Chapter 7

Observational Techniques for Bats

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Introduction

The principal objective of surveying and censusing bats using observational methods is to determine community composition, species richness, and abundance. The methods selected and the kinds of information obtained will vary with the size and mobility of the animals being investigated, observer access to the animals, the available instruments for extending the sensory ability of the observer, and the number of animals present. Before beginning a survey, an investigator should have some knowledge of roosting habits, nightly foraging activities, seasonal movements, and effects of environmental factors—such as local topography, temperature, humidity, light intensity, and habitat structure—on abundance patterns. Knowledge of historical and temporal-spatial patterns associated with a particular species or population may also be important. Observers should be thoroughly familiar with the operation of binoculars, night-vision scopes, video cameras, ultrasonic detectors, or other instruments used to extend their sensory capabilities and should understand their detection limits. Because roost sites of some bat species are relatively easy to locate and often house large aggregations of individuals, they offer considerable potential for assessing population characteristics. Consequently, most efforts to estimate relative or absolute numbers of bats have focused on captures or observations made at or near roosts (e.g., Barclay and Bell 1988; Thomas and LaVal 1988).
Roosting bats

Generally, four observational methods can be used to survey bats in roost situations: direct roost counts, disturbance counts, nightly dispersal counts, and nightly emergence counts. Access to some roost sites may require specialized equipment, knowledge, and skills. Some roost sites may pose safety risks to the observers. The location of some roosts may severely restrict opportunities for observing bats, because of factors such as foliage density or height above the ground or because the roost site may be physically inaccessible (e.g., caves and mines with openings too small for human ingress and egress). To conduct surveys and censuses of bats that occupy caves and mines may require climbing experience, including rope work. A novice should not enter a complex cave or mine unless accompanied by an experienced caver. In situations in which direct access to the interior of a cave or building roost is limited, nightly emergence, dispersal, and disturbance counts offer the best alternatives for estimating colony size.

Estimates of absolute numbers present at roost sites are seldom feasible except for some relatively small, gregarious species. For other species, indices of abundance may be the only type of data that can be obtained. For some gregarious microchiropterans whose roosts are not accessible to observers, nightly emergence counts provide the most reliable estimates of colony size. For some large, gregarious pieropodids, estimates can be obtained by making roost counts, dispersal counts, or disturbance counts.

Direct Roost Counts

RESEARCH DESIGN

Direct roost counts are carried out by groups of observers stationed at designated positions relative to a colony or survey area. Observers should be positioned to ensure unobstructed views of the roosting bats (Wiles 1987), which are then enumerated directly, with or without the aid of binoculars or spotting scopes. Observers are assigned areas and count only those bats in the designated area. The reliability of the estimate depends on the experience of the observers and the visibility of the bats. Photography, videography, and radar can be used to augment direct observations of some species.

The most consistent and reliable counts of large, tree-roosting megachiropterans are made soon after sunrise and during the late afternoon, when wind velocity is low and cloud cover is minimal (Wiles et al. 1989). Under such conditions it may be possible to count the bats in a colony from distances up to 1,000 m from the roost (Wiles et al. 1989). The reliability of a roost count generally decreases with increasing numbers of bats, the inaccessibility of the roost to observers, and the extent to which direct observations are limited by dense foliage (Wiles 1987). In addition, only some individuals of a population may aggregate and be observed.

DATA ANALYSIS

Total numbers of roosting bats are obtained by summing the individual counts made by each observer. The density of bats is determined by dividing the total count by the area surveyed. Population estimates of species that form large aggregations can sometimes be made if all known sites are censused on the same day (Martin 1987). Richards (1990) used a network of interested individuals in Australia, who reported the presence or absence of Pteropus at traditional roosts each month by telephone. He was able to survey a study area that exceeded 250,000 km² rapidly and frequently. Although this approach may not yield reliable colony counts, it can target areas that warrant further investigation by qualified individuals. When trained observers are available, the total number of bats present can be estimated by counting the number of bats roosting in “average” trees and then extrapolating this number to the number of
trees occupied by bats in a given region. Alternatively, the number of bats present can be estimated by counting bats in "patches" or groups and then multiplying the average of these values by the number of patches in each roost tree. These two approaches were used to estimate populations of Eidolon helvum. Although estimates differed by as much as 33%, the trends were in general agreement (Mutere 1980; Barama and Kiregyera 1982).

Bats can be completely censused only in well-defined geographic areas, such as small oceanic islands, or at roost sites. Boats have been used to locate and count the number of trees occupied by pteropodids roosting on small islands (Tidemann 1985; Wiles et al. 1989), although direct visual counts of individual bats may not be possible. Counts of bats occupying dense foliage may underestimate actual numbers by as much as 20% (Wiles 1987).

Populations of some gregarious species may be difficult to assess if their roost sites extend over large areas, and species that roost singly or in small groups often cannot be surveyed or censused effectively. It is not uncommon to find large colonies of pteropodids spread over areas more than 1 km long, especially along water courses. Large colonies of Pteropus spp. in eastern Australia can exceed 100,000 individuals and cover areas up to 5 km long and 50 m wide (Nelson 1965b). Counts made at single locations are likely to underestimate total colony size unless observers can account for colony members that roost at alternate sites (Martin 1987; Wiles et al. 1989, 1991). For example, Tidemann (1985, 1987) found that only about half the population of Pteropus melanotus on Christmas Island actually formed colonies; other individuals were widely dispersed.

Disturbance Counts at Roosts

For disturbance counts at roost sites, bats are stimulated to take flight during the day and are counted as they become airborne (Racey 1979). Disturbance counts can be used when roosting megachiropterans are difficult to observe because of dense foliage or other visual obstructions.

At least two observers are required for disturbance counts. One person enters the roost area and makes loud noises, and the other individual counts bats. Often several "beaters" operating in unison are needed to encourage bats to take flight, although such efforts are only successful over a limited area. Sharp metallic sounds, such as those made by hitting metal pipes or tent pegs together, will cause some species of pteropodids to take flight (C. R. Tidemann, unpubl. data). The vocalizations of animals in very large roosting aggregations may mask the sounds made by investigators, however, making it difficult to use this method effectively. Shouting usually does not induce pteropodids to take flight (Racey 1979), although the noise from a discharged shotgun may do so (Ratcliffe 1931).

Once bats become airborne, they may be counted directly or photographed with a camera fitted with a wide-angle lens. Colony size can be estimated by projecting 35 mm transparencies on a screen and counting the number of bats, with corrections for overlapping topographic features. The success of a disturbance count depends on the sensitivity of bats to disturbance, the skill of the individuals causing the disturbance, and the position of the photographer relative to the flying bats. Obviously, this method will underestimate the number of bats present if some fail to fly (e.g., flightless young) or if others become disturbed prematurely. Videography has considerable potential for estimating colony size, if all bats take flight following disturbance, because the images of bats can be downloaded into a computer and the particles (= bats) counted frame by frame in the laboratory (G. C. Richards, unpubl. data).

Nightly Dispersal Counts

This technique involves counting bats as they disperse nightly from diurnal roost sites. Such
counts are most effective if flying bats are silhouetted against the sky or open ocean and if there are several observers occupying different vantage points (Parry-Jones and Augee 1992). Observers should be at their stations at least one hour before nightfall and should count only those bats that depart within a preassigned arc surrounding the roost. Although decreasing light levels at the time of nightly dispersal may reduce visibility, use of light-gathering binoculars can facilitate counting (Racey 1979; Nicoll and Racey 1981).

Radar can also be used to census night-dispersing pteropods (e.g., Tidemann 1985; Parry-Jones and Martin 1987; G. C. Richards, unpubl. data). An important advantage of radar over direct visual observation is that it can be used equally well both day and night. In addition, individual animals can be detected at distances up to 4 km (groups at much greater distances), a 360° area can be scanned at one time, and the data can be stored on video for later analysis (C. R. Tidemann, unpubl. data). In areas where the view of dispersing bats is uninterrupted, radar can be used to determine dispersal directions. The relatively low portability of the equipment and the relatively high acquisition and operational costs, however, are important disadvantages of radar.

Dispersal counts, like direct roost counts and disturbance counts, provide minimum estimates, because flightless young may remain in the roost when their mothers depart or cling to them when they fly off (Wiles et al. 1989). Bats should be counted only once during a dispersal flight, but many individuals circle the roost area before dispersing.

Roost Counts at Maternity Colonies

Many species of Microchiroptera form large roosting aggregations in caves, mines, buildings, and similar structures, sometimes numbering several million individuals. Because most species are highly susceptible to disturbance during the maternity period, efforts to estimate numbers of bats should be designed to minimize disturbance. This can best be accomplished by making infrequent visits to a colony after adults have departed and before they return from feeding.

Even in the most carefully designed study, it may not be possible to account for all bats present. For example, as the size and complexity of the roost site increase, the probability that all bats will be observed and counted directly decreases. Some species may roost in multiple layers, especially where the roost substrate is irregular (Tuttle 1975). Before undertaking a roost census, investigators should assemble background information on the roosting habits of the target species. Such information should include likely reproductive condition and physiological state of the roosting individuals, times of nightly emergence and return, effects of temperature and precipitation on roosting behavior, and nightly foraging behavior. This knowledge can be used to design a sampling protocol that will reduce disturbance to the bats and minimize sample bias.

For many species, an investigator will need to use a combination of observational and capture methods to obtain an accurate estimate of colony size and composition. An observer can sometimes estimate the number of lactating females present at maternity roosts by counting non-volant pups in the roost following the nightly departure of adults. During the maternity period, it may be possible to use pup counts and the ratio of lactating bats to pregnant bats or to postlactating bats captured in traps or nets at the cave entrance to estimate the number of females present at a given maternity roost (Tuttle 1975, 1979). Using this method, the number of lactating females should equal the number of young present divided by litter size.

Some bat species leave stains from skin oils and urine on the ceilings and walls of caves and mines where they have roosted for many years,
and sometimes one can derive population estimates using this information. Tuttle (1979) estimated the density of *Myotis grisescens* per unit of roost surface and multiplied this value times the ceiling area that was covered by stains to estimate colony size. Colony size also may be estimated by measuring the area on the floor of a cave covered by fresh guano deposits, and multiplying this area by the cluster density of roosting bats (Tuttle 1979; Thomas and LaVal 1988). Estimating cluster density and spatial coverage of bats in maternity roosts can be highly disruptive, however, because of the sensitivity of bats to disturbance during this period (Tuttle 1976a, 1979; Kingsley et al. 1991).

**Nightly Emergence Counts**

Nightly emergence counts made as bats depart from traditional day roosts in caves, mines, tree cavities, and buildings can be one of the most effective ways to estimate the number of bats that roost in inaccessible places or in mines and caves that are unsafe to enter, or that are disturbed by entry of observers into the roosting site. Ideally, such counts should be made repeatedly over several weeks to establish intracolony variation in the number of bats present. Nightly emergence counts are nondisruptive, and they can provide important baseline data for comparing results from different sampling methods (e.g., number of bats captured in the roost vs. emergence counts).

Nightly emergence counts are most effective when departing bats are silhouetted against a clear sky (Kunz and Anthony in press). As with nightly dispersal counts, decreasing light levels at the time of emergence can reduce bat visibility and lead to biased estimates. Use of light-gathering binoculars or night-vision goggles may improve visibility of bats in some situations.

The number of observers required to conduct nightly emergence counts will depend on the size and configuration of the roost site and the number of openings used by the departing bats. Observers should be assigned specific exits or fields of view and should be present at their stations before the onset of nightly emergence to ensure that the earliest departing bats are counted. It is important to avoid counting bats more than once, especially if bats reenter a roost during the emergence period. The number of reentering bats should be subtracted from the total number of departing ones to derive the actual count. As with direct roost counts, nightly emergence counts may underestimate the number of bats present, especially if flightless young are left in the roost when their mothers depart.

Still photography, cinematography, videography, and electronic or mechanical counting devices can be used to count emerging bats (e.g., Daan 1973; Altenbach et al. 1979; Mitchell-Jones 1987; Rodriguez-Duran and Lewis 1987; Thomas and LaVal 1988; Speakman et al. 1992). Such devices allow bats to be censused in the absence of an observer and can provide multiple records over extended periods. Before using such devices, it is important to validate the signals (mechanical or electronic) with visual counts. An advantage of “remote” devices is that recordings of emerging bats can be “viewed” and analyzed independently by different observers. In order to obtain consistent results, however, electronic devices must be maintained in excellent working order, and the power supply must be reliable.

It may not be possible to make reliable visual counts of emerging bats at roosts of exceptionally large aggregations. In these situations, sequentially timed still photographs of emerging bats may provide important data (e.g., Humphrey 1971; Rodriguez-Duran and Lewis 1987). Emerging bats can sometimes be photographed at fixed intervals against an open sky or a white backdrop placed near the cave or mine entrance. Colony size can be estimated by counting the number of bats per photograph and integrating these counts with estimates of flight speed and
the duration of the emergence period. This method assumes that the number of bats in each photograph is independent of the time the photograph was taken. The photographs are treated as stratified random samples of the bat column, from which the colony size can be estimated. This method is used most effectively at roost sites occupied by single species.

Counts of Foliage- and Cavity-Roosting Bats

Censusing foliage-roosting micro- and megachiropterans poses special challenges to the observer, especially if the bats are rare, solitary, or widely dispersed. Methods are usually labor intensive and limited to searching for roosting animals at potential roosting sites or observing their activities at feeding or night roosts. Knowledge of general roosting habits can facilitate the location of bats once the observer has formed a search image based on roost characteristics. Tent-making bats (e.g., Timm 1987; Kunz et al. 1994) and other foliage-roosting species (Constantine 1966; Findley and Wilson 1974; Brosset 1976) often can be found in this manner.

Finding small bats roosting in tree hollows, tents, natural crevices, and foliage involves location and systematic observation of all possible roost sites in a designated area. Because bats are often cryptic, however, other methods may be more fruitful. For example, individuals or groups of foliage-roosting and crevice-dwelling bats can often be located by attaching radio transmitters to individuals captured in foraging or commuting areas and then following those individuals to their roosts. This approach has been used successfully to locate bats that roost in unmodified foliage (Thomas and Fenton 1978; Morrison 1980; Barclay 1989; Spencer and Fleming 1989), in leaf tents (Charles-Dominique 1993), in tree hollows (e.g., Fenton et al. 1985; Luney et al. 1985; Fenton and Rautenbach 1986; Tidemann and Flavel 1987; Kurta et al. 1993), and beneath exfoliating bark (Kurta et al. 1993).

Counts of Hibernating Bats

Ideally, hibernating bats should be counted in midwinter, when the population is at its peak. Human safety considerations and the size and complexity of the hibernaculum will often dictate the number of personnel needed to conduct such a census. To minimize disturbance to hibernating bats, normally no more than two or three observers should participate in a winter census, and each site should be censused no more than once per winter. If bat populations are threatened or endangered, the census should be conducted only every two years.

Because many hibernating bats roost in large, tightly packed clusters, counting all individuals may be difficult or impractical. Instead, population size can be estimated by determining the cluster densities at selected sites and extrapolating those to the total area of the cave covered by the hibernating bats. Because cluster density can vary with species, season, and characteristics of the roost substrate (e.g., Tuttle 1975), estimates of average cluster density should be based on several different clusters at a given site. In addition, because cluster density may show considerable intercave variation, samples should be taken from several different clusters and hibernacula before extrapolating to entire species (Thomas and LaVal 1988).

Survey personnel can estimate cluster density by placing a frame of known dimensions over a cluster and counting each bat within the frame (LaVal and LaVal 1980) or by photographing the frame and cluster and then counting the bats from the photograph. In this way the total ceiling or wall area covered by bats may be estimated from photographs. The geometric properties of clustered bats, however, may introduce sources of error when estimating the total area covered. If the scale of photographs is not known precisely, the camera-to-cluster distance can only
be approximated. The walls and ceilings of hibernacula are often uneven, and a projection of hibernating bats onto a flat plane will have a smaller surface area than the actual colony. If the film plane is not parallel to the colony, the projected surface will be smaller than the actual surface. Stereophotography overcomes these limitations and makes it possible to determine the camera-colony distance and the actual surface of the bat cluster, independent of the irregularities of the cave substrate and the angle from which the photograph was taken (Palmeirim and Rodrigues 1989).

Observers who census hibernating bats should be alert to potential adverse effects of their presence on the bats, because frequent winter arousals can significantly reduce critical fat reserves and, thus, survival (Tuttle 1979; Speakman et al. 1992). Intense or heat-generating light sources (e.g., floodlights, carbide and kerosene lanterns) should be avoided. Roost temperatures and other environmental variables (e.g., light, wind velocity, humidity) should be recorded at the time census data are taken, but prolonged exploration and extensive mapping should be minimized during the hibernation period. Extensive roost mapping should be carried out during the summer when bats are absent from the cave.

Night-vision devices, low-light-level videography, motion detectors, and ultrasonic detectors may aid an observer when assessing the relative numbers of flying bats. Even with such devices, however, it is not always possible to distinguish among different species or to obtain accurate counts. Ultrasonic bat detectors may be valuable for assessing species composition in some habitats, but they cannot be used to determine the numbers of bats present, because they do not distinguish echolocation calls made by one bat from those made by several individuals. Moreover, bat detectors do not detect megachirop- terans and some microchiropterans (e.g., most phyllostomids). Although large megachirop- terans may be observed flying during daylight or twilight hours, dense foliage and irregular topography often limit the ability of observers to assess numbers of bats reliably.

Counts with Motion Detectors

Indirect (remote) census methods minimize disturbance to sensitive colonies and allow for regular and frequent assessment of bat activity with minimum expenditure of time. Such approaches may be used to assess either seasonal or nightly changes in relative numbers of bats. Infrared motion detectors can be used to monitor both winter and summer roosts inside caves and other similar structures (Pierson et al. 1991).

As bats fly through the field of detection, individuals are recorded as a “pass.” Infrared detectors do not distinguish among individuals or species, but they are useful for monitoring roost sites occupied by single species. When motion detectors are used, the motion counts must always be validated with direct observation using night-vision devices.

Ultrasonic Bat Detection

Ultrasonic bat detectors can sometimes be used to identify species of microchiropterans and to
estimate their relative abundances in areas where they commute or forage (e.g., Crome and Richards 1988; Richards 1989; Ahlen 1990; Rydell 1990). A few species have distinctive echolocation calls and are relatively easy to identify; other species are more difficult to identify (Ahlen 1990). Learning to distinguish the echolocation calls of different bat species based on species-specific features such as frequency composition, changes in frequency with time, and duration of pulse repetition rate requires considerable practice, good acoustic memory, and much patience (e.g., Fenton et al. 1983; Miller and Andersen 1983; Pye 1983; Crome and Richards 1988; Richards 1989; Ahlen 1990; Rydell 1990).

When echolocating bats navigate on the wing and search for prey, many emit “cruising” pulses at repetition rates of approximately 2 to 10 pulses per second. Most of the calls are highly structured signals with frequencies that range from 20 kHz to 200 kHz (Pye 1983; Fenton 1988; Ahlen 1990). Calls of some species are frequency modulated and dominated by sweeps from high to low frequencies over a span ranging from 2 to 15 msec. Calls of other species are dominated by a constant-frequency component in which most of the signal remains steady at a fixed frequency, usually for more than 10 msec. When an echolocating bat detects a potential prey item, it typically increases its repetition rate to about 100 pulses per second as it closes in for capture, terminating in what is commonly called a “feeding buzz.” Some species of bats, notably those that glean arthropod prey from surfaces, may not emit a detectable feeding buzz (Fenton and Bell 1979), and species that produce low-intensity calls cannot be detected with most bat detectors.

**INSTRUMENTATION AND RESEARCH DESIGN**

Several types of bat detectors are available, and the reader should consult the literature (Downes 1982; Fenton 1988; Ahlen 1990) for details. Bat detectors can have one or more types of sound-detecting systems to convert ultrasounds into audible sounds: heterodyning, frequency division, and time expansion with digital memory. A heterodyning system has the highest signal-to-noise ratio and potentially the greatest sensitivity of the three detection systems. It is the only system present in the least expensive, and less sensitive, detectors (e.g., Ultra Sound Advice Mini-2, Pettersson Electronik D-100, and Flan and Skye), but it is also included in more expensive models (Ultra Sound Advice S-25 and Pettersson D-940 and D-980). Inexpensive heterodyne detectors can be tuned manually to monitor a selected 10-kHz frequency range. The Pettersson D-940 and D-980 are unique in having a heterodyne system that continuously scans a user-defined frequency range and locks in a digital frequency display when a signal that exceeds an adjustable threshold is detected. Tape recordings of the audio output from either tunable or scanning heterodyne detectors can serve as event recorders, but they do not retain frequency or other information from the original sound.

In contrast to the narrow band and high sensitivity provided by heterodyning systems, frequency division systems offer lower sensitivity but broad band detection. The frequency of incoming signals is divided 10 to 20 times (into the audible range). Some bat detectors (Pettersson D-940 and D-980), retain the amplitude structure of the original call, but in all systems harmonics are lost. Tape recordings of stepped-down calls do permit analysis of time-frequency structure for use in subsequent species identification (Thomas and West 1989). Some detectors (Westec and Titley Anabat II) only have frequency division modes, whereas others (Ultra Sound Advice S-25 and Pettersson D-940 and D-980) have both frequency division and heterodyne features.

Bat detectors with time-expansion systems digitally sample the incoming high-frequency sounds (250–300 kHz) at a high sampling rate
for a few seconds and then play back the stored sample slowed down 10 to 20 times, making it possible for the observer to hear and record the call (Ahlen 1990). Harmonics are retained when the signal is slowed, and resolutions comparable to those obtained with large, expensive tape recorders can be achieved, while permitting field signal storage on a moderately priced cassette recorder (Fenton 1988; Ahlen 1990). The principal disadvantages of time-expansion systems are their decreased sensitivity to weak signals that can be detected by heterodyne detectors of comparable quality and their discontinuous signal (3 sec of capture followed by 30 sec of output). Time-expanded analog signals are easily analyzed with audio frequency hardware and software used for studies of bird song or human speech.

SPECIAL CONSIDERATIONS

It is important that researchers using bat detectors to conduct field surveys validate the sounds produced by each species. Investigators should capture and record representative individuals in the field and establish a reference library of unique frequencies that can be consulted when calls are being analyzed (e.g., Ahlen 1980, 1981, 1990; Fenton and Bell 1981; Woodside and Taylor 1985; Thomas et al. 1987; Thomas 1988). Cruising echolocation calls of most genera and many (but by no means all!) species in a given bat community differ in frequency span, duration, or shape. Once call characteristics are identified, it may be possible to determine activity levels of certain species within or between habitats. Ultrasonic bat detectors have also been used with varied success to determine the presence and relative abundances of bats in several different communities, including those in savanna woodlands in Africa (Aldridge and Rautenbach 1987), tropical wet forests in Australia (Crome and Richards 1988; Richards 1989), old-growth forests in the Pacific Northwest of the United States (Thomas 1988; Thomas and West 1989), rural areas in northern Europe (Limpens et al. 1989; Rydell 1990), and agricultural areas and forest reserves in eastern Europe (Gaisler and Kolibac 1992).

Bat detectors should be positioned at specific locations for both survey and census work, because station counts are more effective than transects at detecting rare taxa (Edwards et al. 1981; Crome and Richards 1988; Thomas 1988; Thomas and West 1989). Use of several detectors at or near ground level and suspended in foliage is appropriate for most survey work. Placement will be dictated by the height and density of the foliage. Bat detectors will be needed for each stratum in highly stratified forest. Fewer detectors are needed to cover the same area in desert regions.

LIMITATIONS

Ultrasonic bat detectors have several important limitations with respect to census and survey work. First, the investigator employing the devices must have a comprehensive knowledge of echolocation, bioacoustics, and methods of sound analysis, and at least a minimal knowledge of electronics. In addition, although some species of bats emit clearly recognizable calls, the call characteristics of others overlap considerably. For example, using broad-band, frequency-division detectors, Thomas (1988) was able to distinguish only eight of 12 species occurring in the Pacific Northwest of the United States. He was not able to distinguish the Myotis species based on their echolocation calls (Thomas 1988; Thomas and West 1989). In a study of a bat community in the rain forest of Australia, however, Crome and Richards (1988) were able to distinguish all 12 species present using a QMC S-100. Gaisler and Kolibac (1992) were able to distinguish only one of five species known to occur in an agricultural area of southern Moravia using QMC minidetectors. Obviously, the ability to discriminate between closely related taxa varies with the experience and skill of the observer.
Another problem with bat detectors is their unequal sensitivity to the echolocation calls of different species (Fenton 1988; Fenton et al. 1992). Bats of several families (e.g., Vespertilionidae, Molossidae, and Rhinolophidae) emit echolocation calls intense enough to be detected with most available bat detectors. In contrast, echolocation calls produced by other bat species (notably members of the Phyllostomidae) cannot be detected except at very close range (Forbes and Newhook 1990; Fenton et al. 1992). This means that some species cannot be censused with bat detectors. Moreover, because dense vegetation and high humidity reduce the propagation of high-frequency sounds, detection limits of bat detectors may vary by habitat and time of night (Griffin 1971; Lawrence and Simmons 1982). The consequence of atmospheric attenuation in the field is a perceived loss of the highest frequencies in calls at increasing distances from the source (Thomas et al. 1987). Because of these numerous limitations, echolocation surveys should not be considered equivalent to songbird surveys.

Richards et al. (1992, unpubl. data) showed that up to 40% of the bats in some communities can be detected but never captured. If the echolocation calls can be distinguished to species unambiguously, the calls can be used to estimate relative levels of “traffic” or “activity” in different habitats. In areas with several species of bats whose echolocation call characteristics overlap, relative activity can be used to identify habitats where mist nets and traps can be used most effectively. Data from bat detectors should be integrated with data from direct observations and captured animals to characterize the composition of bat communities fully.