, chemiluminescent tags (Mini-light Sticks, Chemical Light, Inc., Wheeling, IL, USA) were affixed to the dorsal fur prior to release to allow tracking with the detector. Smaller bats were followed using a spotlight. Rare bats, or those of uncertain identity, were released in a large enclosure or were tethered by a hind foot with a thin thread (8 to 15-m long), allowing the animal to take flight and yet be retained as a voucher for positive identification. Focused sampling was performed at several known roost sites for *Peropteryx kappleri, Saccopteryx bilineata, S. leptura, Eumops auripendulus*, and *E. glaucinus*.

Species were identified with respect to time-frequency structure of echolocation calls using Analook software following the qualitative method of O'Farrell *et al.* (1999). Although in the present survey a number of species and genera were different from those of previous acoustic data, we were able to use existing reference vocalizations to compare those taxa common to Venezuela, the United States (O'Farrell, 1997), and/or Belize (O'Farrell and Miller, 1997, 1999). Species that could not be identified by capture or matched with known reference calls were placed in call structure groups (i.e., sonotypes). Our past experience indicates that families can be separated by general call patterns, and that closely related species tend to exhibit similar call shape structural patterns at different frequency ranges (O'Farrell, 1997; O'Farrell and Miller, 1997, 1999).

TABLE 1. A checklist of insectivorous non-phyllostomid bats recorded in the Henri Pittier (Rancho Grande), Guatopo, and Yacambú national parks, and the Cuare Wildlife Refuge. Previously documented (Pr) by standard collection methods (ASOVEM, 1986; Fernández and Ulloa, 1990; Ochoa *et al.*, 1995; Bisbal and Ribero, 1998) and recorded by acoustic methods (Ar). Only the species detected during the present study are shown in the table, therefore the list is not exhaustive. Unidentified species (sonotypes) are based on vocalizations with time-frequency patterns differing significantly from those species positively identified within a particular genus. Approximate limits of critical minimum and/or maximum frequency are given in parentheses

Family/Species	Locality			
	Rancho Grande	Guatopo	Yacambú	Cuare
Emballonuridae				
Peropteryx kappleri	Ar	Pr, Ar		Pr
P. macrotis	Ar			Pr, Ar
Peropteryx sp. (37–42 kHz)	Ar		Ar	Ar
Saccopteryx bilineata	Ar	Pr, Ar		Ar
S. canescens		Ar		Pr, Ar
S. leptura	Ar	Pr, Ar		Ar
Diclidurus albus	Ar	Pr		
Diclidurus sp. (25–30 kHz)	Ar	Ar		Ar
Noctilionidae				
Noctilio leporinus	Pr			Pr, Ar
Mormoopidae				
Mormoops megalophylla	Pr, Ar		Pr	Pr, Ar
Pteronotus davyi	Pr, Ar	Pr, Ar	Ar	Pr, Ar
P. gymnonotus				Pr, Ar
P. parnellii	Pr, Ar	Pr, Ar	Pr, Ar	Pr, Ar
P. personatus	Ar			Pr, Ar
Vespertilionidae				
Eptesicus brasiliensis	Pr, Ar	Pr	Pr, Ar	
E. furinalis	Pr	Pr, Ar	Ar	
E. fuscus	Pr, Ar		Ar	
Eptesicus sp. (45–48 kHz)	Ar	Ar	Ar	
Lasiurus blossevillii	Ar	Pr	Ar	
L. cinereus	Ar	Ar	Ar	Ar
L. ega			Ar	Ar
Lasiurus sp.1 (50–60 kHz)	Ar	Ar		Ar
Lasiurus sp.2 (25–30 kHz)	Ar			Ar
Myotis keaysi	Pr, Ar	Pr, Ar	Ar	
M. nigricans	Pr, Ar	Pr, Ar	Ar	Pr, Ar
Myotis sp. (53–57 kHz)[1]				Ar
Rhogeessa minutilla				Pr, Ar
Molossidae				
Molossops greenhalli	Pr, Ar	Pr, Ar		Ar
M. temminckii	Pr, Ar			
Molossops sp.1 (30 kHz)			Ar	
Molossops sp.2 (35 kHz)				Ar
Eumops auripendulus		Pr, Ar		Ar
E. glaucinus	Pr, Ar	Pr, Ar		
E. perotis	Pr			Ar
Eumops sp. (14–16 kHz)	Ar			
Molossus molossus	Pr, Ar	Pr, Ar	Pr, Ar	Pr, Ar
M. rufus	Pr, Ar	Pr, Ar		
M. sinaloae	Pr, Ar			
Molossus sp.1 (frequency > *rufus*)				Ar
Molossus sp.2 (frequency > *molossus*)	Ar	Ar		Ar
Nyctinomops laticaudatus	Pr, Ar			Ar
Tadarida brasiliensis			Ar	

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[1] — Morphologically related to *Myotis nigricans* (44–47 kHz) but with higher frequency range

Sonotypes were initially categorized by key structural features (e.g., minimum frequency, maximum frequency) and general shape (e.g., patterns of change in slope). Where possible, sonotypes were assigned to a particular family and genus based on the general patterns in shape of echolocation calls. They were presumed to be distinct species because of variance from those of positively identified species. We used the supposition that size of bats is related to the dominant call frequency, i.e., the smaller the bat the higher the frequency (Jones, 1995; Barclay *et al.*, 1999) when assigning tentative identifications to sonotypes. This relationship has recently been described by a linear model (e.g., Bogdanowicz *et al.*, 1999). Vocal signatures of related species from three genera and representing three families Emballonuridae, Mormoopidae, and Vespertilionidae are provided as examples (Fig. 2).

Voucher specimens of the following species are housed at the Museo de la Estación Biológica de

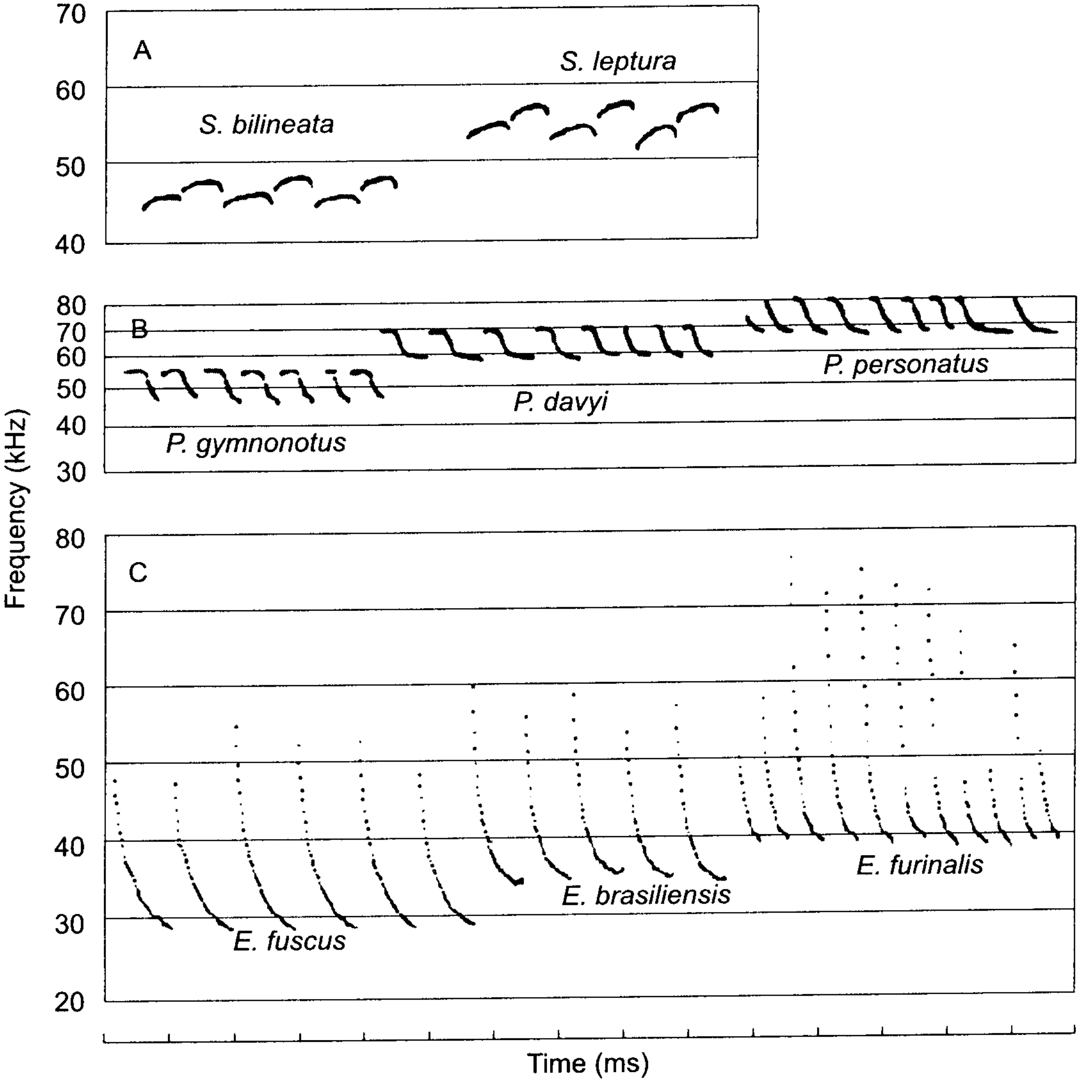

Fig. 2. Comparison of frequency-time display of vocal sequences produced by related species; (A) two emballonurids: *Saccopteryx bilineata* (forearm length, FA = 44–48) and *S. leptura* (FA = 37–43); (B) three mormoopids: *Pteronotus gymnonotus* (FA = 50–55), *P. davyi* (FA = 43–49), and *P. personatus* (FA = 42–48); and (C) three vespertilionids: *Eptesicus fuscus* (FA = 46–52), *E. brasiliensis* (FA = 39–48), and *E. furinalis* (FA = 37–41) showing forearm size versus frequency relationship (forearm lengths from Reid, 1997 and Linares, 1998). The time between calls is compressed to allow more calls per screen. Time tic marks are 10 ms

Rancho Grande (EBRG), Maracay, Aragua State: *Saccopteryx bilineata, S. leptura, S. canescens, Pteronotus davyi, P. gymnonotus, P. parnellii, Eptesicus brasiliensis, E. furinalis, Lasiurus ega, Myotis keaysi, M. nigricans, Myotis* sp., *Rhogeessa minutilla, Molossops greenhalli, Molossus molossus, M. rufus*, and *Tadarida brasiliensis*. In addition, four species (*Peropteryx macrotis, Molossops temminckii, Eumops auripendulus*, and *E. glaucinus*) were identified in the field either by observation or by capture, without retaining voucher specimens. Acoustic voucher files for all species recorded during the study were deposited at the bat acoustic library of the Museum of Southwestern Biology (University of New Mexico, Albuquerque, USA) and the Museo de la Estación Biológica de Rancho Grande (Maracay, Venezuela).

Prior to field sampling, we reviewed published species lists for each locality (ASOVEM, 1986, Fernández and Ulloa, 1990; Ochoa *et al.*, 1995; Bisbal and Ribero, 1998), and a compilation of records from EBRG. This compilation allowed *a priori* evaluation of the local bat fauna and also facilitated the analysis and identification of data gathered during acoustic surveys.

RESULTS

We identified 30 species, representing 15 genera and five families, on the basis of vocal signatures, verified by capture and subsequent recording of released animals or comparison of vocal signatures of verified species from other localities (Table 1). One echolocation pattern was verified by capture as *Myotis* (near *nigricans*) but demonstrated a frequency range sufficiently different from this species to warrant classification as a distinct sonotype. Also, ten sonotypes species showed similarities with vocalization shapes to those of the genera *Peropteryx, Diclidurus, Eptesicus, Lasiurus, Molossops, Eumops*, and *Molossus*. Previous studies documented 13 species that we were not able to identify acoustically during the short survey period.

In general, the species detected that were common to Belize and/or the United States were within the range of frequencies and shapes established for these countries. Predictions for these species were proven correct with subsequent capture. For sonotypes, one emballonurid recorded during the surveys was initially predicted to be *Centronycteris maximiliani* based on the similarity of call shape and lack of variation in maximum frequency to the pattern known for *C. centralis* in Belize (Fig. 3). However, individuals were captured and subsequently identified as *Saccopteryx canescens*. Its call structure lacked the characteristic stepped alternating maximum frequency exhibited

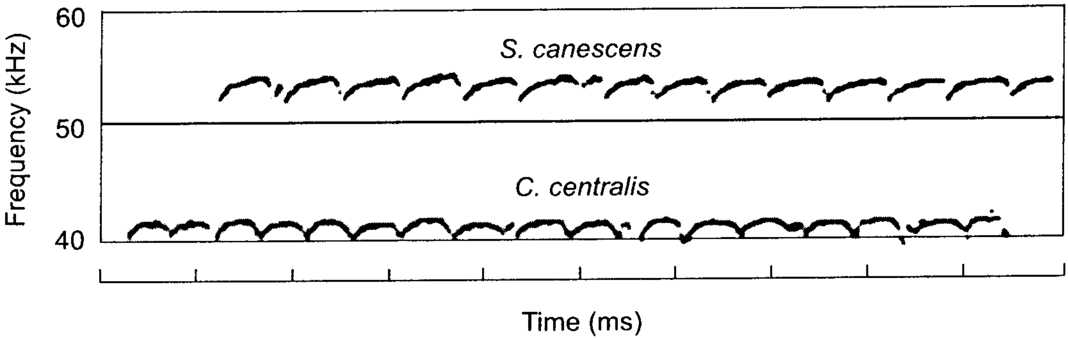

FIG. 3. Comparison of frequency-time display of vocal sequences produced by two emballonurids *Centronycteris centralis* (FA = 43–49) and *Saccopteryx canescens* (FA = 36–41) showing the similarity in call structure that initially led to hypothesising that the latter may be *C. maximiliani* (forearm lenghts from Museo del Instituto de Zoologia Agricola, 1988 and Reid, 1997). To date the vocal signature of *C. maximiliani* remains unknown but is thought to be similar in structure to *C. centralis*. The time between calls is compressed to allow more calls per screen. Time tic marks are 10 ms

by other *Saccopteryx* (Fig. 2A). A vespertilionid intermediate in frequency range between *Eptesicus furinalis* and *E. fuscus* (Fig. 2C) was predicted to be *E. brasiliensis* based on its intermediate size between the other two. This identification was later verified by capture. During supplementary acoustic inventories in the lowlands of the Henri Pittier National Park, we captured and confirmed the vocal signature of *Molossops temminckii* (53 kHz). The pattern of these call pulses were unique for any species examined to date. Based on acoustic similarities with this record and comparisons with unconfirmed calls from Belize, we predicted another sonotype to be *Molossops greenhalli* (25 kHz). This was later verified by capture of this species. Based upon a pattern that appears unique to this genus, we suggest that the similar sonotypes listed in Table 1 as *Molossops* spp. may represent additional species in this genus. Predictions for the remaining species identifications need to be tested.

The contribution of acoustic sampling nearly equaled or exceeded the number of species previously known from Rancho Grande, Yacambú, and Cuare (Table 2). Furthermore, our short-term acoustic surveys added two to nine additional species to previous lists from all locations. Thus, the use of sonotypes increased the known taxonomic richness substantially. Species accumulation for the two localities with the most comprehensive databases (Guatopo and Rancho Grande) demonstrate the importance of further inventory work to more fully characterize bat diversity (Fig. 4). At Guatopo, it appeared that the number of species is near asymptote but the accumulation curve is still steep for Rancho Grande.

DISCUSSION

In the present study, we selected sites that contained a relatively comprehensive baseline inventory established over multiple decades by numerous investigators at all times of the year. Our study provided a snapshot in time within the broader context of a comprehensive database. As acoustic data were collected, we separated calls with similar shapes and frequency ranges into sonotype categories. Based on an expanding library of vocal signatures throughout North and Central America, we were able to predict taxonomic identity for sonotypes. Depending on the amount of experience with different taxonomic groups, these predictions were generally at the family and genus level although species were assigned to those echolocation patterns that compared closely with verified calls in the vocal library. Predictions were tested empirically as species were captured simultaneously

TABLE 2. A comparison of the number of species of non-phyllostomid aerial insectivorous bats identified acoustically by family to the total previously known to occur at four protected areas in northern Venezuela; Pr = previous records based on conventional sampling methods (ASOVEM, 1986; Fernández and Ulloa, 1990; Ochoa *et al.*, 1995; Bisbal and Ribero, 1998); Ar = acoustic records; and Add = number of species added to previous inventories. The taxonomic affinities of sonotypes are hypothesized (number is given in parentheses)

Family	Rancho Grande		Guatopo		Yacambú		Cuare	
	Pr/Ar	Add	Pr/Ar	Add	Pr/Ar	Add	Pr/Ar	Add
Emballonuridae	–/7 (2)	7 (2)	4/5 (1)	2 (1)	–/1 (1)	1 (1)	3/6 (2)	4 (2)
Noctilionidae	1/–	–	–	–	–	–	1/1	–
Mormoopidae	3/4	1	2/2	–	2/2	1	5/5	–
Vespertilionidae	5/9 (3)	5 (3)	5/6 (2)	3 (2)	1/9 (1)	8 (1)	2/7 (3)	5 (3)
Molossidae	8/9 (2)	2 (2)	5/6 (1)	1 (1)	1/3 (1)	2 (1)	1/8 (3)	7 (3)
Σ	17/29 (7)	15 (7)	16/19 (4)	6 (4)	4/15 (3)	12 (3)	12/27 (8)	16 (8)

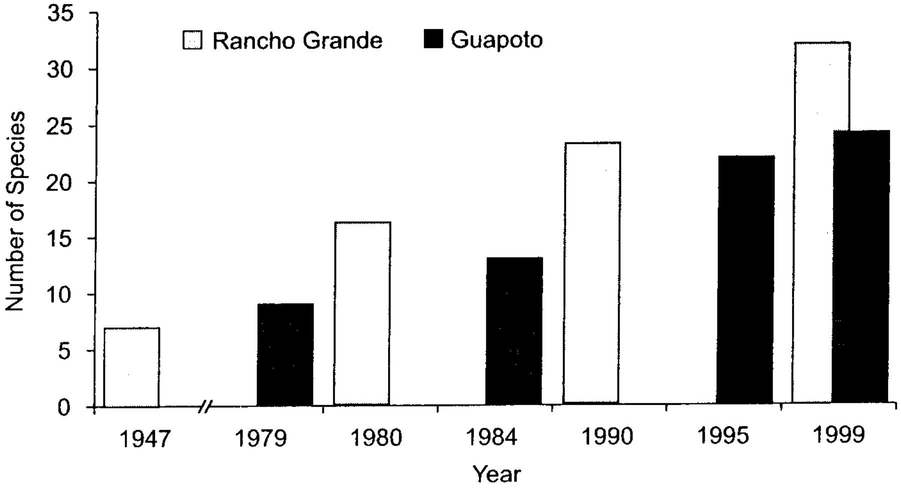

FIG. 4. Species accumulation for aerial insectivorous bats (Emballonuridae, Noctilionidae, Mormoopidae, Vespertilionidae, and Molossidae) recorded in the Guatopo and Henri Pittier (Rancho Grande) national parks. Data prior to the present study correspond to the results of conventional capture techniques (Tate 1947; Eisenberg *et al.*, 1979; Ochoa 1980; Salazar, 1984; Fernández and Ulloa, 1990; Ochoa *et al.*, 1995). Additional data for 1999 (this study) were obtained by acoustic detection and include only those species with confirmed taxonomic identifications

during the acoustic surveys. Of the 30 species identified based on comparison with known vocal signatures (Table 1), 19 were confirmed during the present study. Of these, three were sonotypes representing previously unknown vocal signatures; *S. canescens* was not correctly predicted but *E. brasiliensis* and *M. greenhalli* were. We point out that the acoustic surveys provided an efficient means to survey four diverse sites at a high level of detail with only 45 hrs of field time.

Regarding the identity of the *Myotis* sp. from Cuare (Table 1), a collection of museum specimens indicate the presence of *M. nigricans* in this locality and Rancho Grande. However, vocal signatures between the *Myotis* found at the two sites differ by approximately 10 kHz. Museum specimens from Rancho Grande suggest that *M. nigricans* is common there. In a preliminary examination of external and cranial morphology of four specimens from Cuare, we found an apparent affinity with *M. nigricans*. However, acoustic differences from hand-released individuals at both sites suggest the possibility of a cryptic species of *Myotis* at Cuare and perhaps in other xerophytic habitats on the northern coast of western Venezuela. This may not be unlike what appears to be a cryptic species of the well known *P. pipistrellus* sensu lato found in Europe that also are separated by ca. 10 kHz (Jones and van Parijs, 1993). The *M. nigricans* complex may represent a composite of sibling species (LaVal, 1973; Koopman, 1994). Although morphological comparisons, including those related to bacular differences, were unable to support this hypothesis (LaVal 1973), it is possible that recent advances in acoustic methods may help in identifying cryptic species within the *nigricans* complex (R. K. LaVal, personal communication).

Of the 24 species common to Belize and the United States, little to no acoustic divergence was observed. Although the existence of geographic variation is probable

(Thomas *et al.*, 1987; Barclay *et al.*, 1999), it has yet to be verified (O'Farrell *et al.*, 2000). The concern that intraspecific variability, including possible geographic variation, could prevent acoustic identification (Thomas *et al.*, 1987; Brigham *et al.*, 1989; Barclay, 1999) appears unwarranted. Variation within a species is predictable, within limits, based on behavior and proximity to clutter (O'Farrell *et al.*, 1999). Knowledge of the types and magnitude of variation to expect and general experience with acoustic identification appears to overcome potential problems in categorizing sonotypes and successfully predicting taxonomic identity, at least at the family or genus level regardless of geographic location (O'Farrell and Gannon, 1999; O'Farrell *et al.*, 2000).

Voss and Emmons (1996) reviewed ten Neotropical rainforest 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. Species accumulation curves for Guatopo and Rancho Grande also revealed that complete inventories have not been achieved (Fig. 4). The number of species recorded for these two areas increased dramatically within the past two decades, using conventional capture methods. However, our short effort increased the species lists substantially (Tables 1 and 2). We expect that with more intensive, long-term surveys, and a more comprehensive library of vocal signatures, more species will be added to the known fauna for both areas.

In addition to documenting occurrence and relative abundance, acoustic surveys can provide supplementary information on ecological patterns of species that are not readily sampled by conventional means (e.g., Molossidae, Diclidurinae, and some genera of Vespertilionidae). Rancho Grande, for example, had no emballonurids recorded prior to the present study. In general, this family prefers lowland habitats (Handley, 1976). We detected emballonurids in a mountain pass formed by steep hillsides (1,100 m a.s.l.), which appears to be used as a movement corridor from low coastal areas to inland lowlands (Ochoa, 1980). Capture is difficult at this location because insectivorous bats fly through the pass at canopy level.

Our acoustic survey, in conjunction with past inventory work, still only approximates the true species composition. Our data support the conclusion that acoustic methods are a vital supplement to standard collection techniques, which corroborates studies elsewhere (Kalko *et al.*, 1996; Kuenzi and Morrison, 1998; Murray *et al.*, 1999; O'Farrell and Gannon, 1999). Even when unknown vocal signatures are recorded, it is possible to distinguish the number of sonotypes present and deduce potential taxonomic identity based on general shape and frequency range of vocalization. A determination of species composition by family initially allows assessment of community diversity and highlights the taxa that need further investigation. Acoustic methods also provide a means of assessing other population and community characteristics not addressed in our study (e.g., activity patterns, spatial distribution, and habitat use). An accurate determination of these ecological attributes is relevant to design conservation strategies for aerial insectivorous bats (Kalko, 1995; Fenton *et al.*, 1998).

Focused surveys at more locations during multiple seasons should add substantially to a description of insectivorous bat communities. The existing database was instrumental in making initial identifications and suggested family or generic relationships. Additional survey and captures will continue to expand the comparative database of vocal signatures (e.g., O'Farrell, 1997; O'Farrell and Miller, 1999). Obviously, the more comprehensive the comparative database of vocalizations is, the greater the number of species that will be identified during acoustic surveys. However, a comparative library alone is no substitute for an experienced investigator with regional expertise.

Sonotypes that we assigned to a particular genus based upon unique vocal signatures (see Table 1) may or may not be correct. This will be ascertained with further investigation. We acknowledge that the vocal signature database for Neotropical bats is far from complete. With continued fieldwork, species with yet unmatched vocal signatures will be captured and their identity added to the database. As the database becomes more comprehensive it may be possible to infer a greater range of taxonomic affinities for sonotypes. We also point out the obvious, that in the beginning all species were unknown acoustically.

A prerequisite to making any decisions concerning the preservation of species is knowledge of their existence (Barrowclough, 1992). Acoustic methods provide an additional means for rapidly reassessing distributions of species of the Neotropical non-phyllostomid bat families that have not previously been adequately sampled. Regardless of the lack of a positive identification or a correct prediction for a vocal sequence, the documentation of these bats, even as sonotypes, allows a more comprehensive understanding of their distributions and diversity so thereby we can begin addressing their conservation needs.

ACKNOWLEDGMENTS

This study was possible thanks to the collaboration and assistance of the following persons and institutions: A. Taber, S. Walker, F. Arengo, E. Delgado, B. Mena, C. Tineo, Y. Muñoz, J. Sánchez, E. Pannier, A. Fernández Badillo, E. Fernández Badillo, M. Aguilera, L. Suárez, E. Ochoa, M. Ochoa, J. Manzanilla, M. Bevilacqua, F. Bisbal, T. Oliveira, R. Durán, E. Orellana, A. Trócolis, Instituto Nacional de Parques (INPARQUES), and Dirección General del Ministerio del Ambiente y de los Recursos Naturales Renovables. Financial aid for various portions of the study was provided by the Wildlife Conservation Society, Bat Conservation International, O'Farrell Biological Consulting, the Facultad de Agronomía de la Universidad Central de Venezuela, and the Asociación Venezolana para la Conservación de Areas Naturales. C. M. Miller, R. E. Sherwin, J. Salazar-Bravo, and W. Bogdanowicz commented on an earlier draft of the manuscript.

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Received 16 September 1999, accepted 30 November 2000