A COMPARISON OF ACOUSTIC VERSUS CAPTURE TECHNIQUES FOR THE INVENTORY OF BATS

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To evaluate the efficacy of the Anabat II ultrasonic detector and analysis system for use as a tool for conducting inventories, we compared results of acoustic versus capture techniques in the southwestern United States. We sampled 57 locations using standard methods (mist nets and double-frame harp traps) and simultaneously with an ultrasonic detector (Anabat II). Assuming total number of species obtained by both methods equaled a complete inventory, captures accounted for 63.5% and acoustic sampling 86.9% of the combined species present. Acoustic sampling was capable of sampling bats that routinely flew outside the sampling capabilities of nets and traps. We found no statistical difference between capture and acoustic sampling with respect to species that use low-intensity echolocation. Acoustic sampling of bat communities is a powerful tool but should be used with various capture techniques to perform the most accurate inventory.

Key words: Chiroptera, bats, acoustic monitoring, Anabat, technique comparison, capture methods, community inventory, echolocation

Much of our knowledge of the biology of bats, away from roost sites, has been obtained from animals captured in nets and traps. Often, verification of presence of a species of bat was primarily by capture at roosts, water holes, or along foraging flyways (Kunz and Kurta, 1988), but more recently, biologists have used monitoring of echolocation calls (Bell, 1980; Crome and Richards, 1988; Fenton, 1982; Kalko, 1995; O'Farrell, 1997). However, not all species and not all individuals of a species are equally susceptible to either form of detection, primarily due to differential use of space and variable intensity of vocalizations among species. To compound the sampling problem, bat activity at a site can vary dramatically from 1 night to the next (Hayes, 1997), and a given location may not be used every night by the same assemblage of species. However, each technique has inherent, potentially serious biases (Kunz and Kurta, 1988; Thomas and LaVal, 1988). Under all but the most restrictive conditions, nets and traps sample an extremely small area relative to that used by free-flying bats. Alert bats, particularly those actively foraging, appear to detect and avoid such devices. Such devices actually sample a small proportion of the chiropteran fauna, and some species are missed completely because their normal flight activities are outside the sampling range of the equipment. Acoustic detectors permit sampling a larger area than traps or nets but may not sample adequately species that use low-intensity vocalizations.

Instruments sensitive to frequencies of sounds used by echolocating bats (bat detectors) allow investigators to hear or visualize these ultrasonic calls (Fenton, 1988). Many species of bats produce echolocation calls that appear distinctive (Simmons et al., 1979). Some insectivorous bats in the western United States have been characterized by the frequency-time structure of their search and feeding calls, providing a basis for recognition of species for free-flying individuals (Bell, 1980; Fenton and Bell, 1979, 1981; O'Farrell, 1997). A similar attempt provided an acoustic guide to the identification of bats of Europe (Ahlén, 1990).

Intuitively, assuming the capability to identify species by call, acoustic monitoring generally should yield a more complete inventory of bat species than captures alone. In Europe, ultrasonic detectors were used to establish presence and in some cases identification of species, but no effort was made to verify acoustic determinations of species by capture (Kapteyn, 1991). Only one previous study compared mist nets and ultrasonic detectors for monitoring activity of bats (Kunz and Brock, 1975). The acoustic system that they used was incapable of discriminating species but provided data on presence of bats. They concluded that nets and the ultrasonic detector yielded similar results with respect to activity. A recent comparison of harp traps and acoustic sampling (Mills et al., 1996) concluded that certain species not susceptible to trapping were detected acoustically but that not all species were identifiable.

Our purpose was to compare species richness of bats obtained by captures versus monitoring of echolocation calls. We predicted that more species would be documented using acoustic rather than capture methods. We further predicted that bats using high-intensity calls would be more conspicuous to bat detectors, whereas those using low-intensity calls would be detected more commonly by capture.

Materials and Methods

We used both acoustic and standard sampling (mist nets and harp traps) to survey 57 locations in Arizona, California, Nevada, New Mexico, and Utah (O'Farrell et al., 1999), incorporating the range of elevations and associated habitats representative of the region. Some sites were examined multiple times for 73 distinct nights of sampling. Because faunal composition changes temporally (Hayes, 1997), each night of sampling was considered an independent event. Sites sampled multiple times were visited in different seasons or years.

Acoustic sampling was performed using an Anabat II bat detector (Titley Electronics, Ballina, New South Wales, Australia), linked to either an IBM-compatible laptop computer or a cassette recorder (CTR−76, Tandy Corporation, Fort Worth, TX). Tanks, troughs, waterways, and flyways were sampled using mist nets or a combination of mist nets and double-frame harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia). Type and quantity of collecting devices were influenced directly by the physical characteristics of each location. Up to 10 nets (>280 m^2 of collecting surface) and two harp traps (9 m^2 of collecting surface) were deployed. Capture and acoustic sampling were conducted simultaneously, usually until midnight and in some cases all night.

Although we tried to be consistent, constant monitoring of the detector was not always possible, especially in times of intense activity of bats when we had to tend nets. Monitoring the screen of the computer was important in observing and selecting high-quality sequences of calls (O'Farrell et al., 1999). Generally, the detector was placed at a central location. When constant monitoring was not possible, the detector was propped at a 45° angle and, whenever time allowed, the screen of the computer was examined for vocal sequences and appropriate series were saved.

We identified species acoustically by comparing calls with an ever-expanding library of vocalizations. The reference library contained calls of known species, obtained by a variety of methods (O'Farrell et al., 1999), including visual recognition by spotlighting a free-flying bat, capture of a vocalizing individual, recording at roosts of known species, and hand-release of individuals with or without chemiluminescent tags. We examined all calls obtained during monitoring and used only those sequences that contained a frequency range and structural characteristics known to be diagnostic for a species (O'Farrell et al., 1999). If there were doubt or overlap with other species, these sequences were disregarded.

For several less common species, we initially used reference calls obtained from other sources. Calls from *Eumops perotis* were obtained from individuals exiting and foraging near a roost in California (C. Corben, pers. comm.). Calls of *Euderma maculatum* were obtained from a locality where a large population of the species is known to occur (Poché, 1975). We recorded calls from free-flying individuals that emitted

TABLE 1.—*Summary of the occurrence of species determined by capture and acoustic methods at 57 sites in the southwestern United States.*

Species[a]	Both methods[b]	Capture[c]	Acoustic[d]
Antrozous pallidus	30	3	10
Corynorhinus[e] *townsendii*	1	10	0
Eptesicus fuscus	23	3	18
Euderma maculatum	0	0	2
Eumops perotis	0	0	5
Idionycteris phyllotis	2	0	4
Lasionycteris noctivagans	12	3	14
Lasiurus blossevillii	0	0	1
Lasiurus cinereus	12	5	6
Myotis auriculus	5	1	0
Myotis californicus	20	1	10
Myotis ciliolabrum	13	4	4
Myotis evotis	2	3	0
Myotis occultus[f]	6	1	2
Myotis thysanodes	10	3	3
Myotis volans	14	7	4
Myotis yumanensis	9	1	11
Nyctinomops macrotis	1	2	7
Pipistrellus hesperus	17	1	14
Tadarida brasiliensis	13	0	21
Total	188	48	136

[a] Nomenclature follows Jones et al. (1992).
[b] Number of sampling events that a species was verified by both techniques simultaneously.
[c] Capture indicates the number of sampling events that a species was verified only by capture.
[d] Acoustic indicates the number of sampling events that a species was verified only by acoustic means.
[e] *Plecotus* (Frost and Timm, 1992; Tumlison and Douglas, 1992).
[f] *Myotis lucifugus occultus* (Hoffmeister, 1986).

characteristically human-audible calls; those calls consistently fit those described for *E. maculatum* in Canada (Leonard and Fenton, 1984). Finally, we identified calls from *Nyctinomops macrotis* by visually comparing our recordings with those from Simmons et al. (1978) and, later, from known free-flying bats.

Although we did not establish the maximum distance at which each species was detected, we estimated the greatest distance at which some bats could be detected by the Anabat detector under conditions in this study. Estimates of linear distance were conservative, based on pacing from the position of the detector to a reference point adjacent to the bat, but no allowance was made for height above the ground. The best acoustic information came from monitoring bats active during twilight conditions.

To evaluate efficiency of the two techniques, we compared number of times a species was detected by capture only, acoustic only, and both methods simultaneously. That allowed a qualitative examination of susceptibility to each method by species. A second comparison was made of the number of species detected at each locality by capture and acoustic sampling separately using a Mann-Whitney *U*-test (Zar, 1984). To examine efficacy of acoustic sampling for bats that use low-intensity calls, we used the log-likelihood test with frequencies of captures as expected values. We tested the null hypothesis that there was no difference between capture and acoustic methods for bats using low-intensity calls.

RESULTS

We captured and recorded 20 species of bats at 57 locations (Table 1). We recognized that both techniques likely missed species that were capable of avoiding the respective device or that flew outside the area sampled by these devices. However, for comparison, we assumed that, at a given locality, the total number of species detected by both methods represented a complete inventory. Based on that assumption, captures accounted for 63.5% and acoustic sampling 86.9% of the combined species present.

A greater number of species were detected by acoustic means than by capture for all sites combined. The number of species detected was greater for acoustic sampling than captures ($U = 6053$, $P < 0.01$), thereby rejecting the null hypothesis of equality between methods. Of the 73 sampling events, 39 had more species detected acoustically, 15 had more by capture, and 19 had the same number by each method. Although acoustic surveys accounted for more species than those conducted by capture, the combination of methods was more successful in detecting bat species than either method alone.

The differential response to capture and acoustic methods by each species (Table 1) provided insight into the limitations of each technique. Four species (*Corynorhinus townsendii, Myotis auriculus, M. evotis*, and *M. volans*) were detected by capture more times than acoustically. *M. auriculus, M. evotis*, and *M. thysanodes* tended to emit low-intensity calls and, based on our observations, were detected only at distances <15 m. However, *M. volans* used louder calls and could be detected at distances >15 m. We found that *C. townsendii*, outside roosts and in hand-released situations (O'Farrell et al., 1999), produced low-intensity calls that could be detected only at distances <5 m. However, with the current low sample size, no significant difference was found in frequency of detection between capture or acoustic sampling among the four species that used low-intensity calls (2-by-4 contingency table, $G = 6.62$, $P > 0.05$). Fourteen species (Table 1) were detected acoustically more times than by capture. Those species emitted high-intensity calls and, based on our observations, could be detected at distances >30 m. Most of those species also tended to fly high, avoiding capture.

Discussion

A limited number of studies have been conducted using calls to assess feeding behavior (Barclay, 1982, 1988; Fenton, 1982; Fenton and Bell, 1979). The relation between design of calls and foraging behavior has been used in an ecomorphological examination of communities of bats (Aldridge and Rautenbach, 1987; Brigham et al., 1997; Saunders and Barclay, 1992). General use of habitat and faunal assemblages also have been examined with the aid of ultrasonic detectors (Bell, 1980; Crome and Richards, 1988; Fenton et al., 1977, 1983; Kalko, 1995; O'Farrell, 1997). These studies suggest that monitoring calls of echolocating bats can be a valuable tool for defining structure of local faunas of bats and describing use of various habitats.

As we predicted, significantly more species were detected using acoustic sampling than capture. These results are even more striking, given that the detector usually was placed in a central location, and in many instances, acoustic monitoring was intermittent so that large numbers of bats could be removed from nets. Failure to detect certain loud species (e.g., *Nyctinomops macrotis, Lasiurus cinereus*, and *Eptesicus fuscus*; Table 1) during all sampling events probably reflected our inability to monitor equipment constantly, as these and other species using high-intensity calls are detected easily. Of the 20 species examined in our study, only four were documented more frequently by capture than by acoustic methods (Table 1). Two of them (*M. auriculus* and *M. evotis*) are known to glean or at least forage in vegetative clutter and emit calls of low intensity that attenuate rapidly (Faure and Barclay, 1994; Fenton and Bell, 1979). Similarly, our ability to detect *C. townsendii* acoustically was limited by distance. These three species and *M. thysanodes* forage in clutter (Black, 1974), where low-intensity calls are adaptive. *M. volans*, however, forages in open areas (Black, 1974) and uses loud calls that we detected at distances >15 m. We found that placing acoustic equipment in flyways or periodically moving into different microhabitats enhanced detection of quiet bats. Uninterrupted monitoring of equipment aided in detecting presence of *M. volans*.

Importance of acoustic sampling for achieving a more complete inventory of species was demonstrated clearly by Kalko et al. (1996) for bats on Barro Colorado Island. After decades of intense sampling by capture, five additional species (7.5% increase) were detected using acoustic methods. All five taxa were species that roost in inaccessible areas and tend to fly or forage at great heights. In the United States, bats that have similar roosting and foraging behavior (e.g., *Lasionycteris noctivagans*, *L. cinereus*, *T. brasiliensis*, *N. macrotis*, and *E. perotis*) are represented poorly in collections (Table 1). Standard capture methods cannot sample at high altitudes at locations in the open or above tree canopies.

It is clear that acoustic sampling can be a powerful tool for performing inventories. However, no single method provides a complete inventory. Although we detected significantly more species acoustically than by capture, a combination of methods provided a more complete inventory. Capture is critical to collecting such information as sex ratio, reproduction, and parasite load. Each sampling technique has inherent biases that must be considered for the specific habitat and faunal assemblage being examined. Mist nets and harp traps are differentially effective and must be deployed in as many microhabitats as possible (Kunz and Kurta, 1988). In the Neotropics, mist netting has been particularly effective for leaf-nosed bats (Phyllostomidae), but traps are more effective for other families (LaVal and Fitch, 1977; Tuttle, 1976). In Malaysia, mist nets were most effective for large bats, particularly Megachiroptera, and harp traps collected significantly more small bats of other families (Francis, 1989). Francis (1989) used harp traps of two different designs, with two or four panels of wires. Significantly more bats were captured in traps with four panels of wires, but some individuals flew through both types of traps.

As part of designing a protocol to survey forested regions of Australia, Mills et al. (1996) compared results from harp traps and tape recordings made in conjunction with Anabat detectors. Recordings were not taken at each trap site but as observers walked transects along forest trails between sites where traps were stationed. A third party analyzed tape recordings at a later time. They trapped 13 species, identified five by call, and an additional six aggregates that could not be separated to species because the sequences of calls were too fragmentary. However, they documented two species and six aggregates acoustically that were not captured.

A comparison between our study and that of Mills et al. (1996) cannot be made completely. Although not all calls or sequences could be identified in either study, the majority of our recorded calls were identifiable due to primary use of a laptop computer, as opposed to a tape recorder, and we did not involve a third party who had no first-hand knowledge of field and recording conditions. Ability to identify species with the Anabat system is enhanced by use of a laptop computer, knowledge of conditions during collection of data, and experience in the field (O'Farrell et al., 1999).

Our results show that acoustic sampling is significantly more productive than standard collecting techniques but that the concomitant use of capture methods provides a more complete inventory. This does not mean that anyone with minimal training can employ either method (O'Farrell et al., 1999) and produce an accurate inventory. If habitat is not properly sampled, quality recordings are not obtained and an experienced person is not available to evaluate recordings, the survey will be inadequate and potentially misleading.

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