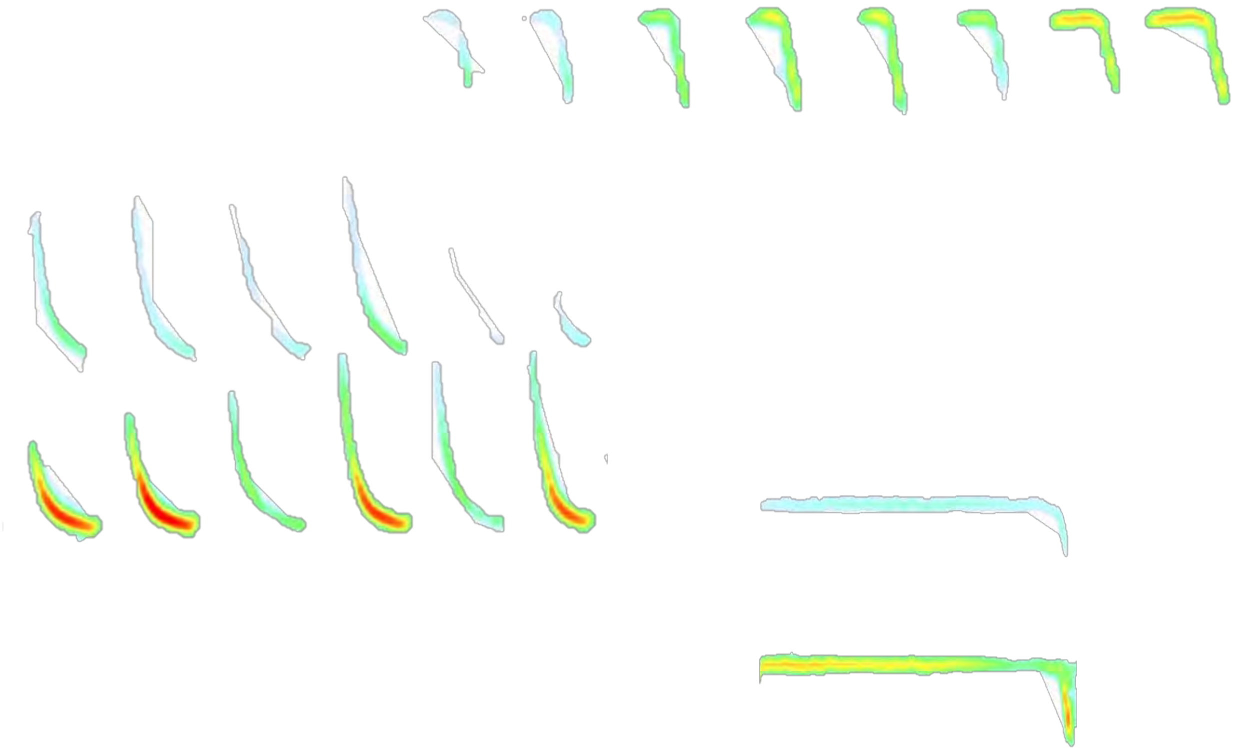
Bat Echolocation Research

A handbook for planning and conducting acoustic studies

Second Edition



Erin E. Fraser, Alexander Silvis, R. Mark Brigham,
and Zenon J. Czenze

EDITORS

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Dedication

This book is dedicated to the bat researchers who have preceded us, to those who work alongside us, and to those yet to come.

Foreword

Echolocation provides an acoustic window on the behavior of most species of bats. Donald R. Griffin's book (*Listening in the Dark: The Acoustic Orientation of Bats and Men*) gave us a preview of what we might hear through this window. This Handbook illustrates how a small window has turned into a giant screen. The study of bat echolocation has progressed from a boutique curiosity and source of wonder to a discipline spanning areas of science from neurobiology through behavior, ecology, evolution, and environmental science.

Many people who study bats use echolocation as a focus for their work. To some this means, for example, neurobiology, communication behavior, or environmental assessment. Whatever the goal, diversity is an underlying and overarching reality. At one level, diversity means that different species take quite different approaches to echolocation. At another level, individual differences remind us that echolocation is a conscious behavior. The same bat may, for instance, use quite different echolocation calls over the course of a night, a season, or its life. How much of echolocation behavior is inherited, and how much is learned?

The diversity of bats is one element in the study of echolocation. However, the diversity of projects that researchers undertake, the array of equipment they use, and the range of approaches involved are as important. Diversity is a multi-edged sword, and apparently contradictory results could reflect different data sets or perspectives, as well as expectations.

As usual, this means that the library is one of the first stops en route to a project. From there keeping abreast of new findings about bat echolocation is a significant challenge. This requires constant efforts to keep up with the relevant literature. But just which literature is relevant? We must remember that changes in technology can change our perspective of what is possible. Learning to listen is a good motto. Listen to the bats and to the colleagues.

Donald Griffin famously referred to bat echolocation as a "magic well" because each time you visited it, you learned something new. Bats continue to surprise us, perhaps because they have not read the literature.

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January 2020

Editors’ Foreword

Overview

The field of bat acoustic monitoring has changed dramatically in recent decades. Since 1950, the tools required to monitor bats acoustically have progressed from cumbersome equipment available only to academic specialists to small, portable devices, some of which are relatively inexpensive.

These technological changes have been tracked by a growing community of enthusiastic practitioners devoted to using acoustic methods to research and monitor bat communities around the world. Bat echolocation remains a vibrant area of basic research. Specialists in this area—working at the frontiers of what we know about bat echolocation—are increasingly joined by many practitioners who are most interested in acoustic detection as a tool. As bat populations are threatened by factors such as white-nose syndrome and wind energy, there are increasing mandates to monitor local populations. Acoustic monitoring is often the best way to address these requirements. In response to a 2006 survey about typical practices for conducting acoustic surveys of bat populations in Canada and the US, most respondents had less than five years of experience and were able to devote less than 20% of their professional time to their bat work (Weller and Zielinski 2006). Although this research has not been replicated recently, we assume that the number of people in this position (having both limited experience and time for acoustic bat work) has increased.

The novice or part-time practitioner of bat acoustic monitoring faces many challenges. There is a bewildering diversity of hardware and software available, each with a unique set of capabilities and associated assumptions. Study design and equipment deployment must be given careful consideration, all with the aim of collecting a massive data set in a form (digital files of high-frequency sound) that most biologists have little experience with. Ultimately analyzing the many terabytes of data that are inevitably collected during an average acoustic survey can be overwhelming.

Handbook Objectives and Scope

Our goal has been to produce a Handbook that provides a brief, comprehensive guide that summarizes current relevant information and best practices in bat acoustic monitoring. We hope that this will be useful to practitioners with varying levels of experience and knowledge. The scope is global, but there is a substantial North American and European bias in the community of researchers studying bat echolocation. This reality is reflected in many of the examples given in the text. However, we have made a concerted effort to create a resource that is broad enough to be helpful to biologists who work anywhere in the world to monitor communities acoustically. Furthermore, we have structured the Handbook in a way that recognizes that different research questions and approaches will be necessary depending on the amount of previous research that has been done on a particular bat community.

The Handbook is a product of the Second International Symposium on Bat Echolocation Research: Tools, Techniques, and Analysis, which occurred in Tucson, Arizona, in March 2017, and was organized by M. Brock Fenton, Janet Debelak Tyburec, and Brian W. Keeley. The Symposium brought together more than 100 participants from around the world, including many leaders in bat echolocation and monitoring science; manufacturers of all the leading bat echolocation recording hardware and software; and many interested biologists hoping to learn more about best practices in acoustic monitoring. A main goal of the Symposium was to connect practitioners using acoustic monitoring with those conducting research about bat acoustics. This Handbook is an extension of that goal.

To make the Handbook as representative as possible of the knowledge and practices used by the current research community, many experts in bat echolocation and monitoring research were involved in each step of its production. The editorial group prepared and circulated a proposed Handbook outline before the 2017 Symposium and then consulted conference participants in both large and small group settings over the course of the meeting. After the Symposium, 51 invited contributors wrote the sections and provided the example acoustic recordings that make up the Handbook, and the entire document was reviewed by four professional bat biologists. We are tremendously grateful to all contributors and reviewers for their hard work in synthesizing and summarizing the complex business of recording and analyzing bat echolocation calls.

Of course, acoustic techniques are just one approach to researching and monitoring bat communities, and are more or less appropriate in different situations. The benefits and drawbacks of using acoustic methods, compared with other approaches, are briefly discussed in the Introduction. However, the assumption of this guide is that readers have already assessed the options available to them and have decided that acoustic monitoring is the best method to address their question.

Contents

The Handbook summarizes all the key steps in conducting an acoustic survey of a bat community, including project planning, strategies for data collection, approaches to analysis and interpretation, a guide to purchasing a bat detector, and a series of case studies. Chapter 1 (“Introduction to bat echolocation”) provides a broad introduction to the theme, including a discussion of why and how bats echolocate, and a brief description of acoustic data, as well as what can be discerned about a bat community using acoustic techniques. Chapter 2 (“Acoustic survey design”) focuses on acoustic survey design, stressing the importance of identifying a clear research question and approach, and summarizing some of the most common questions that researchers investigate using acoustic techniques. Chapter 3 (“Bat detector choice and deployment”) discusses the difficult task of choosing the appropriate detector and summarizing the different technological approaches, as well as the trade-offs involved with selecting one style of detector over another. Chapter 4 (”Echolocation call identification”) focuses on strategies for identifying recordings of echolocation calls, starting with a discussion of the challenges associated with this task, an overview of both manual and automated approaches, and a section on using and creating call libraries, which is crucial for researchers working in areas where bat communities have received little or no study. Chapter 5 “Data, analysis, and inference”) deals with data management, analysis, and inference. It includes a discussion about strategies for data management that contains a section on the nature and use of databases. Furthermore, it describes different approaches to statistical analyses, many of which are intuitively linked to the suggestions for study design in Chapter 2. Chapters 2 through 5 each conclude with a

"Some additional suggestions" section, which were sent to us when we asked a group of bat acoustic experts what they considered to be some common pitfalls associated with the technique. The final chapter of the Handbook ("Case studies") includes five case studies, each of which summarizes a previously published study or studies that used acoustic survey techniques. The goal of this section is to demonstrate how many of the principles discussed throughout the Handbook have been applied in real-life scenarios. We selected the case studies to provide examples from a range of geographic locations, using various detecting technologies, and asking diverse questions about bat communities. Throughout the Handbook, when photos or recordings of individual species are provided and labeled, we have identified the species of interest by scientific name and by the common name provided by the online resource, *Bats of the World: A Taxonomic and Geographic Database* (Simmons and Cirranello 2020), unless stated otherwise.

On behalf of all contributors to the Handbook, we hope that this guide will help demystify the process of eavesdropping on bats and promote high standards in future acoustic studies of bat activity.

Erin Fraser, Alex Silvis, Mark Brigham, and Zenon Czenze

Three buffy flower bats (*Erophylla sezekorni*). © Joroen van der Kooij, Bat Conservation International.

Glossary

Term	Definition
Acoustic data	Information about bats collected using a detector that records sounds. These data are usually in the form of recordings of echolocation calls, but in some cases, they represent manual identification from real-time detections. Acoustic data may be raw sound files or may be values extracted from those files.
Acoustic guild	Groups of bats sharing echolocation call characteristics adapted for use in specific habitat types. For example, species with high-frequency, short, large-bandwidth calls that tend to forage in clutter versus groups with low-frequency, long, low-bandwidth calls that tend to forage in the open.
Acoustic survey	Sampling bats by recording and analyzing their echolocation calls.
Active recording	A method of recording echolocation calls whereby researchers actively orient a bat detector to follow bats as long as possible in real time in an effort to produce longer call sequences and higher quality calls than passive recording.
Microphone arrays	Three or more simultaneously recording microphones deployed in a known and fixed spatial configuration. Enables determination of the 3-D position of a bat during echolocation call emission. Used to assess call intensity, directionality, and emission direction.
Attenuation	Loss in sound intensity follows the inverse square law: sound pressure level halves for each doubling of distance, i.e., –6 dB for each doubling of distance. Sound is attenuated owing to spherical spreading and absorption by the atmosphere, which increases with temperature and humidity, and scattering (e.g., reflection).
Automated classifier	Automatic call recognition and identification; software that allows for quantitative call ID.
Automated ID	A form of echolocation identification in which recorded files are filtered and identified with algorithms or a software program that compares the statistical properties of multiple parameters of a recorded call to a library of known calls, to classify them to a known species or group of species. Also known as quantitative call ID.
Bandwidth	The range of frequencies through which an echolocation call sweeps. Narrow-bandwidth calls sweep through a few frequencies over time, whereas broad-bandwidth calls sweep through many frequencies
Bat pass	A single crossing of a bat through a detector's zone of detection; see "call sequence."
Bio-sonar	Synonym for "echolocation."
Broadband detector	A bat detector that can simultaneously detect a range of ultrasonic frequencies.
Call	A brief, continuous emission of sound; see "pulse."
Call amplitude (intensity)	The energy contained in an echolocation call, often measured as decibels at a set distance from the bat. A characteristic that affects the distance at which a call can be detected.

Call classifier	Tool that classifies bat calls or call sequences to species or group from call or call sequence characteristics. May be qualitative or quantitative.
Call library	A collection of bat calls, known to be produced by specific species, that allows comparison to calls with unknown identity and may be used by an automated classifier or as a training and reference tool.
Call parameters (morphology)	Properties of a call (statistical or qualitative) that aid in describing the shape and frequency range of echolocation calls.
Call sequence	A series of echolocation calls produced by a single individual. A single flight (crossing) of a bat through a detector's zone of detection. See "bat pass."
Clutter	Obstacles that can affect a recording of echolocation calls (e.g., foliage, trees); may cause either scattering echolocation calls due to reflection and blocking or bats adjusting their normal search-phase calls in response to obstacles resulting in changes in call parameters.
Constant frequency	CF; a type of call that remains at one frequency over the entire call duration. These calls are of high duty cycle leading to considerable pulse-echo overlap. Bats using CF calls typically exhibit Doppler-shift compensation.
Decibel (dB)	A measure of the amount of pressure exhibited by a sound wave, often used to measure call "loudness."
Detector	Electronic equipment capable of detecting ultrasound (echolocation calls) that is normally above the range of human hearing and produced by bats. Many also allow for these sounds to be recorded.
Directional microphone	A microphone that is more sensitive to sound arriving from certain directions.
Doppler shift	A property of sound that results in an apparent change in frequency because of an object's movement. A sound source moving towards a microphone is perceived as a higher frequency and vice versa.
Duty Cycle	DC; The percentage of time during which a bat is producing a pulse (low DC is <25% and high DC is >25%).
Echolocation	An orientation system used by bats and other animals based on generating sounds and listening to the returning echoes to locate obstacles and prey.
Feeding buzz	The terminal phase of an echolocation sequence that results in numerous rapidly produced calls during the approach to a potential prey. The calls are so closely spaced that, to the human ear the output from a detector sounds like a buzz. These calls typically lack many of the species-specific characteristics needed for identification.
Filters	Statistical processes that remove undesirable noise such as insects, electrical interference, etc., from recordings of echolocation calls.
Frequency	The number of sound waves that pass a fixed place in a given amount of time and measured in hertz (H; 1 wave per second) or kilohertz (kH). Frequency is equal to the reciprocal of the period of the sound wave.
Frequency division	A type of bat detector that reduces the frequency of echolocation calls so that they may be heard by humans or stored more easily by dividing the frequency of sound by a set number called the division ratio (*n*).
Frequency modulated	FM; a type of echolocation call that varies or "modulates" in frequency throughout the call, with no pulse-echo overlap. Low DC.

Frequency response	A quantitative measure of the output spectrum of a system or device used to characterize the system's dynamics. It is a measure of magnitude and phase of the output as a function of frequency compared with the input.
Full spectrum	Bat detectors in which all desirable information about the recorded sound is preserved in real time, including frequency and amplitude.
Harmonics	Harmonic frequencies are integer multiples of the fundamental frequency. Some bats alter the amplitude of harmonics by selective adjusting during sound production. They can be used to assist in pinpointing an insect's location. These are sometimes referred to as overtones.
Heterodyne	A type of bat detector that lowers the frequency of echolocation calls so that they may be heard by humans or stored more easily by mixing with a known signal frequency, thereby resulting in a narrow-band detector.
Interspecific variation	Variation in the parameters of echolocation calls among different species.
Intraspecific variation	Variation in the parameters of echolocation calls among individuals of the same species.
Kilohertz	kHz; 1000 hertz; the most common unit of measure of the frequency of sound.
Known call	Echolocation calls recorded from bats of a known species.
Manual ID	Identification of call sequences through visual and/or auditory comparison with a known call library; accuracy can be highly variable, based on researcher experience. Also called qualitative call ID.
Metadata	Data that provides information about other data.
Minimum frequency	Found in frequency modulated (FM) calls. Represents the lowest frequency produced.
Mobile transect	A method of bat echolocation sampling in which the researcher moves at specified times, often at a known or constant rate, and records echolocation calls at a series of set points in space for a set time.
Narrow-band	A detector that can only record calls from a small frequency range at a specific time. See also heterodyne.
Oscillogram	A two-dimensional graphical display of sound amplitude as a function of time.
Omni-directional microphone	A microphone that can detect equally in all directions (i.e., has a spherical zone of detection).
Passive recording	Sampling echolocation calls by a spatially fixed detector at a single point in space; opposite of active sampling and active recording.
Peak Frequency	Represents the frequency with the greatest amount of energy in a call, typically near the minimum frequency. An important parameter for identifying many FM calls.
Phonic groups	Groups of bats using echolocation calls categorized by similarity in frequency; may include groups of species or genera, or categories such as "high," "medium," or "low." See "sonotype. "
Power spectrum	The distribution of power of various frequency components that compose an echolocation signal.
Pulse	A brief, continuous emission of sound, commonly referred to as a "call."

Qualitative call ID	See “Manual ID.”
Quantitative call ID	Identification of calls or call sequences based upon measured parameters of the call or call sequence; see “call parameters.”
Search-phase call	The type of echolocation call emitted by bats when commuting or foraging; characterized by consistent call characteristics.
Sampling rate	A setting on an acoustic detector that describes the number of equally spaced samples that are taken for each 1 s of signal, and the bit depth is the number of bits used for encoding each sample in memory. For example, a sampling rate of 48 kHz and a bit depth of 16 bits means that we take 48,000 equally spaced samples per second of signal.
Signal-to-noise ratio	A measure of call quality that compares the relative amplitude of desirable and undesirable components.
Sonogram	A picture made from collecting information about the echoes bouncing off an object.
Sonotypes	May refer to a distinctive acoustic signature that can identified and quantified within a recording, but which may not be identified otherwise. Researchers working in little-studied bat communities may identify sonotypes if the echolocation calls of all species present have not been previously documented. May also refer to a group of species or genera whose calls are not distinguished acoustically. See “phonic group.”
Sound	The physical properties of a sound wave include amplitude of the vibration, which humans interpret as loudness or intensity, and frequency, which is the speed of the vibration. Human ears perceive this as the pitch of the sound.
Sound pressure level (SPL)	Sound pressure is measured in decibels (dB) on a log 10 scale relative to a reference level.
Spectrogram	A visual representation of the spectrum of frequencies of sound as they vary with time or some other variable.
Speed of sound	340 m/s (in air).
Time expansion	A type of full-spectrum bat detector that reduces the frequency of recorded calls by electronically stretching them over a longer time period so they may be heard by humans and stored more easily.
Ultrasound	Sounds above the range of human hearing (typically set to above 20 kHz).
Wavelength	The distance traveled in one wave cycle, i.e., from crest to crest. For sound waves, the wavelength is equal to the speed of sound divided by frequency.
Zero-crossings	A detector type that calculates frequencies by measuring the time between moments of zero sound pressure, which corresponds to the period (one cycle) of the wave.

Greater horseshoe bat (*Rhinolophus ferrumequinum*) catching moth, multiple exposures. © Stephen Dalton/Minden Pictures, Bat Conservation International.

Chapter 1. Introduction to Bat Echolocation

Introduction

A basic assumption of this Handbook is that readers have already made the decision to use acoustic methods—instead of, or in addition to, many other potential approaches to bat research—to address a research question(s). To guide this decision process further, the introductory chapter of the Handbook provides a brief primer on the evolution and ecology of bat echolocation, discusses some characteristics of acoustic data, and provides a brief list of questions to consider when deciding whether or not to use acoustic techniques.

Evolution of echolocation in bats

Fossils indicate that flight and echolocation have been present in bats for at least 45 million years, and indirect evidence based on fossilized moths indicate possibly as long as 75 million years (Gáll and Tiffney 1983). Whether flight or echolocation evolved first in bats has been vigorously debated based on morphological and molecular evidence (Eick et al. 2005; Novacek 1985; Simmons et al. 2008; Speakman and Racey 1991; Teeling et al. 2000). The current consensus is that echolocation evolved after flight (Schnitzler et al. 2003; Simmons et al. 2008), with echolocation used first for spatial orientation then subsequently for food acquisition (Schnitzler et al. 2003).

Spatial orientation by echolocation is accomplished by measuring the distance to a target object using the time delay between an emitted signal and the corresponding return echo, with directional sensitivity in hearing providing information on angles and precise locations of individual objects (Moss and Schnitzler 1995). It is apparent that, using the same information from echoes, spatial orientation and prey target acquisition are accomplished simultaneously by foraging bats. Spatial orientation and navigation at small, medium, and large scales requires a broader input resolution compared with foraging (Schnitzler et al. 2003). Tracking and acquisition of aerial prey requires resolution of target speed, distance, and relative location, and the rate of echolocation calls increases (feeding buzzes) as distance to prey decreases, allowing more fine-tuned resolution.

Much like aircraft, bats come in various shapes and sizes. Like aircraft, bat maneuverability and speed are related to body mass, wing loading (weight divided by wing area), and aspect ratio (wingspan divided by wing area). These physical characteristics are the primary determinants of where bats can fly safely and, thus, the environmental conditions with which they are associated. Bat physical attributes also correspond with echolocation call characteristics, like frequency range and shape, which themselves correspond to dietary preference (Aldridge and Rautenbach 1987; Denzinger and Schnitzler 2013; Norberg and Rayner 1987). Generally speaking, bats that use highly "cluttered" conditions (i.e., areas with many structural obstacles) have higher call frequencies than species that use less cluttered conditions (Aldridge and Rautenbach 1987; Neuweiler 1989). The strength of the association between general foraging strategy and echolocation is such that bat biologists often discuss bat foraging guilds rather than families or genera (Denzinger and Schnitzler 2013). Although the relationship between habitat association, call characteristics, and diet follow reliable patterns, significant variation occurs among species owing to divergent evolution (Jones and Holderied 2007; Jones and Teeling 2006) (Figure 1-1; Figure 1-2).

In addition to echolocation calls used to navigate and identify prey, many species also communicate socially using "social calls." The purpose of social calls include, but are not limited to, facilitating group cohesion (Chaverri et al. 2013; Furmankiewicz et al. 2011), identifying familiar and unfamiliar individuals (Voigt-Heucke et al. 2010), and increasing foraging efficiency (Wright et al. 2014). Social calls may or may not be ultrasonic, but in most cases, they differ substantially in structure from echolocation calls.

So why do we sample echolocation calls? Because many bats use echolocation to navigate and forage, they emit calls almost continuously while active and flying. This constant production of sounds provides a reliable way of documenting that bats are present and, more specifically, what species

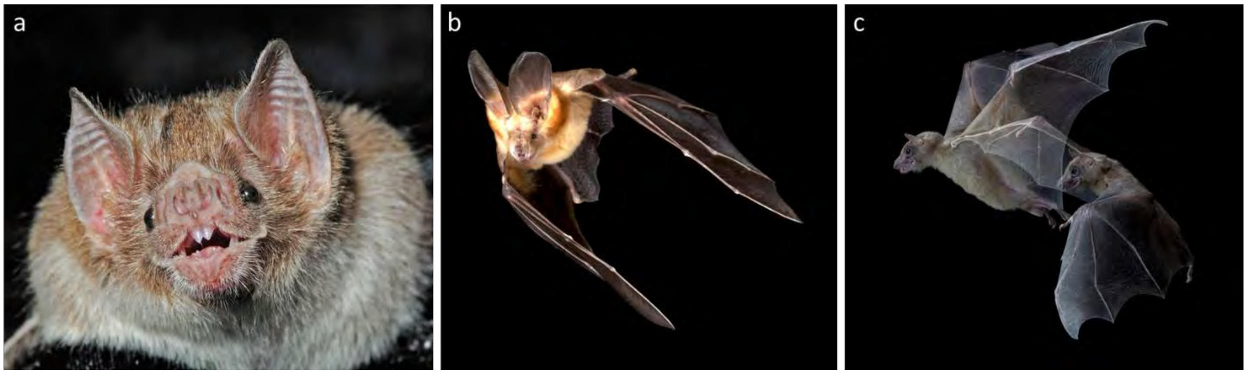

Figure 1-1. Modes of echolocation. *Most echolocating bats emit echolocation calls from their open mouths, e.g., (a) the common vampire bat (*Desmodus rotundus*). Approximately 300 species, including (b) Egyptian slit-faced bat (*Nycteris thebaica*), instead emit calls through their nostrils (Jakobsen et al. 2018). Unusually, at least two species of Old World fruit bats, including (c) the Egyptian rousette (*Rousettus aegyptiacus*), create calls by clicking their tongues (Fenton and Ratcliffe 2014). © Sherri and Brock Fenton.*

may be present and what the animals are doing. However, none of this can be achieved unless we use the appropriate sensors to collect these data.

What are “acoustic data”?

At the broadest level, “acoustic data” may be defined simply as data pertaining to sound. In the context of bat acoustic studies, the term acoustic data refers to sounds made by bats. However, acoustic data may also be used to refer to a range of specific kinds of data, depending on context. For example, both recordings of bats and quantitatively measured parameters from an individual call qualify as acoustic data. Less commonly, acoustic data may refer to data about data, such as the type of equipment used to record calls, or the date and environmental conditions when recordings were made. However, these last examples are better classified as metadata.

It is helpful to think of acoustic data as being either “primary” or “derived,” where primary data are those collected directly from bats, i.e., recordings. To facilitate this discussion, it is worth taking a moment to address terminology. In this Handbook, we follow the traditional wording, as formally defined by Loeb et al. (2015), that a single sound made by an echolocating bat is a “call” or “pulse,” whereas a series of calls, recorded as an echolocating bat flies by a recording station, is referred to as a “bat pass” or “call sequence.” All four terms are common in the literature and both pairs are used interchangeably throughout the Handbook, although we have most frequently used “call” and “call sequence.” Depending on recording setup and study objectives, primary data typically fall into one of three categories: entire bat passes/call sequences; individual calls/pulses; and components of individual vocalizations. Derived data, then, are those created based on processing or analyzing these primary data. Derived data may be qualitative or quantitative, although the

Figure 1-2. High and low duty cycle echolocation. *One challenge of echolocation is that loud outgoing calls may mask quiet returning echoes. Most bats use low duty cycle echolocation, which means that they produce broadband calls that are interspersed with relatively long periods of silence, thereby separating pulse and echo in time. About 160 bat species, including members of the Old World families Hipposideridae and Rhinolophidae, such as (a) the Bornean horseshoe bat (*Rhinolophus borneensis*), and a few species in the New World genus,* Pteronotus, *such as (b) the Mesoamerican mustached bat (*Pteronotus mesoamericanus*), use high duty cycle echolocation, meaning that they produce relatively constant frequency calls with little temporal separation, relying on the Doppler-shifted change in frequency to separate pulse and echo (Fenton et al. 2012). Image (a) © Sherri and Brock Fenton. Image (b) © Ch’ien Lee/Minden Pictures, Bat Conservation International*

difference between qualitative and quantitative data is decreasing, as increasingly powerful machine-learning algorithms are developed. Perhaps the most common derived qualitative data are patterns of multiple calls within a recorded file, or the structure of an individual call. Many bat biologists may qualitatively describe a file or call by "how it looks." Some examples of terminology for qualitative data include "hockey stick shape," "upsweep," "downsweep," and "flat." Many qualitative parameters from a recording may also be described quantitatively. For example, a file containing multiple vocalizations may be qualitatively described as having an undulating minimum frequency that can be quantitatively summarized as the standard deviation of the minimum frequency of the call. Derived parameters often quantify specific aspects of a call, such as bandwidth, slope (in frequency modulated calls), duration of call, and time between calls, among other measures.

In subsequent analyses, the metrics of interest (response variables) are often some combination of the primary and derived data. Researchers often report metrics of primary acoustic data (e.g., number of calls recorded, number of bat passes recorded; or sometimes, in studies during which recordings are triggered, the number of files recorded). These results may be informed by derived data; for example, measured parameters of all recorded calls may allow reports of primary data to be categorized in various ways, including but not limited to species, genus, sonotype, phonic group, or acoustic guild.

Acoustic data, therefore, are both audio recordings and spreadsheets of numbers and words (i.e., quantitative and qualitative). When reviewing acoustic studies, as well as when preparing to undertake an acoustic study, it is critical to understand what constitute the data that will ultimately be used for inference, and how primary data may be turned into derived data.

What can we learn using acoustic techniques?

Studies of bat acoustics are incredibly varied about topic, study system, study organism(s), and study design. Summarized broadly, studies of bat acoustics often seek to answer questions from within common topical domains: 1) biodiversity or community structure; 2) distribution; 3) activity patterns and habitat selection; 4) behavior; 5) population monitoring; and 6) phenology. Although these are common domains, studies using bat acoustics are not in any way limited to these. Indeed, continual improvements in acoustic hardware and software, coupled with decreasing costs, suggest substantial opportunity for acoustics to be used in an ever-widening domain of topical areas. Indeed, clever study design, new hardware, and advanced analytics now permit studies that were not feasible 10 years ago.

As with all technological fields and scientific methods, there are limitations to what can be learned from acoustic data. Perhaps the greatest current limitation is that distinguishing among individuals, between males and females, or between juveniles and adults is not generally possible. This limitation distinguishes bat acoustic studies from many other wildlife investigations that rely on remote sensing, particularly those using camera traps, which may allow researchers to determine the qualitative data described above. However, combining acoustic detectors with other sensors, such as cameras or advanced acoustic arrays consisting of

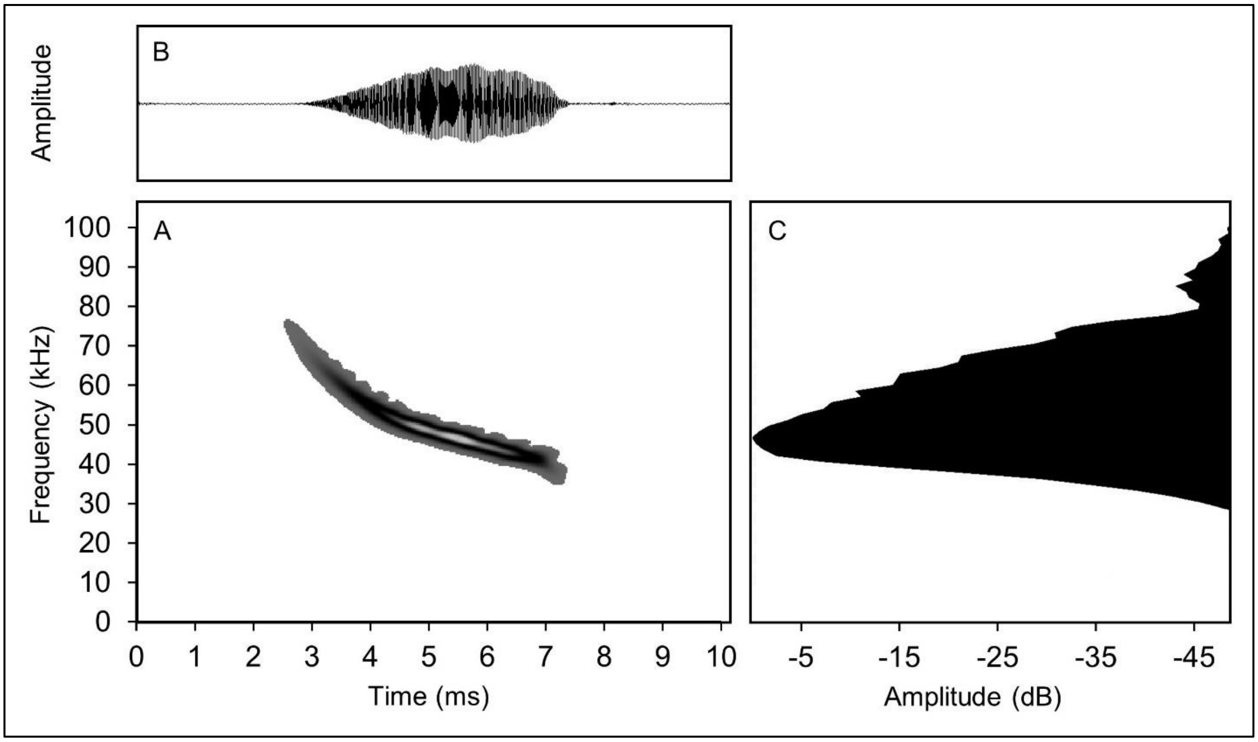

Figure 1-3. Recordings of echolocation calls: the output. *Recordings of a little brown myotis (*Myotis lucifugus*) echolocation call may be viewed through three kinds of output: (A) a spectrogram, which shows changes in call frequency over time; and (if the recording is made using full-spectrum technology) (B) an oscillogram or time domain, which shows changes in sound amplitude above a noise floor over time; and (C) a power spectrum, which shows variation in sound amplitude across frequencies. Note: zero-crossing recordings do not contain information about call amplitude and so may only be viewed as spectrograms.*

multiple microphones, may reduce these limitations. Similarly, such limitations may be rendered moot when use of controlled laboratory experiments is possible. Current technological limitations are only one factor that constrains what may be learned using acoustics. Acoustic studies are also limited by the way detectors are used, including the recording parameters selected, sampling design, and how detectors are placed and configured relative to surrounding clutter, but these limitations can be addressed more readily by the researcher.

How do we visualize acoustic data?

Acoustic recordings are typically displayed as spectrograms that depict frequency plotted against time. If data are recorded in full-spectrum format, spectrograms typically include information on the intensity of the recorded sound (Figure 1-3). In contrast to full-spectrum recordings, data on intensity are not available from zero-crossing recordings. However, intensity information may be retained in zero-crossing format if the data are derived from full-spectrum recordings. The methodology to do this has not been widely applied to date.

Full-spectrum data may also be displayed as an oscillogram or time domain, which represents sound amplitude plotted against time. Amplitude is presented on the *y*-axis, and time on the *x*-axis. Frequently, oscillogram information is paired with the spectrogram, as in many figures in this Handbook. Full-spectrum recordings may also be visualized as a power spectrum, which illustrates variation in sound amplitude across frequencies.

Acoustic data are not usually displayed on linear or "true time" axes. Rather, both the frequency and time axis are adjusted to represent specific features of interest in the call more clearly. Because individual echolocation calls of many bat species are brief (only several milliseconds in some species), the most common adjustment to spectrograms is to stretch, or slow, the time axis, thereby making the shape characteristics of a call more evident. Many acoustic programs (software) also provide a "compressed time" option that removes "empty space" between individual calls. This option is particularly useful when the time axis is stretched, as the spaces between individual calls are increased. Removing empty space permits more calls to be displayed concurrently, thus providing a better overview of patterns in the data. Data must be evaluated in both true and compressed time modes because each format may mask relevant details.

Adjustments to the frequency axis also are common; perhaps the most frequent adjustment is to use a logarithmic rather than linear scale. A logarithmic scale provides several benefits: it allows a broader frequency range of calls to be displayed. This is a useful feature when the bat community in a study area includes species that use high and low frequency, and it reduces the skewness of frequency modulated calls towards high frequency values.

Is acoustic monitoring the right approach for your projects?

For readers who are still wrestling with whether acoustic techniques are the best approach for their specific research initiatives, we provide a brief primer in the form of a list of questions to consider before purchasing detectors and certainly before heading into the field. The last thing you want is to invest time and resources into acoustic monitoring, only to realize too late that you cannot use the data collected to achieve your research goal. If you answer yes to the following questions about your project and local bat community, then acoustic monitoring may be the best approach for your research. If the answer to some of these questions is no, then you may want to consider alternate methods, such as capturing bats, conducting roost emergence counts, engaging in hibernacula surveys, or something else.

To help determine whether acoustic approaches are appropriate for a given project, it may be helpful to consider the following questions:

Question 1 – Research objective(s): Will acoustic monitoring address your research objective(s) (Figure 1-4)? Acoustic monitoring may allow researchers to gain great inferences about local bat communities and study systems, but there are also many research questions that acoustic monitoring alone cannot answer. Prior to investing in an acoustic-monitoring project, it is essential to identify the specific research objective(s). See Chapter 2 ("Acoustic Survey Design") for examples of the kinds of research questions often addressed using acoustic-monitoring techniques.

Question 2 – Local bat community: What proportion of the species in your study area echolocate or are reliably detectable with a bat detector? Quiet or non-echolocating bats will create high false negatives when making

***Figure 1-4. Bat research methods.** Acoustic monitoring is just one approach to researching bats. Alternatively, or in addition to acoustic techniques, bats (a) like this fringe-lipped bat (*Trachops cirrhosus*) may be observed and counted as they emerge from their roosts; or (b) may be captured using harp traps, hand nets, or in the case of this big brown bat (*Eptesicus fuscus*), a mist net. Once bats have been captured, researchers may collect data on age, sex, body size, and condition; collect tissues samples for various subsequent analyses; or attach transmitters to remotely collect information about aspects of the bat's biology. Image (a) © Michael Durham/Minden Pictures, Bat Conservation International. Image (b) © Ch'ien Lee/Minden Pictures, Bat Conservation International.*

inferences about the bat community if you rely solely on acoustic monitoring.

Question 3 – Call library: Is there an existing echolocation call library for your study area that you can access? If there is no call library, all is not lost. It is possible to learn a lot about a bat community without being able to identify some or all recordings to species; however, it is helpful to know in advance if this is the situation. You also may build a call library, but this can take substantial resources and time, requiring many nights of trapping and investment in the appropriate equipment to record the calls of hand-released bats. To learn more about building a call library, see Chapter 4 ("Echolocation call identification") and Case study 5 ("Bats in the Ghats: Building a call library to study the impacts of agriculture on bats in a biodiversity hotspot").

Question 4 – Species identification: If the bats in your area are readily detectable, and a good call library exists, can the focal species be distinguished from sympatric bats using call morphology? Some species overlap considerably in call morphologies, which will limit the ability to use acoustic information to distinguish among species and model species-specific activity and trends.

Question 5 – Time: Do you have enough time to answer your question? Some research questions may be addressed relatively quickly (over weeks or months), while others may take years. Remember that monitoring activity to characterize trends over time can require a minimum of 5–10 years of continuous data collection. Also, if your goal is to examine long-term temporal differences, do baseline acoustic data exist for the study area? Past data collection equipment and protocols may need to be considered if there is intent to compare the data you will collect to those from previous monitoring efforts.

Question 6 – Equipment: Do you or will you have the appropriate equipment to record and analyze calls? Bat detectors and software required for call analysis are expensive and different research projects/bat communities have different technological needs. For example, some species groups in some regions (e.g., Rhinolophidae and Hipposideridae) can echolocate at frequencies above the default recording ranges of common brands of detectors. Much of the heavy lifting in data analyses can be done directly by software containing auto-classifiers, but you need access to an appropriate software package. It is important to assess whether your research budget will allow for acoustic monitoring using the technology that is necessary to meet your objectives.

Question 7 – Expertise: Do members of your research team either have expertise or the willingness to gain expertise in all stages of the acoustic-monitoring process? Even with enough time and resources to collect the data, without the skill to analyze them and classify the calls recorded, the research goal may be unachievable. Although software packages exist to streamline call identification, it is crucial to remember that no software is infallible. The onus is on you to verify the accuracy of auto-classifiers to quantify error rates, and you must be aware of implications of both false negatives and false positives to address your research question.

Conclusion

It is not easy to determine whether acoustics are the most appropriate method to answer a given question. The point of this Handbook is to provide an overview of theoretical topics, along with practical advice gleaned from collective decades of experience, to help you evaluate whether an acoustic study is indeed appropriate, and, if it is, to help you design, plan, and conduct one. However, it is impossible to provide guidance to address every situation in which acoustics may be considered, because of the diversity of bats and their behavior, logistical constraints, and varying levels of knowledge about bat communities worldwide.

For more specifics on the physics of bat echolocation, as well as deeper evolutionary and ecological background, see:

- Metzner, W. and R. Müller. 2016. Ultrasound production, emission, and reception, in: Fenton, M.B., A.D. Grinnell, A.N. Popper, and R.R. Fay (Eds.), *Bat Bioacoustics, Springer Handbook of Auditory Research*. Springer, New York, pp. 55–91.
- Moss, C.F. and H.-U. Schnitzler. 1995. Behavioral studies of auditory information processing, in: Popper, A.N., Fay, R.R. (Eds.), *Hearing by Bats, Springer Handbook of Auditory Research*. Springer, New York, pp. 87–145.
- Schnitzler, H.-U., C.F. Moss, and A. Denzinger. 2003. From spatial orientation to food acquisition in echolocating bats. *Trends in Ecology & Evolution* 18, 386–394

A hoary bat (*Lasiurus cinereus*) in flight. © Michael Durham/Minden Pictures, Bat Conservation International.

Chapter 2. Acoustic Survey Design

Introduction

In this chapter, we describe strategies for planning and conducting common types of studies that use acoustic techniques, as well as the different types of sampling approaches that can be used. Although this chapter describes some current best practices, it is not meant to be exhaustive. There are doubtlessly many new applications of acoustic techniques that will increase our knowledge of bat biology, and researchers are encouraged to exercise their creativity and innovation!

Study design, simply put, is the process of determining how to allocate time and resources to get the most precise answer to research question(s). The first steps in beginning an acoustic study of bats, or indeed any scientific endeavor, is to develop hypotheses and formulate research questions. Determining the questions and objectives is the most important step for identifying study design. Questions that are commonly addressed using acoustic data include: 1) Which species are present at a given site? 2) What environmental features influence presence and activity at a particular location? 3) What are the habitat associations of individual species? 4) How does land management affect presence and activity? 5) How does activity change temporally, both intra-annually and over many years (i.e., population monitoring)?

Once the objectives have been identified, evaluate whether acoustic methods are appropriate and, if so, what specific equipment is best. In some cases, the decision to use acoustics may be straightforward, e.g., if the study is designed to replicate work conducted elsewhere, if bats cannot be safely handled, and if acoustics are appropriate and equipment is on hand. In other cases, the decision to use acoustics may be less straightforward, e.g., if equipment costs are an issue or if alternative methods offer greater benefits. If you are still deciding whether acoustic techniques are appropriate for your research/monitoring project, see Chapter 1 ("Introduction to bat echolocation"), which includes a list of questions to help guide your decision-making.

Once the objectives are known and it is clear that acoustic methods are the best approach, you must create a study design, which is essential for the success of any research project. Although each project is different, we provide some general advice for common scenarios that can help with developing an appropriate study design. To decide on the optimal design, identify the metric(s) of interest, constraint(s), and relevant variable(s) for the objectives. Furthermore, it is crucial to determine the level of sampling effort necessary to provide the desired level of confidence/accuracy/precision. The optimal study design will vary based on your specific objectives and will be affected by the density of bats, their distribution, and their behavior. Therefore, the design needs to be customized for your objectives. Given the uniqueness of each study and the imperfect information confronting researchers prior to surveys, it is impossible to give uniform detailed advice on survey design. All the study types described as follows need to be customized to individual study systems.

Finally, many practical considerations accompany each type of study design. Chapter 3 ("Bat detector choice and deployment") focuses on selecting an appropriate bat detector, but once the detector is in hand, it is still important to consider how it may best be deployed and the best strategy for accumulating acoustic data. Chapter 2 ("Acoustic survey design") concludes with a brief description of the various acoustic sampling approaches.

Common study types and survey foci

Stages of knowledge

The research questions that can be asked about a bat community may depend on the amount and types of research that have previously occurred in the area of interest or adjacent regions. We present the following information with the idea that most readers of this Handbook, particularly consultants and agency biologists, will be taking a taxon- or systems-based approach to their work (i.e., their focus will be to best understand which bats are present and active in their particular area(s) of study and how this may change over time). Researchers pursuing more hypothesis driven research may find that the trajectory described as follows applies less to their work.

Researchers working with a community that has been well studied for many years may have a good idea of the types of bats present, as well as the habitat associations of different

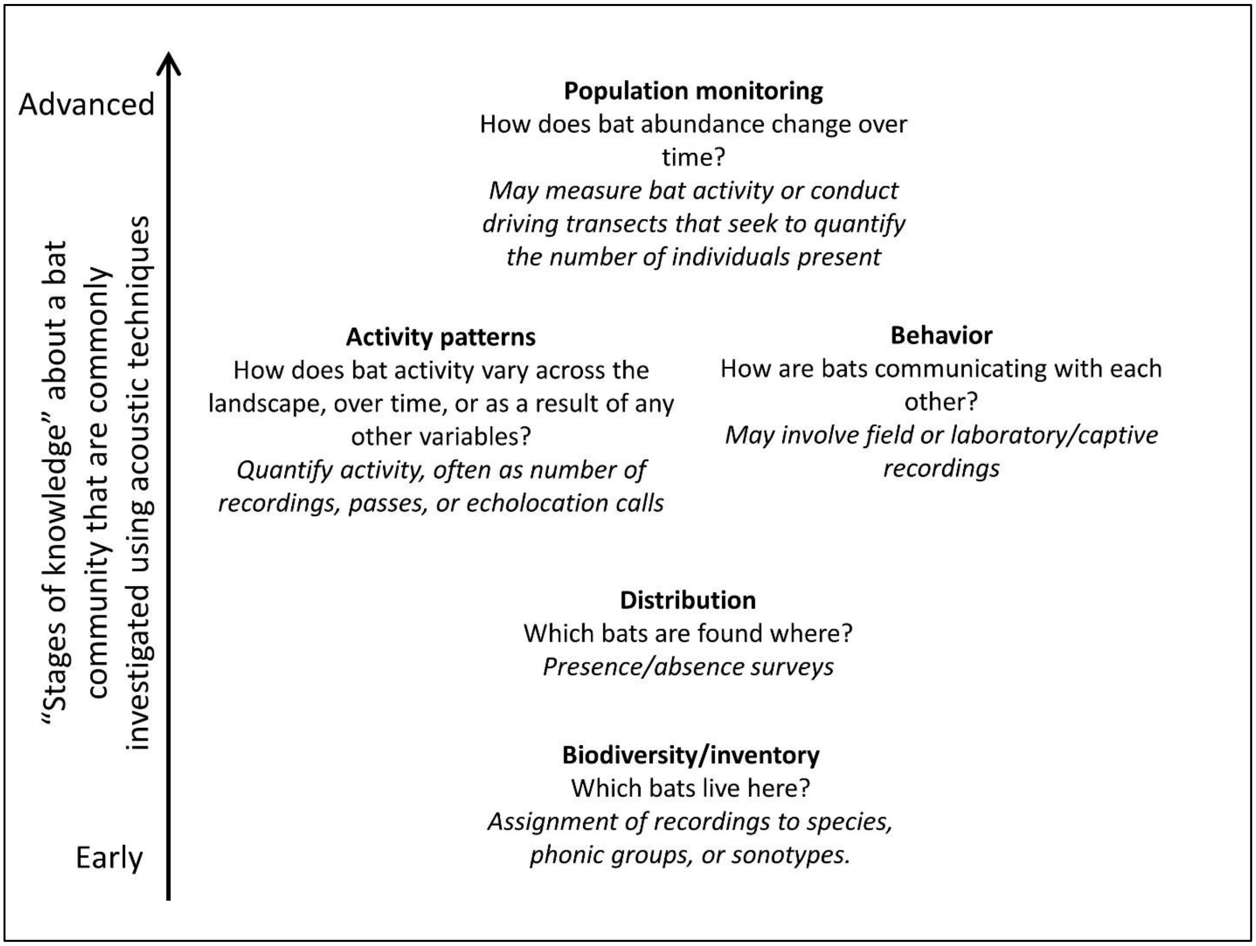

Figure 2-1. Stages of knowledge about bat communities. *Types of studies that may be conducted about a bat community using acoustic monitoring techniques. Study type in bold; example research questions in non-bold; suggested methodology in italics.*

species. This background knowledge can inform research projects that pursue emergent and specific questions having to do with variation in bat activity, behavior, or population monitoring. Researchers working with a little-studied community in a part of the world where little research has previously occurred may be more limited. Building a call library or completing a biodiversity inventory may be a useful first step but is not necessary for all study objectives. Although research rarely proceeds in a predictable and linear way, Figure 2-1 illustrates a typical progression of research questions or "stages of knowledge" that researchers may progress through regarding a bat community over multiple years of acoustic monitoring. Of course, this list is flexible and only a suggestion; researchers may design studies that skip stages or pursue multiple stages concurrently. However, Figure 2-1 provides some context for a reader to assess the stages of knowledge about their local bat community. Each of the study types identified in Figure 2-1 are then discussed in more detail later in the chapter.

A common limitation in acoustic studies is the absence of well-developed call libraries that allow researchers to assign recordings to species, genus, or sonotypes/phonic groups. Although these resources are ideal or necessary for many research questions, it is also possible to learn much about a bat community even if all recordings cannot be identified. Recordings may be grouped according to similar call characteristics (also called sonotypes) that can be identified afterwards. Furthermore, predictable relationships among call characteristics, bat morphology, and habitat use may allow researchers to generate new and testable hypotheses based on sonotypes commonly recorded in a region where there has been little study.

Species diversity

The assessment of species diversity within an area requires specific sampling designs that might differ from those used to investigate activity or occurrence. Owing to species-specific variation in detection probabilities and abundance in a study area, the sampling effort required to record all species present at a local or regional scale will mainly depend on the ability to detect elusive and rare species (Meyer et al. 2011; Skalak et al. 2012). For acoustic sampling to be optimized, and given that both time and money are limited, surveyors need to find the best trade-off between sampling effort and cost.

The answers to the following questions should help produce the optimal sampling design: "when?", "how long?", and "where to place the detectors?"

The "when?" is easiest to answer because several studies have tested the optimal duration of acoustic sampling within a night (Froidevaux et al. 2014; Skalak et al. 2012). The most efficient strategy is passively sampling the entire night (from sunset to sunrise), because it covers the bimodal peaks of bat activity and increases the likelihood of recording elusive and rare species.

The recommendations regarding "how long?" vary depending on the type of detector used, as well as regional and site-specific differences. However, many studies argue that sampling for a repeated number of nights is required, because rare and elusive species are more likely to be missed when sampling takes place for only one night (de Torrez et al. 2017; Froidevaux et al. 2014; Newson 2017; Obrist and Giavi 2016; Skalak et al. 2012).

The answer to "where to place detectors?" is mainly determined by the research questions, the number of detectors available, and by site or landscape characteristics. When working in complex habitats such as forests, within-site variability should be considered, and detectors deployed simultaneously in different micro-habitats that reflect the three-dimensional (3-D) space used by bats (Froidevaux et al. 2014; Kubista and Bruckner 2017). For large-scale studies, particularly in heterogeneous landscapes, increasing the number of detector locations can help, given that spatial variation in bat activity is often higher than temporal variation (Moreno and Halffter 2000). Conversely, deploying detectors at sites of great importance for bats, such as perennial standing water bodies, may reduce the number of detectors required (de Torrez et al. 2017). Although Adams et al. (2005) advocated the use of lights to increase sampling efficiency, this approach may deter light-averse bats, which would, therefore, be missed from the survey (Froidevaux et al. 2018).

Presence/absence

If the goal is to determine whether individual bats or specific species/members of sonotypes/phonic groups are present, using repeated surveys of sample sites may be appropriate. Employing repeat surveys allows the use of occupancy models to estimate and correct for imperfect detection of species (MacKenzie et al. 2002). MacKenzie and Royle (2005) calculated the optimal number of repeat surveys per sample sites under various circumstances. In general, if the probability of detection is low or the probability of occupancy is high, more repeat surveys at individual sample sites are warranted. If the scope of the project needs to be reduced, then the number of repeat surveys is fixed and the number of sample units is adjusted. If repeat surveys are cheaper than surveys at new sites, the number of replicates can be increased to the highest level possible. Under certain conditions of occupancy and detection, more efficient study designs may allow repeat surveys to cease after a species is detected or to not proceed with surveys if a species is not detected during the first visit (while surveys do proceed at sites where the species was detected (Specht et al. 2017)). However, MacKenzie and Royle (2005) argued that surveyors should expect detection heterogeneity and, therefore, should continue surveys even after detection of a species. The above recommendations assume that the true detection rate is known prior to surveys. The more likely case, though, is that this value is unknown. Then the best strategy is to assume a low detection probability and increase the number of repeat surveys (Clement 2016).

Standard occupancy models assume that bat passes can be correctly identified; however, this assumption may be difficult to meet (Barclay 1999). Recently developed, false-positive occupancy models allow an estimate of misidentification rates and can adjust occupancy estimates accordingly (Royle and Link 2006) using either acoustic data or acoustic information combined with capture data (Miller et al. 2011). The initial application of this false-positive occupancy modeling technique to acoustic and capture data suggested that misidentification rates could be quite high and significantly bias standard occupancy models (Clement et al. 2014). Clement (2016) provided advice on study design when misidentifications from acoustic surveys are a concern, and suggested that in surveys for a single species with known detection rates, surveyors should use only acoustic techniques (if detection rates are high and false-positive rates are low) or only capture surveys (in the other case). If acoustic methods are selected, the number of repeat surveys should be increased relative to the recommendations of MacKenzie and Royle (2005), although the proportional number of additional surveys needed cannot be generalized well across systems and species. More misidentifications would require more surveys (Clement 2016). However, if detection rates are unknown prior to surveys, a good hedging strategy is to perform both repeated acoustic and repeated capture surveys. It is worth noting that occupancy modeling still can be used when misidentification rates are high if recordings are categorized to phonic groups, sonotypes, or acoustic guilds.

Activity patterns

Let’s say we want to compare the activity of a given species in two habitats. If there are a vast number of sample units available, and the selected units are far enough apart, they can be considered independent samples. For simplicity, we also assume (for now) that we have an unlimited supply of bat detectors and that each survey has the same cost, i.e., surveying two sites once each costs the same as surveying one site twice. When we use bat activity as a metric, we must make several assumptions. Key among these are that recorded calls meaningfully represent bats' use of a site (Hayes 2000), that calls can be identified to the correct category (e.g., species, sonotype/phonic group), and that detection rates are the same at different sites. Typically, activity will vary spatially and temporally within each habitat, in addition to the hypothesized inter-habitat effect. Often, simulation studies are a useful tool to decide the best design and we simulate data using the following mixed-effects model:

$$ln(y_{sn}) = \beta_0 + \beta_1 h + \tau_s + \eta_n + \varepsilon_{sn},$$

where $ln(y_{sn})$ is the natural log of bat activity at site s during night n, β_0 is the intercept (also average bat activity in habitat 1), β_1 is the effect of habitat 2 on bat activity, τ_s is the random effect for the survey site, η_n is the random effect for night, and ε_{sn} is the error term. In this simulation, parameter values are based on convenience, but during study design, they should be selected based on biological knowledge. In this simulation, the goal is to select a study design to maximize our ability to obtain a significant estimate for β_1 given a fixed survey intensity budget. Therefore, we vary the number of (simulated) sites and nights surveyed subject to the constraint that $s \times n \leq$ budget. After simulating data, we fit the above model and note if the estimate of β_1 is significant or not. We repeat this many times and identify the values of s and n that most often yield a significant estimate for β_1. The optimal design is to set $n = 1$ and $s =$ budget.

A number of publications advocated for repeat sampling at survey sites (Hayes 1997; Sherwin et al. 2000; Gannon et al. 2003; Milne et al. 2005; Fischer et al. 2009). Many of these contended that nightly variation in bat activity is high and that repeat sampling will improve estimates of activity within a survey unit. Although this contention is correct, if the objective, and indeed the objective of many studies, is to estimate the difference between two habitats rather than to estimate activity within a single survey unit.

Multiple surveys of a single site are not independent and, therefore, provide less information for the model than surveys of additional sites. Using the same logic, if there is spatial variation within sample units, more information is gained by increasing the number of sample units surveyed rather than subsampling each sample unit. Similarly, if the number of detectors is limited, the recommendation remains to move the detectors frequently to maximize the number of sites surveyed. However, if it is cheaper to survey one site repeatedly than to survey many sites, then the optimal design could include repeat sampling because more total surveys could be completed. Alternatively, if the objective is to estimate activity at a specific location (e.g., a toxic spill site), it may not be possible to find replicate sample units, in which case repeat sampling may be the only option for increasing replication. Furthermore, if the research question is focused on changes in activity through time, or covariates that vary through time (e.g., meteorological), repeat surveys would be more appropriate. In addition, systemic variation in activity within sample units may be important to investigate. For example, if activity differs above and below the canopy, and inferences at both levels are required, then multiple detectors must be deployed within a sample unit.

Behavior

Recording sounds emitted in known behavioral contexts

The first step in behavioral studies focusing on bat acoustic communication is to record the sounds emitted by individuals. Researchers must identify situations in which bats naturally produce specific sounds or recreate the conditions to elicit the sounds of interest. To date, the most common types of social signals are produced within roosts (e.g., aggressive calls) or under captive conditions (e.g., distress or isolation calls). However, other types of signals, like contact or mating calls, are not emitted regularly under natural conditions, and thus will be difficult to record.

Although rarely recorded in smaller groups, aggressive calls are perhaps one of the most common signals emitted by bats that live in large colonies (Pfalzer and Kusch 2003; Gadziola et al. 2012; Prat et al. 2016). These signals are often composed of syllables that differ in duration, bandwidth, and amplitude (Gadziola et al. 2012; Lin et al. 2015; Walter and Schnitzler 2017). In the field, recording aggressive calls at roosts is common, but take care to minimize echoes. Captive studies solve this issue by housing bats in anechoic chambers (Pfalzer and Kusch 2003). In the laboratory, aggressive calls can be elicited by placing two bats, in short succession, in a small box (simulating an owner–intruder situation), by placing several bats in a larger room where they can roost and interact, or by irritating them with mild tactile stimulation (Bastian and Schmidt 2008; Gadziola et al. 2012; Prat et al. 2016; Walter and Schnitzler 2017).

Bats emit distress calls when movement is restricted (e.g., when they are handled; Gillam and Fenton 2016). Distress calls are distinctive as they are low frequency, multisyllabic, and more audible than other social calls (Carter et al. 2015; Lin et al. 2015; Hechavarría et al. 2016). Because distress calls are usually loud, it is easy to make high-quality recordings. Distress calls can be recorded from bats entangled in mist nets or while holding them in an acoustically insulated chamber (Carter et al. 2015; Hechavarría et al. 2016).

Isolation calls are regularly produced at the roost, specifically by pups separated from their mothers (Gillam and Fenton 2016; Figure 2-2). These calls allow mothers and pups to find each other, particularly when they live in large, noisy clusters (McCracken and Gustin 1991; Scherrer and Wilkinson 1993). If pups are widely separated in the roost, easily accessible, and their mouth movements can be clearly seen, isolation calls can be recorded when adults leave to forage (Fernandez and Knörnschild 2017). To record isolation calls in the laboratory, temporarily separate a pup from its mother and gently stroke the pup in the hand or place it in a separate chamber (Bohn et al. 2007; Knörnschild et al. 2013; Engler et al. 2017).

Contact calls are emitted by group mates that become separated during flight to maintain contact while locating food or roosts and by individuals that have located a roost and are announcing its location to group mates (Wilkinson and Boughman 1998; Carter et al. 2009; Chaverri et al. 2010; Schöner et al. 2010; Arnold and Wilkinson 2011; Carter et al. 2012; Chaverri et al. 2013; Gillam et al. 2013). Regardless of context, the most challenging question in recording contact calls is "how to predict flight direction or the location of a new roost site?" To answer this question, place microphones within a small area that includes potential roosts, or outfit bats with colored light-emitting diodes to track group

Figure 2-2. Isolation calls by bat pups. *A group of Brazilian free-tailed bat (*Tadarida brasiliensis*) pups that have temporarily been left by their mothers in a cave in the southern United States. Female bats display a remarkable ability to identify the calls of their own offspring among hundreds or thousands of other pups (Gillam and Fenton 2016). © J. Scott Altenbach, Bat Conservation International.*

movements while recording acoustic signals (Wilkinson and Boughman 1998; Chaverri et al. 2010; Montero and Gillam 2015). If you have identified a roost, maximize data collection by placing recording instruments near the roost and focus sampling efforts during the time when most individuals return (Arnold and Wilkinson 2011; Gillam et al. 2013). Contact calls are not very loud and, if recorded far from the animal emitting them, recordings with low signal-to-noise ratio will result.

Mating calls are emitted during the mating season and are associated with courtship and territoriality. To record them, you should first understand the reproductive cycle of your focal species and focus your efforts during female estrus. Although males of several species court females at roosts and may copulate during the daytime, the data are scant, and we do not know the mating habits of most species (Ortega and Arita 1999; Behr et al. 2004; Chaverri and Kunz 2006; Tan et al. 2009; Toth and Parsons 2013). Several studies describe mating calls by males to court females or defend territories (Behr et al. 2004; Knörnschild et al. 2014; Lin et al. 2015; Smotherman et al. 2016; Bartoničková et al. 2016). To collect acoustic data that can be used to unequivocally assign specific behaviors (i.e., courtship or territoriality) to certain calls, it may be necessary to use synchronized audio and video in concert with directional microphones. Sampling should be focused when animals are most active at the roost (Behr et al. 2004), or audio and video equipment may be left at the roost for extended periods (e.g., all night). For species with highly synchronized postpartum estrus, data collection should be focused shortly after parturition (Knörnschild et al. 2014).

Unraveling the function of sounds

A major obstacle in studying acoustic communication by bats is to determine the behavioral context under which signals are emitted, and their function. We know that bats produce multiple social calls while roosting and foraging, but their functions are seldom understood. However, with diligent observation, simultaneous audio and visual recordings, and sound experimental design, we are beginning to learn the function of many cryptic vocalizations.

Direct observations of bats engaging in conspicuous courtship displays (e.g., males hovering over females, especially during estrus; Voigt and Von Helversen 1999; Voigt et al. 2008), and accompanying audio recordings (Behr et al. 2004) have contributed to our understanding of the acoustic underpinnings of sexual selection in bats (Knörnschild et al. 2016). Further, direct observations in the field, coupled with audio recordings and playback experiments, show that bats use contact calls to locate roosts and group members (Chaverri and Gillam 2016). In addition, by simultaneously placing microphones in a bat's flight path and within an occupied roost and then releasing an individual, we know that some species may use a call-and-response system that allows flying individuals to discriminate between conspecifics that are flying and those that have located and entered a suitable roost (Chaverri et al. 2010). Playback experiments in a flight cage confirm that these acoustic signals are important for maintaining contact during flight and for detecting roost sites (Chaverri et al. 2013).

Figure 2-3. Vocalizations of Egyptian rousettes. *Several colonies of Egyptian rousettes (*Rousettus aegyptiacus*) were recorded in captivity to understand better the functions of their various vocalizations (Prat et al. 2016). © Steve Gettle/Minden Pictures, Bat Conservation International.*

There are times when no obvious behavior is associated with a specific vocalization, either because both are rare or because the amount of physical and acoustic interactions among group members precludes individual observations and clear sound recordings. To overcome this, more acoustic and video data are needed over longer periods. Alternatively, or in addition, recording captive bats housed in acoustically isolated chambers may be needed. Several colonies of *Rousettus aegyptiacus* were continuously monitored with video and audio for 75 days, generating an enormous database (ca. 162,000 vocalizations) that allowed specific sounds to be associated with behavioral contexts, as well as identifying the senders and receivers (Prat et al. 2016) (Figure 2-3). By focusing on identifying calls based on their temporal and spectral characteristics and then assigning similar vocalizations to a specific behavioral context, captive *Murina leucogaster* and *Eptesicus fuscus* were found to emit 17–18 syllables, most of which were ascribed to behaviors related to aggression, appeasement, distress, mating, contact, and grooming (Gadziola et al. 2012; Lin et al. 2015).

Designing behavioral experiments using sound: recommendations for sound recording and playback/call broadcast

Most behavioral experiments that use acoustic data include sound playback. To conduct this type of study, consider several issues before starting. First, the sounds used for playback should be recorded with a microphone that will not significantly alter the signal's spectral components. This means using microphones with a moderately flat frequency response (i.e., resulting in the range of frequencies in a signal of interest being recorded at similar intensity). If such a microphone is not available, apply filters to sound files to compensate for the different intensities at which the call components were recorded. Most manufacturers readily share a microphone's frequency response. Use this to gauge microphone suitability or, alternatively, to generate filters that modify sounds accordingly. Resolution of recordings should be at least 16 bits per sample. The number of samples made per second is the sampling rate and must be fast enough to record the highest frequencies of interest (Nyquist Theorem), including multiple harmonics if desired. Using highly directional microphones makes it easier to record only the sounds of interest and get high signal-to-noise ratios that will increase the quality of files for playback. Choose speakers for playback with a moderately flat frequency response over the desired range of frequencies. If more than one speaker is needed for simultaneous playback, ensure that the speakers have the same frequency responses and sound intensity.

Once sounds of interest have been recorded, they can be edited to remove unwanted signals. Using high-pass filters will remove noise under a specific frequency threshold. An important issue for playback studies is that different signals must be included to avoid problems associated with pseudoreplication (McGregor 2000). For example, a project aimed at evaluating the ability of mothers to discriminate among isolation calls from their pup versus foreign young must not use only one isolation call from either test subject. A positive response towards playbacks could be interpreted as either a preference for that particular, but more problematically, to that specific signal.

Population monitoring

Tracking changes in and among populations is a key method for addressing questions related to human effects, disease, and management activities. Methods commonly used to estimate population sizes include mark–recapture, distance sampling, double observer sampling, and point center counts. Typically, these techniques require sightings of individual animals, possibly repeated over time, or at least, reliable documentation of presence of an individual of the species of interest (Lebreton et al. 1992; White 2008; Thompson 2013; Rovero et al. 2013). Given that many bats are cryptic and difficult to capture, let alone recapture, use of these techniques is not well suited to estimate population sizes, particularly across large spatial scales. The use of acoustics to do this is appealing as a lower cost and less effort-intensive option. Acoustic studies may also improve detection probability of the species of interest. However, acoustic data cannot be used currently to distinguish among individuals, between sexes, or even among species in some cases. These inherent constraints restrict the ways that acoustics can be used to monitor populations.

Given these limitations, the use of acoustics to monitor bat populations requires modified sampling designs and statistical analyses, as well as acceptance that the bounds of inference will be narrower than what may be the case for other species and the ability to detect small population changes reduced. So how then, can bat populations be monitored acoustically?

Population-monitoring techniques

Generating counts of individual bats using acoustic techniques is challenging, as multiple recordings may be made by multiple bats or by one bat passing by the microphone multiple times. Many studies report bat passes/calls/recordings, which are all proxies of bat activity and cannot be transformed to estimates of individual bats. At present, there are only three methods that use acoustics to generate counts of bats. Pioneered by cetacean biologists (Mellinger et al. 2007; Marques et al. 2009), microphone arrays generate counts of animals by triangulating the origin of sound using time delay among individual microphones (Efford et al. 2009; Blumstein et al. 2011). Owing to the rapid attenuation of ultrasound in air, the number of microphones needed to monitor a population currently makes this technique unfeasible (Koblitz 2018). Successful use of acoustics to estimate avian population density (Dawson and Efford 2009), continued development of statistical techniques in cetacean acoustic-monitoring programs, and advances in microphone technology (including individual recording units integrating multiple microphones, thereby acting as a mini-array), give confidence that this method will become feasible in the future.

In contrast to microphone arrays, mobile acoustic transects generate counts of bats using a single microphone (Roche et al. 2011; Whitby et al. 2014) by limiting the chance that any individual is recorded twice. Specifically, movement speed along the transect is higher than the speed of the animals, and transect configuration is determined such that bats cannot cross the transect line again before the observer (i.e., the transect does not have a curve or angle that would allow a bat to cut back in front of the observer). Thus, in theory, each recording represents an individual bat passing through the detection area of the microphone. If multiple individuals of the same species are recorded at the same time, it remains impossible to distinguish among them.

Generating counts of individuals using active stationary sampling requires that sampling duration be long enough to document numbers of bats effectively, but short enough to limit multiple detections of the same animal. In practice, this is difficult to achieve and requires skilled operators who can distinguish between freeflying individuals with accuracy. For a more detailed description of active sampling, see the section on sampling approaches later in this chapter. Due to the difficulty of ensuring that no bat is counted multiple times, counts generated using active acoustic monitoring may best be thought of as pseudo-counts. Active stationary monitoring can be quite accurate, as long as the sampling protocol is adequate and observers are highly trained. A notable example of active stationary monitoring with heterodyning detectors is the National Bat Monitoring Programme (NBMP) in the United Kingdom, which relies on volunteers to gather data. Power analysis using data from NBMP indicates an ability to detect a >50% population decline over 25 years for some species (Barlow et al. 2015).

Although counts of individual animals are the preferred basis for assessing population dynamics, broad trends may be derived using measures such as activity levels and dynamic occupancy models. Biologists commonly assume that the number of files recorded by passive detectors (i.e., activity) is related to the number of bats living near that site. If this assumption is reasonable in a study system, long-term passive monitoring of activity patterns at stationary points may provide a measure of long-term changes in bat populations. However, interpretation of data based on trends in activity patterns in the context of population sizes should be highly tempered. The function defining the relationship between activity levels and population levels is undefined. For example, a 25% decrease in activity may not reflect a 25% decrease in population. More generally, it is unlikely that the relationship between activity and population size is strictly linear, given inter and intraspecific interactions (Jachowski et al. 2014). Consequently, passive activity monitoring to assess population trends should be paired with additional measures of population size. The North American Bat Monitoring Program (NABat) is a notable example of the use of passive activity data in conjunction with other data, including those from acoustic transects as well as visual counts at summer and winter roosts, for population monitoring (Loeb et al. 2015).

When changes in population distribution are of interest, assessment of patterns of colonization and extirpation among distinct populations or habitat patches can be informative. An assessment of population “turnover”, i.e., a change in status from occupied to unoccupied, or vice versa, can indicate population expansion or contraction. Although such assessment can incorporate population counts or activity levels, this approach works well with binary data indicating presence or absence.

In some cases, it may be necessary, given differences in ecology and detectability among species, to combine multiple methods to assess bat populations. In other cases, a combination of multiple methods may be a useful way of addressing limitations in equipment, personnel, or funding. Combinations of different methods may also provide hierarchical understanding of populations. For example, a metapopulation study assessing colonization and extirpation among habitat blocks using passive acoustics may benefit from subsampling among occupied blocks using acoustic transects. This combination would provide information on change among populations, along with specific population sizes, while reducing overall sampling effort (achieved by not sampling in unoccupied blocks).

Designing population-monitoring studies

When designing a population-monitoring study, it is common to first determine the population to be monitored, what measure of population is of interest, and for how long the monitoring needs to be undertaken. If a population is to be monitored over several years to detect trends, it is also important to identify the level of change that is of interest. Answering these questions will determine the location, spatial scale, and duration of the study. Selecting the population of interest, although simple in theory, is difficult in practice, as discrete populations of individual species may be difficult to identify, given bats’ ability to travel long distances quickly. This will be particularly difficult when multiple species or a community must be monitored, because of differences in population structures and space use among species. Spatially balanced study designs are well suited to environmental studies generally (Stevens and Olsen 2003; Brown et al. 2015) and bats specifically (Rodhouse et al. 2011, 2012; Loeb et al. 2015). This design may be of particular use when monitoring populations of multiple species, as sampling intensity can be scaled spatially to account for differences among species.

Although statistical power analysis is beneficial for any scientific study, it is particularly useful for studies intended to monitor changes in populations. Power analysis conducted prior to initiation will provide guidance in determining the sample size necessary to detect the level of population change of interest. Power analysis can also be conducted after a project to define the degree of change that is detectable. This can be useful for validating the study methodology and for providing context if no change was detected. Using prospective power analysis to refine study design requires that the statistical methods used to analyze the final data set must be selected in advance. For advanced statistical techniques, such as occupancy models and mixed-effects models, calculation of power can be difficult, as actual methods of calculation may not be well defined or readily available in statistical software (Osenberg et al. 1994; Martin et al. 2011; Guillera-Arroita and Lahoz-Monfort 2012; Johnson et al. 2015). In these cases, it is still helpful to conduct power analysis using a simpler version of the analytical method (Gerrodette 1987). When designing studies to monitor populations of multiple species, it is important to consider power for each species. For example, a study designed to detect a 25% change in population of a common species may be insufficient to detect a much more critical 10% change in population of an already rare species. In multi-species studies, it is best to design around the smallest effect size of interest.

For long-term studies, the ability to replicate sampling protocols between years is critical. Ideally, study design is repeated identically each year, including sampling locations, equipment, and personnel. This is impractical given real-world logistics, equipment degradation, staff changes, land access changes, and funding availability. Fortunately, studies may be designed to account for these differences. Changes in sampling intensity are well tolerated by balanced sampling designs, such as Generalized Random Tessellation Stratified (GRTS) sampling, which allow effort to be scaled up or down without compromising study design. The NABat is one example of a large-scale initiative using this approach. Changes in equipment may be accounted for, albeit imperfectly, by conducting comparative studies in which equipment is paired and set to record in the same conditions. Differences in numbers of recordings on a nightly, hourly, or per minute basis then may be addressed directly in the analysis portion of the study, through use of correction factors or categorical predictor variables. Personnel may be similarly calibrated, although this is only needed when active observation is required.

Sampling approaches

In general, bat detectors can be used either actively or passively. Depending on the species and question of interest, most detector types can be used in various ways, and each approach comes with inherent benefits and drawbacks. Acoustic monitoring is not “one size fits all” and there is no method that can answer all questions for all species. To execute any of the approaches described as follows successfully, it is necessary to deploy detectors in the best way possible. See Chapter 3 (“Bat detector choice and deployment”) for strategies for optimal detector deployment.

Active acoustics

Active detection requires manual control and adjustment of detector orientation. This method dates from when detectors were unable to record sound files and immediate interpretation of sounds using the unaided ear was necessary. The use of heterodyne detectors, which allow operators to tune the device to specific frequency ranges and hear characteristics of sounds emitted by the target bat, is a potential approach for active detection compared to recording and subsequent analysis. Modern detectors that can record are overtaking the use of heterodyne detectors, as recorded files are used increasingly for species identification.

Ideally, the aim is to keep a bat in the zone of detection to maximize call quality and the duration of the recording. The major benefit of this method is that observations of a bat's flight behavior, size, color, and other visual cues can be made in real time, while simultaneously recording acoustic characteristics to aid in the identification of call sequences (Limpens 2002).

The major drawback is that this is the most labor-intensive method of acoustic monitoring and requires a high degree of expertise. However, with practice, long sequences of high-quality calls can be recorded, which are critical for accurate acoustic identification. This method is a primary way to collect voucher calls for call libraries (see Chapter 4, "Echolocation call identification"). There are two primary ways in which active acoustics are used in research: point counts and active transects.

Point counts

Active point counts involve a researcher remaining at a single location (point) and recording bats for a predetermined amount of time. The researcher adjusts the orientation of the microphone while recording presence–absence and activity data.

Active transects

Active transects typically involve recording while on a predetermined route. A researcher, on foot or in a vehicle, adjusts the orientation of the detector microphone while traversing the route and collecting data on presence/absence or activity. If the goal is to educate new researchers or the community about bats in your area, there is no better or more engaging way than taking a "random walk" with an active detector.

Passive acoustics

Passive deployments do not involve a researcher changing the orientation of the microphone. Instead, a detector is set and left to record. A benefit of passive deployment is that recording bouts can be replicated and randomized appropriately for most statistical analysis. The main drawback is that there are many ways a detector can fail, resulting in loss of data. Regardless, many acoustic-monitoring studies employ stationary or mobile passive deployments. Passive stationary deployment is most common, especially to determine presence/absence and habitat use of bats, whereas mobile acoustic transects are best for population monitoring.

Stationary acoustics

Stationary acoustic deployments involve a "set it and forget it" technique that involves a researcher leaving a detector at one point for a time (days to years) without checking it. This allows placement of multiple detectors on a landscape in a short period, and multiple locations can be sampled simultaneously over a predetermined time frame. Because activity patterns vary across both time and space, careful consideration of survey effort (number of sites and number of nights per site) is required to address research objectives.

Stationary detectors are effective when research objectives concern presence/absence. Passive, stationary deployments are also appropriate to answer questions regarding activity patterns; however, do not confuse activity with abundance. If you record 10 bat calls, passive acoustics cannot determine if this is 10 bats each passing the microphone 1 time, 1 bat passing 10 times, or a combination thereof.

When using stationary acoustics for either presence /absence or activity studies, the best practice is to account for detection probability. In presence/absence studies, the use of occupancy techniques accounts for the detection probability of a species, based on equipment and environmental factors. Accounting for detection probability in the context of activity is more difficult. In this case, detection probability of each bat pass must be calculated. Currently, the best methods to do this are double observer methods.

Depending on the research objective, passive deployments can be short or long term. Regardless of duration, proper detector placement and orientation is important. Raise the microphone as far off the ground as possible (>3 m). This reduces the effects of vegetation and insect noise, which reduce the instrument's ability to detect bat calls. Recordings from detectors placed less than 50 m apart can vary significantly, depending on the impact of vegetation or background noise. See Chapter 3 ("Bat detector choice and deployment") for a more in-depth discussion about best practices for deploying stationary detectors.

Short-term deployments are typically measured in days or weeks and are an excellent choice for surveys of individual species. Long-term deployments often last months to years. Long-term deployments may be used for monitoring efforts and to study migratory patterns and seasonal cycles. Detectors are often weatherproof and powered by an external battery (sometimes recharged by solar panels). For these deployments, be aware of battery life and data-storage capability. Even if detectors can operate independently for a long time, check them often to assure that they are functioning properly. A guideline for how often to check is simply "how many data are you willing to lose."

Mobile transects

Mobile transects can be conducted by continuously recording while moving (e.g., using a car or boat) with the microphone(s) oriented so that the zone of detection is above the vehicle. This method is similar to active transects; however, the researcher does not change detector orientation or vehicle speed as bats are encountered. Mobile transects were developed in Sweden in the early 1980s and used to monitor populations and evaluate habitat use (Ahlén 1980, 1983; Jüdes 1987; de Jong and Ahlén 1991; Rydell 1991; Blake et al. 1994).

This method can overcome the high spatio-temporal variation in bat activity by sampling a large geographic region in a short time. This allows researchers to collect large amounts of quantitative data about populations of abundant and easily identifiable species. Further, because this method only requires one piece of equipment per transect, established transects can be monitored using citizen science, which reduces the burden of monitoring programs on researchers (Whitby et al. 2014). This method is not useful for studies of rare species or those that avoid transects (i.e., roads, rivers, or paths).

Unlike other acoustic methods, mobile transects can provide an index of abundance (number of calls recorded) and are most appropriate for monitoring efforts. This method can detect small declines in a species population (Roche 2011) and, although initial abundance can be low, this has little effect on the power of monitoring efforts. Consistency within transects between years is important. Some differences can be accounted for in modeling efforts (e.g., temperature), although others (e.g., change in detector or microphone type) cannot. Furthermore, abundance estimates are possible because a mobile transect is conducted at a speed faster than bat flight. Mobile methods that are slower than bat flight speed (e.g., bike) likely do not meet the assumptions critical for abundance estimation. Thus, vehicle speed should be chosen by determining the flight speed(s) of the species of interest.

Mobile transects may also be appropriate to evaluate habitat use. Locations can be embedded in recordings, allowing the abundance of bats to be related to proximity of habitat features. Multiple stationary detectors used simultaneously are better at answering most questions concerning habitat use than are mobile transects. However, if the number of detectors is limited, mobile transects can provide some insight into habitat use if the study is carefully designed and implemented.

Summary

The goal of this chapter has been to provide foundational knowledge about some common study types that employ acoustic techniques to investigate bat populations and to introduce readers to basic approaches to acoustic sampling, with an emphasis on both taxon- and system-based research. The field of bat acoustics is constantly changing, and it is important to realize that this chapter is not exhaustive. Creativity in study design is a must, and acoustic techniques have been used to approach a range of other research questions. For example, acoustic monitoring may be used in phenological studies, allowing researchers to monitor known or potential hibernacula entrances, bridges, and maternity roosts to determine seasonal arrival and departure times of migrants and peaks of seasonal activity at swarming sites. Similarly, acoustic monitoring can be used in disease surveillance, allowing researchers to detect movement of bats in and out of hibernacula and to determine levels of aberrant daytime flight, which is symptomatic of white-nose syndrome in North American bats. Case study 3 ("Going, going, gone: Declining bat activity in summer following the arrival of white-nose syndrome in upper New York State") at the end of this Handbook provides a good example of one such project.

In conclusion, every proposed acoustic study is unique and includes different constraints and opportunities, ranging from the number and types of bat species present to the budget available to the accessibility of sites. The descriptions in this book are just the first step in study design, providing a springboard for creating and modifying the optimal study design to address unique research questions in varying sets of circumstances.

Some additional suggestions

1. Ensure bat presence and/or activity surveys are conducted for an appropriate duration.

Bat activity varies widely from night to night at a single location. Some protocols for passive surveys to confirm species presence suggest that two nights are sufficient to document the presence of a species at a site. However, there can be an order of magnitude difference in the number of bat passes per night, sometimes even between two consecutive nights. This will influence the measure of species diversity.

2. Be skeptical of "manufacturer's recommended" detector settings. Understand the ramifications.

Many protocols encourage researchers to "use the manufacturer's suggested settings" for bat detectors. When manufacturers provide user settings it is because they are aware that different gain, sensitivity, trigger level, and signal-to-noise ratios are appropriate for different recording objectives and/or field conditions. Therefore, instructions like, "set your detector to a sensitivity level of 7," can be misleading. Do not assume that identical settings on different detectors will return comparable data. Calibrate detectors to meet the specific goals of the study.

Brazilian free-tailed bats (*Tadarida brasiliensis*) emerge from a cave at dusk. © Jonathan Alonzo, Bat Conservation International.

Chapter 3. Bat Detector Choice and Deployment

Introduction

Once you have decided that acoustic monitoring is the best method for your study, the choice of detector can be daunting (Fenton 2000.) Budget inevitably guides many equipment choices, but the selection of hardware should ideally be driven by your reasons for buying it. If you are using a detector for outreach and education, then an immediate visual or audio output is more important than many other features. If your goal is to perform academic, management, or conservation research, then hardware choices will be driven by study objectives and may vary with location, bat community, and research questions.

In this chapter, we first discuss the thought processes involved in selecting the best detector. In doing so, we provide a brief summary of the main types of detector, a discussion of some of the trade-offs that you may consider when choosing an instrument for your study, and a list of questions that you might ask vendors to help you make an informed decision. Second, we provide guidance on how to deploy the detectors that you use most effectively.

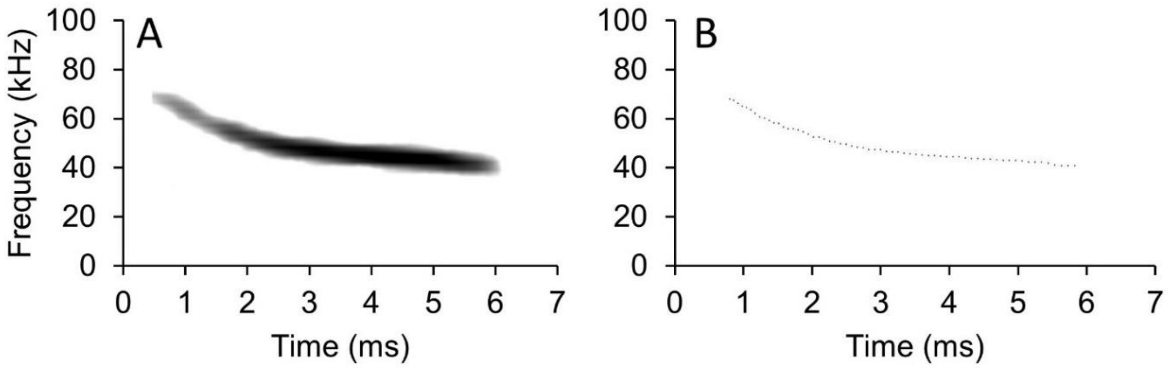

***Figure 3-1. Full spectrum and zero-crossing recordings.** Examples of spectrograms of (A) full spectrum and (B) zero-crossing recordings of the same little brown myotis* (Myotis lucifugus) *echolocation call.*

Bat detector types

Bat detectors can be heterodyne or broadband. Heterodyne detectors are tuned to a narrow range of frequencies and convert sounds of those frequencies to audible (to humans) sounds in real time. This provides a quick method to listen for bat presence. Similar to experienced birders who can bird "by ear," well-trained specialists may identify bat echolocation calls to species or sonotype/phonic group simply by listening to the output of a heterodyne detector (Barataud 2015). Heterodyne detectors provide little information about call structure, but are a low-cost tool that can be used easily in citizen-science monitoring efforts and are effective for community outreach and education about bats and echolocation.

Survey efforts typically require broadband detectors, which record a range of frequencies simultaneously, to identify species, especially in communities where calls vary in frequency (Limpens 2002). Broadband detectors mainly use zero-crossing (frequency division) or Fourier analysis to process digitally recorded calls. Zero-crossing analysis is simple and fast with low digital storage requirements, although it can only analyze a single harmonic and is limited by a loss of amplitude information (Figure 3-1). Fourier analysis gives information on amplitude, frequency, and duration of echolocation calls. Fourier analysis typically uses untransformed, real-time signals, resulting in little information loss, but the analysis is computationally demanding (Parsons et al. 2000; Parsons and Szewczak 2009). There is disagreement about the relative value of the two methods. Each has its trade-offs. Zero-crossing is a quick, simple method, but detects fewer calls than the information-rich Fourier analysis (Adams et al. 2012). Fourier analysis requires more battery life and data storage than zero-crossing analysis, but can evaluate an entire call, including harmonics and amplitude information.

Trade-offs in detector hardware

The main trade-offs to consider when selecting a broadband bat detector include (*i*) the recording quality and type needed to complete the required observation or analyses, (*ii*) the field characteristics of the detectors (e.g., battery life, weatherproofing), and (*iii*) cost. We discuss each in turn and provide a list of questions (see box at the end of the chapter) that can help you to learn about each of these characteristics as you research the different types.

i. Recording quality and type

The bat community being studied and the resolution in call analysis required will both influence choices of hardware and detector settings. For example, the highest frequency echolocation calls will dictate the required sampling rate. A sampling rate must be at least twice that of the highest frequency of interest (Nyquist Frequency). If the bat community contains few high-frequency bats, and/or if capturing these high frequencies is unnecessary (e.g., not all bat passes need to be identified to species level, higher harmonics are not important, etc.), then a lower sampling rate can suffice (Figure 3-2). Sampling rates of 500 samples per second (kHz) or higher are used by many researchers, but 256 kHz will record sounds up to 128 kHz, which can suffice for recording of many North American species when information about only the fundamental harmonic is desired.

Figure 3-2. The importance of sampling rate. *A detector capable of recording with a high sampling rate would be required to detect the presence of this Percival's short-eared trident bat (*Cloeotis percivali*), which typically echolocates at frequencies greater than 200 kHz! © Sherri and Brock Fenton.*

The data format of recordings also is an important consideration. To identify species from calls, automated call analysis software may accept only full-spectrum or zero-crossing input, so it is important to collect the type of data required by the software package being used. It is critical to realize that although full-spectrum files can be converted into zero-crossing format (there are several software packages that will do this), you cannot convert zero-crossing into full-spectrum data. It is thus recommended that, if you are uncertain about the required data format for post-field processing, full spectrum data be collected. Recording of zero-crossing files by the detector (rather than deriving this format from full-spectrum recordings during post-processing) is referred to as "native zero-crossing."

If you are not using a call analysis software package, manual identification using a reference library is easier if calls are recorded in the same format as the reference library. If you plan to compare data with those from past surveys, choose similar hardware, as detectors vary in detection efficacy (e.g., sensitivities), which can result in different depictions of the same bat community, limiting the value of comparisons among surveys (Adams et al. 2012).

ii. Field characteristics

Survey duration and site location/accessibility all influence choice of detector. Regardless of the characteristics of a field site, a detector needs to be able to maintain power, store sufficient data, survive the elements, and be transported to the deployment location.

When determining what detector to use, some questions to consider and/or ask vendors about are listed below. Where necessary, we have expanded on some of the questions in italics.

- **What is the frequency response of the microphone?** *"Flat" microphone responses mean the microphone has relatively similar sensitivity to all frequencies of interest. It is a good idea to use a microphone with a similar response to the one that was used to collect reference library recordings; this is critical if frequency amplitudes are being considered in call identification.*
- **What is the frequency recording range of the detector and microphone?** *This must be able to sample your highest and lowest frequencies of interest. See Chapter 4 for some examples of the variation in the frequencies of echolocation calls.*
- **How directional is the microphone? Is there an option to switch among microphones with different directionalities?** *Directional and omnidirectional microphones are deployed differently and have different pros and cons.*
- **What are the signal-to-noise ratio characteristics? Are they adjustable?** *This will determine how close to the microphone the bat needs to be to trigger a recording, and how often noise might falsely trigger your detector.*
- **What is the detector storage/memory capacity? What are the scheduling capabilities for detector recording?**
- **Does the detector record in full spectrum, native zero-crossing, or have the option to do either?**
- **How much does the detector weigh? How portable/resilient is it?**
- **How tamper resistant is the detector and is it secure from theft?**
- **How weatherproof is the detector/microphone? Are there some conditions where they should not be used?** *For example, some microphones may have a windscreen that when wet and frozen blocks ultrasound. Some detectors have limitations on safe operating temperatures.*
- **What is the average battery life? Does extreme cold or heat affect this?**
- **Can the detector be connected to external power?**
- **Can batteries (detector power, internal clock) and storage capacity be monitored?**
- **Is the internal clock battery user-replaceable? Will the detector still function if this battery dies?**
- **What happens during a power failure or other component failure?**
- **Can the detector record GPS coordinates and associate them with individual recordings? Does it log and how often?** *For example, some detectors only log a waypoint once per minute, which may not be enough for a driving transect.*
- **Does the detector have any additional sensors?** *For example, temperature and humidity.*
- **Can the data be downloaded remotely? Can the detector send remote alerts?**
- **Does the detector have self-diagnostics? How do you know if the detector is functioning properly?**
- **Does the detector have speakers or a place to plug in a headset to listen to bats or other ultrasonic sounds in the environment?**
- **What length of microphone cables can be used and how does signal degrade with cable length?**

Surveys in remote locations that require many nights of sampling may benefit from detectors with a long battery life, high data-storage capacity, and remote data access. Local climate is important for determining the amount and type of weatherproofing that is required, as well as the estimated life of the microphones. Detector size and mass are important if researchers need to hike to distant sites, and detector appearance and locking mechanisms may be important for security in high-traffic areas.

iii. Budget

The most influential aspect for most researchers when choosing detector hardware is usually cost. Detectors vary in price depending on a range of features including, but not limited to, weatherproofing, data storage, temperature sensors, and GPS capability. However, some key features, like microphone quality, directionality, sampling rate, and recording technology will determine the ability to detect bats and should actually be the priority.

Effective bat detector deployment

Once you select the detector that you will use, give careful thought to deployment. Various characteristics of detector deployment, including location, orientation, and settings, can have a substantial impact on the quality of recordings (Figure 3-3; Figure 3-4). The following list highlights some important considerations.

i. Settings

When using a zero-crossing system, determine whether you need to set the noise floor for your detector or if this is automatically set. If automatic, it is critical to plug your microphone in and then start the detector in the area where it will be deployed. It is also important to know how often the noise floor is automatically recalculated, and whether you can program the detector to do this at a custom interval. If using full-spectrum recording, use a sampling rate appropriate for capturing the highest frequencies of the bats of interest (Nyquist Frequency; see previous description).

ii. Recording search-phase calls

Deploy detectors along a flyway where bats are likely to commute. This placement will increase the likelihood that the bats will be producing stereotypical search phase echolocation calls, which will make them most likely to be identifiable. Recording on a bat's route from a roost to a drinking or feeding area will increase the likelihood of recording search-phase calls rather than social calls or feeding buzzes. Recording in a low-clutter location will also maximize the chance of obtaining search-phase calls rather than those produced in reaction to clutter.

iii. Recording social calls

Deploy detectors near a roost, but make sure that the microphone is placed some distance from the exit to avoid capturing early-phase and social calls that may limit identification. If you are making full-spectrum recordings, avoid oversaturated recordings caused by recording bats that are too close to the microphone. You can reduce oversaturation by decreasing the gain or increasing the distance of the microphone to the bats.

iv. Detector properties

Some physical properties of detectors can negatively impact your recordings. A housing over the microphone to protect it from inclement weather will reduce detection distance and can lead to potentially spurious sounds or reflections captured in the recordings. Microphone cables connecting aspects of your system have limits. If they are

Figure 3-3. Examples of bat detector deployment. *Actual bat detector deployments demonstrating a small sample of the variety of deployment techniques. Bat detectors, microphones, and deployment devices are highlighted in lighter shaded areas of the images. Image (a) shows a bat detector attached to a tree with a locking cable and microphone elevated on an extensible pole; sampling area is sub-canopy and comprises open forest understory and the small stream seen in the background © Alexander Silvis. Image (b) shows a microphone elevated on a pole attached to a snag; sampling area is above canopy © Darrian Washinger. Image (c) shows a microphone deployed on a fence post with the bat detector at the bottom of the post © Erin Swerdfeger. Image (d) shows a long-term acoustical monitoring station comprising a directional microphone, detector, and power supply in weatherproof housing accompanied by a solar panel; this system includes remote data upload using cellular technology © Alexander Silvis.*

long, check with the manufacturer that the cable you plan to use does not severely attenuate signal transmission.

v. Factors in the local environment

To optimize recordings, anticipate changes in sunset/sunrise times, as well as daily and seasonal weather. Check your recording site with a simple heterodyne detector before

Figure 3-4. Sampling flyways. *Bat detector deployed along a forest path that serves as a flyway for bats. Detector is attached to a tree, whereas the microphone is elevated on a pole and positioned to the side of the path and away from the immediate acoustic shielding of the tree; both are highlighted in the lighter shaded areas of the image. Always consider whether vehicles or people may collide with detectors and other equipment when sampling along flyways like roads or hiking paths. © Alexander Silvis.*

deployment and assess other local sources of ultrasonic noise. Factors like wind, rain or snow, insect calls, or nearby devices like irrigation sprinklers can turn what may have seemed like an acoustically quiet site into a horrible one. Wind is especially challenging. You should secure cables and straps, cut long grass, and remove flagging tape, all of which can create noise. Move detectors away from dripping/running water, localized insect noise, and electromagnetic interference. Through acoustic assessment and due diligence, you may find that a change in position of just a few meters can make a huge difference in recording quality.

vi. Clutter

Any clutter near a microphone will cause unwanted reflections of sound back into the path of the incoming signal. Remember that the ground is also clutter, so elevate the microphone sufficiently to reduce reflection of sound from the ground. The height of the microphone should be made based on the technical capabilities of the microphone used. A minimum height of 3 m is generally recommended to improve signal-to-noise ratio, reduce echo distortion, and also increase the vertical reach of the detector’s detection volume for omnidirectional microphones. When determining microphone deployment height, also consider whether you may exclude recording particularly low-flying species. It is best to set microphones in areas where the ground cover will dampen echoes, for example, leaf litter or grass, as opposed to over a paved surface or near water, unless study objectives are specific to areas with the latter kind of ground cover. Ideally, have the microphone aimed at an opening through any forest canopy to allow unobstructed detection of species foraging above. If you are actively recording ultrasound while driving, the roof of the vehicle becomes the ground, so you must elevate your microphone well above it or keep it close to the roof and direct the microphone downward at the roof. Microphones pointed down at the roof will record only reflected signals, sometimes reducing recording quality. Elevating the microphone on a pole about 2 m above the roof and using an upward pointing directional microphone will reduce road noise. A test run is useful, because different factors can affect recordings, such as use of electric versus combustion engines, gravel versus paved roads, directional versus omni-directional microphones, microphone housing, etc.

vii. Camouflaging detector equipment

When possible, place detectors to blend in with the surroundings while keeping microphones away from clutter and vegetation. For example, direct your microphone out into a flyway from a pole extending from a prominent shrub rather than simply placing a bare pole in the ground. Conspicuous placement in a flyway may attract attention from humans, other wildlife, or even the bats if they are accustomed to flying in an area free of obstacles.

viii. Keeping equipment safe

For longer-term deployments, be aware that cables and gear are attractive to chewing rodents, scratching cows, web-building spiders, nest-building insects, and even humans (Figure 3-5). Damage to cables or other parts of the system will ruin a recording session, so protection is critical. Take precautions like using a split tube loom covering on cables (i.e., thin corrugated plastic tubing that slips over cables easily and is available at most automotive supply stores). Indicator lights, particularly those that blink, will attract curious (and potentially malicious) humans and wildlife. Whenever possible, disable lighting, enclose your gear, or cover any lights with opaque tape. Reduce attractive scents when deploying detectors by using latex gloves or hunting spray. Expect the unexpected and check your system at regular

Figure 3-5. Damaged field equipment. *Bat detectors deployed in the field are subjected to many hazards. For deployments in areas where rodents are common, (a) placing detector hardware inside protective cases can be a worthwhile investment — remember to check cables frequently, as these often are more difficult to protect © Cori Lausen. Equipment should always be checked after severe weather events, as (b) lightning and wind can severely damage or destroy equipment and data © Rachel Hamilton. It is not always possible to protect equipment, as (c) inquisitive large mammals, such as this family of black bears, and people can overpower or outmaneuver protective cases © Ontario Ministry of Natural Resources and Forestry. Ensuring that no food residue is transferred to equipment following a luncheon in the field can reduce the risk of exposure to some species.*

intervals (frequency determined by the amount of data you are willing to lose).

ix. Microphone detectability

When recording bats on a walking transect, note that the microphone will pick up bats that are flying behind or above you. Knowing the directionality of your microphone (which is important for all applications not just for walking transects) will allow you to judge whether you have recorded the bat you observed. You can ensure you are recording the desired animal by listening to the sounds you detect in real time and correlating them with the observed movement of a bat.

x. Check and double-check

Before walking away from your passively deployed detector, test that it is working! Use a source of ultrasound (e.g., snapping fingers, rattling keys) with the detector turned on to ensure that your microphone is working, all cables are properly attached, and the detector settings are appropriate. When programming your detector, double check that you are using the right values for time zones and longitudes. Double check the power supply, settings, and connections before you leave. It is often (and perhaps even usually) the simplest things that ruin a recording session, and any of these can be avoided.

Summary

Choosing a detector can be intimidating, with a seemingly endless array of technical specifications. The topics discussed in this chapter should provide a support framework to make detector selection easier.

Some additional suggestions

1. Do not assume that any bat detector will work for your project.

There is no “one size fits all” bat detector that can be used to perform all applications. The preferred detector of even the most experienced bat acoustic biologists may not be right for you and your needs. Researchers must understand the survey conditions and unique demands that are placed on a detector. It is like buying footwear: no type of shoe can do everything, but each type can do something.

2. Invest time learning about the limitations of your chosen bat detector.

Bat detectors have many settings and options that allow users to maximize performance depending on the location or species of interest. A new bat detector should not be handed to a novice with the instructions: “sample the bat activity and species diversity” in a habitat of interest. You should spend time getting to know the settings on the units and how different options return different quality recordings.

3. Keep it simple.

Do not become enamored with the newest gadgets and discard older hardware like heterodyne detectors. Modern full-spectrum detectors offer previously unimaginable options for monitoring and identifying bats including live spectrograms and automatic species identification. However, when it comes to getting a feel for how bats behave in the field, the option of the old-fashioned (and cheap) heterodyne detector remains a good one.

Curaçaoan long-nosed bat (*Leptonycteris curasoae*) feeding at an agave blossom. © Bruce D. Tauberg/Bat Conservation International.

Chapter 4. Echolocation Call Identification

Introduction

One of the greatest challenges faced by biologists conducting acoustic surveys is what to do with *all those recordings.* Bat detectors can be deployed remotely for weeks at a time and, while in the field, they can record hundreds of thousands of calls that take up terabytes of storage space. The goal of many acoustic studies is to identify these recordings to the species level or at least to sonotype/phonic group. Researchers may be unsure about how to proceed with identification. In many cases, it is simply not possible for humans to examine each recording manually, so they must rely on software-based automated analyses. But which approach is best? Even with the available software, should biologists conducting acoustic monitoring be able to identify echolocation calls manually? How best to deal with uncertainty in identification? All these questions require careful consideration. Echolocation call identification is one of the most contentious issues surrounding the use of acoustics. Figure 4-1 offers a light-hearted take on this long-standing discussion.

In this chapter, we begin by summarizing the overall process of call identification, elaborating on strategies for both manual and

Figure 4-1. A humorous point. *This clever cartoon was found in the archives of Dr. Thomas Kunz. We believe that it was drawn by Dr. Kunz and features Dr. Brock Fenton while alluding to bats producing echolocation calls that are audible to humans. The cartoon is an example of the really good fun had by these two biologists. It also illustrates two of the main messages of this Handbook: 1) the potential for acoustic techniques to help researchers make exciting discoveries about bats in ways that might otherwise not be possible and 2) the uncertainty inherent in identification of bats from recorded echolocation calls. The echolocation calls of spotted bats (*Euderma maculatum*) are distinctive, having the most energy at around 10 kHz. In the southern Okanagan Valley in British Columbia (Canada), some naturalists were familiar with the calls, but attributed them to an insect because "everyone" knows that bat echolocation calls are ultrasonic. Both Drs. Kunz and Fenton substantially advanced our knowledge of bat biology, mentoring many students and producing large bodies of work. This cartoon was used with the permission of Dr. Kunz's family and Dr. Fenton.*

automated approaches, as well as the benefits and drawbacks of each. For a reminder on the ways that recordings of echolocation calls can be visualized, see Figure 1-3. We then discuss one of the main reasons that identification can be so problematic — namely, the tremendous intraspecific variation that exists in echolocation calls. We finish with a discussion of call libraries, which are necessary for use in training novices in manual identification, as well as for developing automated classifiers. We also include a section on best practices for producing call libraries, given that many biologists are working in areas where the local bat community has received so little study that the creation of a library is the first step in their acoustic-monitoring efforts.

Call identification process — overview

The process of using specialized broadband detectors to record echolocation calls allows high-frequency sound to be transformed into a form that can be measured and visualized using purpose-built software. For a reminder of the types of recordings that are typically made, see “Bat detector types” in Chapter 3 (“Bat detector choice and deployment”), which discusses heterodyne, zero-crossing/frequency division, and full-spectrum recorders. As discussed in Chapter 2 ("Acoustic survey design"), echolocation data may be used to address a multitude of ecological, biological, and behavioral questions. To answer many of these questions, it often is necessary first to analyze recordings of echolocation calls and identify species, genera, or sonotypes/phonic groups present in the recorded information. Typically, identification is performed at the file level, with files often corresponding to bat "passes." Less commonly, identification is performed within a file. Identification within a file is most common when long files are recorded, such as when detectors are programmed to record continuously, rather than for predetermined periods or in response to specific acoustic triggers.

Identification of calls to species is a technically difficult task owing to interspecific similarities (often those within the same genus) and intraspecific variation within species' calls. In some cases, identification to species is not possible because of an inability to distinguish reliably among calls of individual species. In these circumstances, identification to genus, or species group or complex, may be the best approach. Identification to species may not be possible when little is known about the calls made by individual species within an area, as may be the case in many species-rich ecosystems that have received relatively little study. In these circumstances, identification of calls to phonic or morphological (e.g., constant frequency, frequency modulated, upsweep, downsweep) groups may occur. Although bats are capable of making a variety of calls, echolocation call frequency and call morphology typically are correlated with body size and habitat (Aldridge and Rautenbach 1987; Bogdanowicz et al. 1999). Thus, identification to phonic or morphological group can provide ecological insights to a community even when individual species identities are unknown. When identifying calls to phonic or morphological group, remember that social calls and feeding buzzes are typically not correlated with body size or habitat.

Regardless of whether calls are identified to species, or phonic or morphological group, the process of identification itself is fairly simple and can be categorized into three steps: 1) **detect** bat call information in a recording; 2) **parameterize** characteristics of the call, and 3) **identify** the call based on its parameters. As a process, these steps are consistent, regardless of whether calls are identified by humans or software. For example, an observer with a heterodyne detector identifying free-flying bats in real time detects the call using the detector and parameterizes it based on the frequency band to which the detector is tuned, as well as other characteristics of the sound perceived by the operator, who then identifies it based on their knowledge and experience. Similarly, call identification software must first detect the presence of echolocation calls within a recording, collect measurements to quantify patterns (parameterize) from those calls, and then use a software-specific algorithm and call library to assign a likely identification.

The call-identification process may involve performing these three steps only once, as in the two previous examples, or iteratively. Pairing identification by software with human manual identification is an example of an iterative process: an operator may use one or multiple software programs to complete each of the three identification steps and then manually complete them again to check or "vet" a subset of the automated identifications.

Similarly, a human identifying bat calls may review the recorded data to find files with bat calls (detect), assess the frequency range of the calls (parameterize), and then separate those files based on call-frequency range (identify). After this initial screening, the human identifier may then review the sorted call data again to determine which files are echolocation calls and which are social calls (detect), then measure characteristics of echolocation calls (parameterize) and identify echolocation calls to species based on measured parameters (identify).

The consistency in these three stages of echolocation call identification does not preclude tremendous variability within these steps among individuals, research programs, or software. Indeed, there are almost as many unique approaches within these steps as there are bats. We discuss these steps in more detail in the following.

Detecting bat calls

In general, detecting calls may be performed manually by humans, automated with the use of computer software, or as a combination of the two. Detection of echolocation data by humans may be auditory, visual, or a combination of the two, and may occur in real time or after the fact if echolocation call data are recorded.

Auditory detection of echolocation call data requires that calls are audible to the human ear and that the observer has some knowledge about the sounds that bats make. Ultrasonic echolocation calls can be made audible through frequency division, time expansion, or heterodyning. In contrast to bird song, bat echolocation calls are not designed to convey information about species or individuals (Barclay 1999). Because echolocation calls are used for navigation, these calls commonly follow a consistent pattern whereby sounds are emitted at regular intervals, with a decrease in the interval when increased resolution of the surrounding environment is needed (e.g., in cluttered areas) or when prey are being approached (e.g., feeding buzz). As heard through heterodyne or frequency division detectors, echolocation calls emitted by bats may sound like a series of regular "tcks". In species for which social calls are important for reproduction, it may be possible to identify species by mating "songs" (e.g., Barlow and Jones 1997.)

Visual identification of echolocation calls requires that calls be visible in real time on a detector or be recorded and viewed using software capable of displaying sonograms. As with auditory detection, visual detection of calls requires that the observer have some information about what bat calls look like. This Handbook includes examples of echolocation calls recorded globally (Figure 4-2). From a scientific perspective, recording echolocation calls for subsequent analysis often is preferable to real-time identification, as more time may be spent on the identification process.

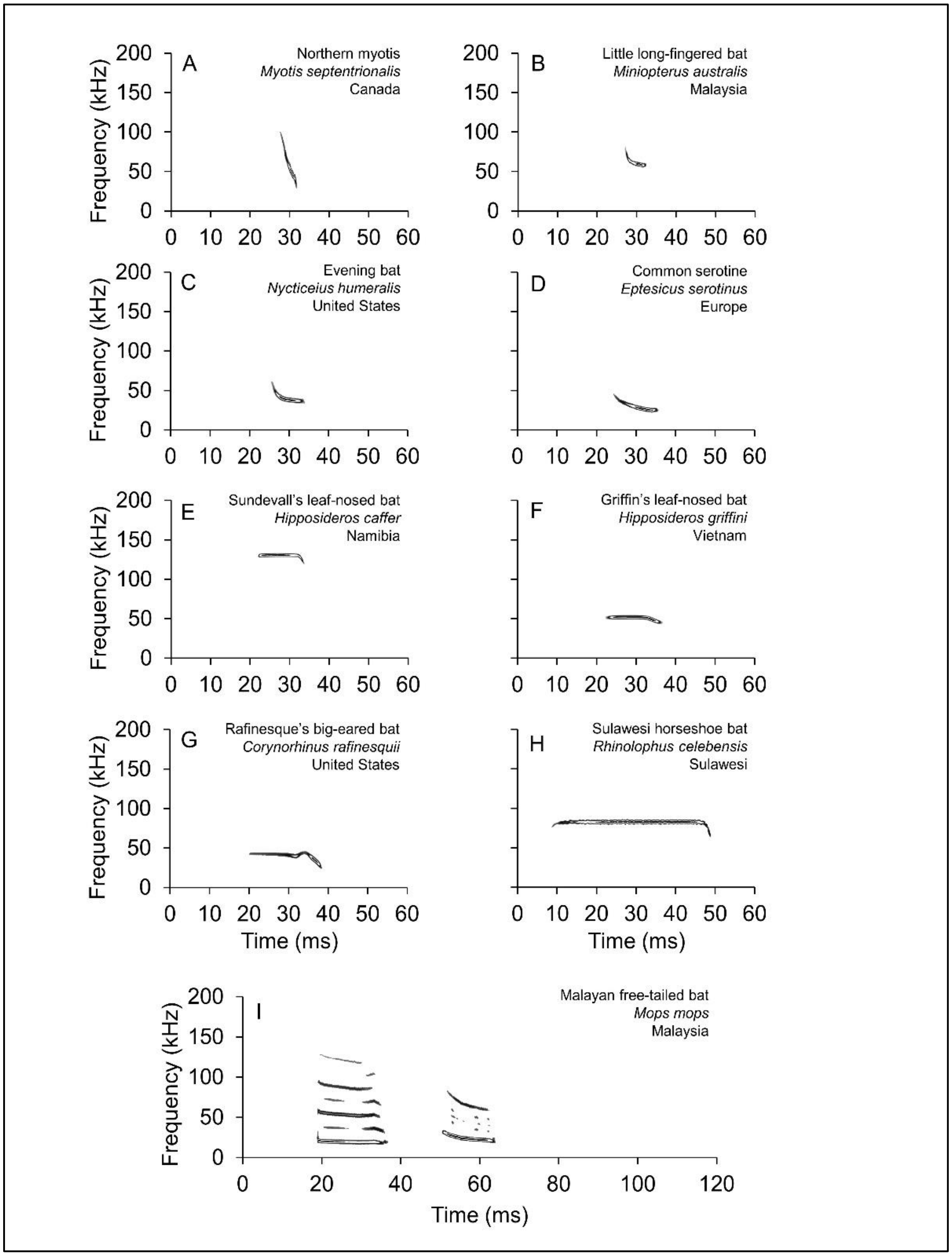

Figure 4-2. Examples of search-phase echolocation calls from bats around the world. *There is huge variation in the structures of the search-phase echolocation calls of different bat species, as illustrated in this small selection of spectrograms of full spectrum recordings: (A) northern myotis* (Myotis septentrionalis) *(Canada); (B) little long-fingered bat* (Miniopterus australis) *(Malaysia); (C) evening bat* (Nycticeius humeralis) *(United States); (D) common serotine* (Eptesicus serotinus) *(Europe); (E) Sundevall's leaf-nosed bat* (Hipposideros caffer) *(Namibia); (F) Griffin's leaf-nosed bat* (Hipposideros griffini) *(Vietnam); (G) Rafinesque's big-eared bat* (*Corynorhinus rafinesquii*) *(United States); (H) Sulawesi horseshoe bat* (Rhinolophus celebensis) *(Sulawesi); (I) Malayan free-tailed bat* (Mops mops) *(Malaysia). Note that typical calls may be frequency-modulated sweeps (A, B, C) or constant frequency (E, F, H), be relatively high frequency (E) or relatively low frequency (G), be extremely short (A) or very long (H). Although most bat species have one type of typical search-phase echolocation call, a small number of species may alternate among two or more different call types in a predictable pattern (alternating call types represented by I).*

Automated detection of echolocation calls using software may be accomplished using various methods, algorithms, and software. However, all techniques fundamentally involve pattern recognition. Historically, pattern recognition was based on expected characteristics of bat calls. This technique required some level of knowledge about the characteristics of echolocation calls made by bats within the area of interest, thereby historically limiting the application of automated detection to well-studied communities.

Automated detection of bat calls is often referred to as “filtering.” In some cases, filters may be designed by users, and in others, they may be preset. This step involves identifying calls through removal of non-search–phase calls, feeding buzzes, fragmentary calls, etc. This process serves to separate calls that are produced by bats but are not identifiable to species versus those calls that are of sufficient quality for accurate species identification. Despite the importance of this step in the acoustic identification process, it is extremely difficult, as there are no clear-cut boundaries for this determination. Instead, this is a balancing act in which acoustic identification is better when more files are identified, but the chances of misclassification increase with lower-quality calls. Thus, the better the recordings, the more data that can be extracted. This is particularly important for species with low-intensity calls and those species that exhibit significant overlap with other species. For example, the northern myotis (*Myotis septentrionalis*) has a low-intensity echolocation call that commonly results in low-quality recordings. When northern myotis were common on the North American landscape, the filtering out of some files from this species did not have a major impact on estimates of presence/absence. However, with the massive declines associated with white-nose syndrome, the impact of filtering out some files is more pronounced and can have dramatic influence on the results obtained. Overall, there are two approaches that can help to minimize this issue (there will always be low-quality calls recorded, so the issue cannot be eliminated). First, software developers must continue to refine filtering processes to minimize these impacts, and, second, users of acoustic detectors should work to improve recording conditions so that optimal recordings are made and analyzed.

Today, machine learning is increasingly being implemented to detect bat calls within recordings. Machine learning does not require knowledge of echolocation calls within an area and may be particularly useful in regions where little is known about the bat community. Detection of calls using machine learning depends on deep-learning algorithms that can identify patterns without subjective input. The avoidance of subjective input has various advantages, including an improved ability to detect calls when levels of background noise are high. Mac Aodha et al. (2018) developed an open-source tool in the Python programming environment that is freely available through GitHub (https://github.com/macaodha/batdetect). To date and to our knowledge, no commercial software uses machine learning to detect echolocation calls.

Parameterizing bat calls

Bat calls may be parameterized at the level of both the individual call and the entire file, using qualitative or quantitative measures or a combination of both. How calls are parameterized will depend in large part on the data type. For example, a call recorded in zero-crossing does not include information on call intensity, whereas a full spectrum call does.

Qualitative parameterization may be performed using both auditory and visual perception. If calls are detected using auditory perception (i.e., a human operator uses hardware or software to hear a modified version of the original call), then parameterization may be based on frequency range and timing/rhythm of calls within call sequences. If calls are detected using visual perception (i.e., a human operator views them using a software viewer), then parameterization may be based on the pattern of individual calls within a call sequence, and the shape and frequency range of the individual calls.

Quantitative parameterization of calls can be performed manually by humans or using call analysis software. What parameters are measured from an echolocation call and/or call sequence, as well as how they are measured, can vary, and whether parameters are measured at the individual call level or for an entire call sequence varies among brands of software. A variety of data may be extracted from acoustic recordings and used to aid identification efforts. Commonly measured parameters are broadly similar across software, with most seeking to describe the shape of the call. Figure 4-3 illustrates some of the commonly used measurements, and Table 4-1 lists more and provides definitions. Measurements may be of call frequency, amplitude, or a combination of the two. Measurements of call amplitude are important not just to quantify a call's peak frequency, but also because particularly low- or high-amplitude recordings may be missing important spectral information and may not be appropriate for analysis. The inclusion of amplitude information allows for analytical approaches that use only high-quality recordings. Many software packages that allow automated identification may use hundreds of measurements from calls to assign identifications.

However, as discussed previously, implementation of machine-learning techniques for call identification represents a fundamental change in how calls are parameterized: rather than measuring individual calls, machine learning characterizes the entire body of information present in the call sequence. Moreover, whereas algorithms for parameter extraction in traditional call analysis software are relatively straightforward, machine-learning algorithms may not be easily interpretable.

Identifying bat calls

Species identification may be done manually by humans or automatically by software and is usually based on recordings of search-phase echolocation calls, i.e., the calls the bats make as they are commuting or searching for food. However, there is increasing evidence that some species may also be identified based on social calls, the calls they make when communicating with other bats. Most of the following discussion refers to identification of search-phase calls. In the best-case scenario, recordings of echolocation calls can be identified to species based on a series of species-specific call characteristics. For example, Figure 4-4 (A, B) is a spectrogram of a full-spectrum recording of two widespread North American species, a hoary bat (*Lasiurus cinereus*) and an eastern red bat (*Lasiurus borealis*). The frequency and time characteristics of these calls are clearly distinct in many ways and the two can be

Table 4-1. Commonly measured parameters of individual bat echolocation calls and their abbreviations.

Parameter	Description
Fc	Characteristic Frequency, i.e. the frequency at the right hand end of the portion of the call with the lowest absolute slope (the Body).
Sc	Characteristic Slope, or the slope of the body of the call.
Fmax	Highest frequency recorded in the call.
Fmin	Lowest frequency recorded in the call.
Fmean	Mean frequency of the call, found by dividing the area under the call by the duration.
FME	Frequency of most energy, also called peak frequency, i.e. the frequency of the call with the greatest amplitude (cannot be measured in zero-crossing recordings, which lack information about amplitude).
S1	Initial slope of the call.
Tc	Time between the start of the call and the point at which Fc is measured (i.e. the right hand end of the body).
Fk	Frequency at the knee; the body of a call is said to start at the knee, which usually is a point where a dramatic change of slope occurs.
Tk	Time from the start of a call to the knee.
Dur	Time from the beginning of a call to its end.
TBC/IPI	Time between calls (also called "interpulse interval")

readily distinguished. In other instances, the reality is not straightforward, and species recognition can be more difficult or even impossible. For example, Figure 4-4 (C, D) shows spectral data of the echolocation calls of two European species, *Eptesicus serotinus* and *Eptesicus nilssonii.* There is a great deal of overlap in the call characteristics of these two species, making it virtually impossible to distinguish reliably between them.

In acoustic surveys, it is normal to be unable to differentiate acoustically among all species that are present, and recordings may be identified to more general groupings. Several terms are commonly used to describe these groups, and there is some overlap in the meaning of the terms depending on their context. The calls made by complexes of two or three species or genera with indistinguishable call characteristics (e.g., *Myotis* spp. or *Lasionycteris noctivagans/Eptesicus fuscus*) may be referred to both as sonotypes (Jung et al. 2012; Núñez et al. 2019) or as phonic groups (Ober and Hayes 2008). To complicate the *Eptesicus* example given in Figure 4-4, members of the European genera *Vespertilio* and *Nyctalus* also have calls that are similar to those of the *Eptesicus* species, and members of these three genera are often not distinguished

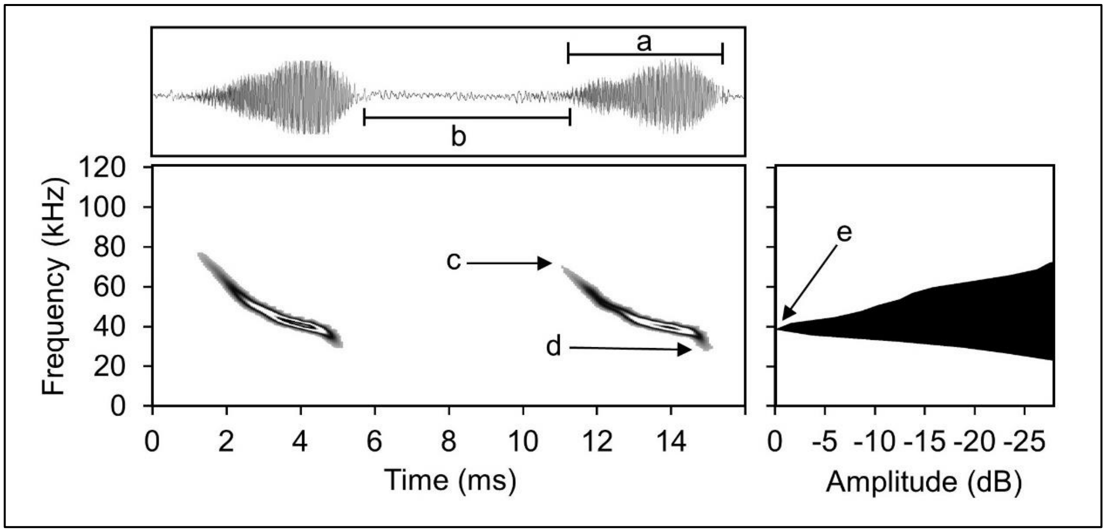

Figure 4-3. Common metrics for quantifying echolocation call structure. *Time domain/oscillogram, spectrogram, and power spectrum outputs are used to demonstrate some common measurements for parameterizing a full-spectrum recording of a bat call. (a) Duration (Dur); (b) Inter-pulse interval (IPI) or Time between calls (TBC); (c) Maximum frequency (Fmax); (d) Minimum frequency (Fmin); e) Peak frequency or frequency of most energy (FME).*

in acoustic surveys and grouped as one sonotype/phonic group (Figure 4-5).

The term sonotype may also be used to describe the groupings of like echolocation calls that may be assembled following a survey of an unknown bat assemblage. In this case, a given sonotype may be the final identification (Estrada-Villegas et al. 2010) or may be matched later to a known species or genus with previously described call characteristics (e.g., Hintze et al. 2016; Silva de Araújo et al. 2016). The term Phonic group may also be used to describe more coarsely defined groupings, e.g., "high" and "low" frequency (O'Keefe et al. 2014) or "large-bodied 25" (referring to a group of large bats with echolocation calls terminating at 25 kHz) (Buchalski et al. 2013). "Phonic type" often differs slightly in usage from phonic group in that it refers to distinct groupings of characteristic call types produced by one putative species (e.g., Barlow and Jones 1997; Thabah et al. 2006). The presence of phonic types within in a species may serve as evidence that the one species, in fact, contains multiple cryptic species.

Last, and less commonly, calls may be characterized to acoustic guild or simply guild (Meyer et al. 2004; Rogers et al. 2006). These categorizations invoke documented associations between call structure and typical habitat usage, allowing researchers to make inferences about the behaviors of the bats being recorded (e.g., Meyer et al. 2004; Rogers et al. 2006).

Countries with highly diverse fauna and a variety of ecosystems are usually host to a complex assembly of bats and, consequently, call diversity. Niche overlap occurs frequently and discerning different species (morphologically and acoustically) can be difficult. For example, Mexico has high bat diversity, including approximately 138 species, 83 of which are insectivorous and emit relatively high-intensity calls. Since it is challenging to identify these bats to species, many are grouped by guilds.

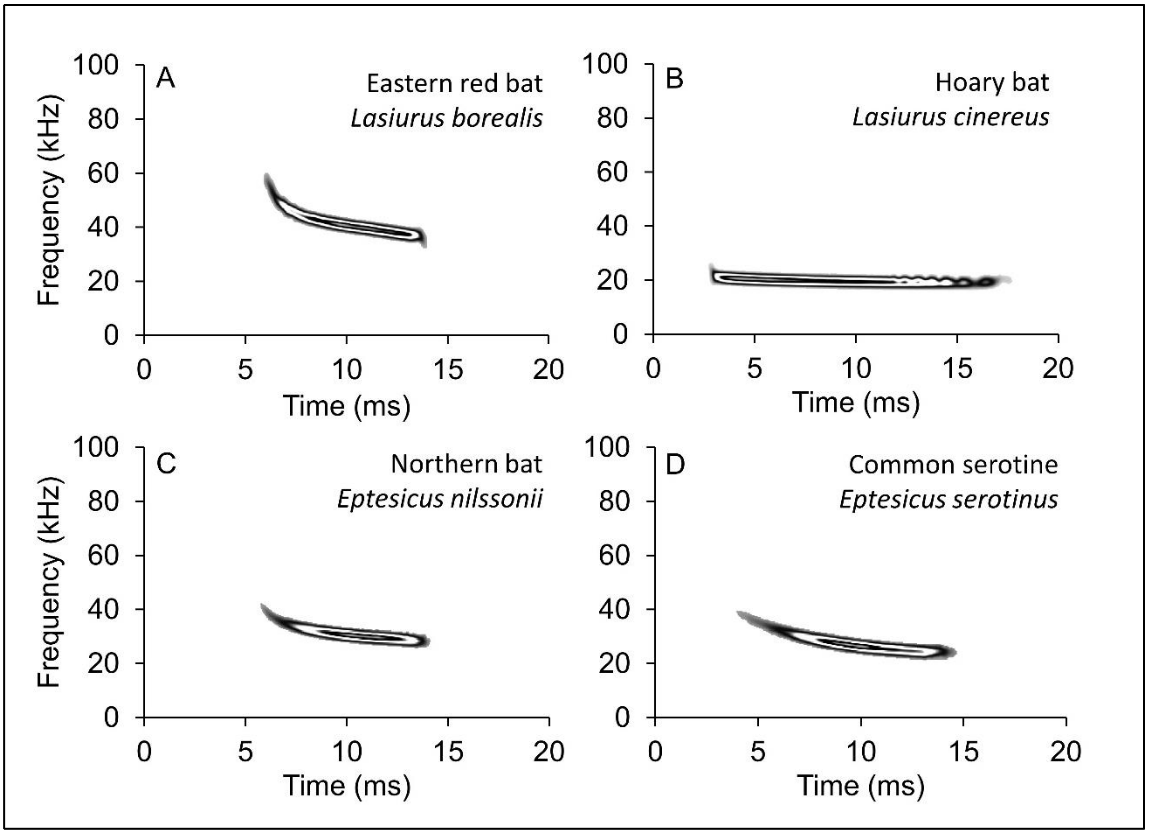

***Figure 4-4. Difficulties in conducting species-level identifications**. Spectrograms showing the search phase echolocation calls of the congeneric North American species, (A) eastern red bats* (Lasiurus borealis) *and (B) hoary bats* (Lasiurus cinereus)*, are very distinctive and in most cases, can be easily distinguished. In contrast, the calls of the European species, (C) northern bats* (Eptesicus nilssonii) *and (D) common serotines* (Eptesicus serotinus) *are extremely similar and cannot be reliably distinguished. The latter pair must usually be identified as belonging to a sonotype that may also include species of* Vespertilio *and* Nyctalus*, which also have similar calls. All recordings were made using full-spectrum technology.*

In almost all acoustic surveys at least some recordings must be categorized as “unknown.”

Acoustic identification efforts can be improved by limiting the species under consideration to only those that may reasonably be found in the study area. Most software packages with automated identification functions provide classifiers that allow the researcher to limit the species under consideration to only those thought to be found locally. A researcher conducting manual identification of calls may generate their own similar list. For an illustration of the importance of geography in call analysis, see Table 4-2 (“Echolocation call identification guidelines: a suggestion for managers”), which assigns a difficulty level to the identification of different species in various regions. The difficulty of identifying a given species differs among regions depending on which other species are present. However, it is important to note that the ranges of many bat species are not well defined, and many researchers have been surprised by the appearance of a species previously undocumented to their area in their acoustic recordings.

Table 4-2. Echolocation call identification guidelines: a suggestion for managers. *Tabular guidelines for conducting acoustic identification of recordings made of a hypothetical bat community (based on one developed by the Swiss Bat Bioacoustics Group). Each species is rated for ease of identification and likely misclassifications are included for each. Depending on the species identified, managers may take identifications at face value or, for more cryptic call types, may request corroboration from an external expert. Note that the need for validation of some species identifications varies among regions within the larger study area*

		Region																							
Species (Sonotype)	Difficulty of acoustic identification	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	…	n	**Possible confusions**
Genus species 1	B	2	2	2	1	2	2	2	2	2	1	2	1	2	1	1	2	2	1	1	2	2	2		1	*Genus species 2*
Genus species 2	A	1	1	1	1	1	1	2	1	1	1	2	2	1	1	1	1	1	1	1	1	2	1		2	*Genus species 1, Genus species 3*
Genus species 3	C	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	*Genus species 2*
Genus A	C	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2		2	*Genus species 1, 2, 3*
Sonotype X	C	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	1		1	*Genus species 1, 3*
Species complex Z	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	*Genus A, Sonotype X*
…	…																									

Difficulty of acoustic identification	
A	easy - can usually be identified with little experience
B	intermediate - identification can be challenging but is usually possible with few years of experience
C	difficult - Identification usually only possible with several years of experience

0	No validation needed
1	Expert validation needed if first record in region or first record in respective or adjacent XxY km square (past DATE)
2	Expert validation mandatory

It is critical to recognize that classification of calls, particularly to the species level, is not error free. That is, 100% accuracy cannot be achieved. In fact, given the level of intra-specific variation in echolocation call characteristics, and the level of inter-specific overlap in echolocation call characteristics, it is reasonable to expect that accuracy rates may range between 75% and 90% at best. Additionally, it is vital to understand that identification of calls to species depends upon a thorough understanding of the intra-specific range of variation in the echolocation calls of each species within the area of interest, as well as the inter-specific similarities of the species within the area of interest. Thorough understanding of the echolocation call characteristics of the bats within an area typically occurs through development and review of a reference call library. In summary, acoustic recordings provide a powerful, but often limited, tool to assess the identities of the bats in a region or habitat. The success of call identification also varies among species and regions.

Manual identification of bat calls

Alongside the recent proliferation of automated species identification software packages is an increased interest in manual identification of bat calls to provide a check on automated identification results (e.g., Heim et al. 2015). This process is sometimes referred to as "vetting" and is a somewhat contentious issue within echolocation call identification. Proponents of manual identification note the inevitable unreliable responses provided by all automated algorithms, arguing that these errors are often detectable and may be corrected manually by the user, given that users know how to identify calls manually and have sufficient knowledge of bat biology (Russo and Voigt 2016). The chief concern in using manual identification techniques is that there may be substantial variation in the qualitative identification results within and among researchers. Furthermore, there is little standardization in the processes used for manual call identification by different researchers (Fraser 2018; but see Reichert et al. 2018). Finally, it may be tempting to only use vetting procedures to look at a small subset of target recordings from a sampling effort (e.g., only those automatically identified as threatened and endangered species), which can remove context and provide more focus on false positives than on false negatives. One recommendation to avoid this second issue is to either vet all files (e.g., Heim et al. 2015) or only a random subset. Either approach allows the user to identify potential systematic issues within the automated identification results but takes the focus away from biases that may be associated with individual target recordings.

Figure 4-5. Giant noctule (*Nyctalus lasiopterus*). *© Jeroen van der Kooij, Bat Conservation International.*

Manually identifying bats based on echolocation calls is a skill that requires theoretical knowledge and practice. Different approaches have been proposed to identify calls manually; however, we focus on the most common two. The first approach involves using a heterodyne detector to identify bats in a qualitative way, through listening. The operator establishes the "best-heard frequency" (i.e., roughly corresponding to the frequency of maximum energy) and assesses sound tonal properties and "rhythm" (i.e., call rate) to identify bats detected in flight. The method is cheap and quick, but it is highly subjective, requires considerable practice, and is only effective where species diversity is low with little risk of overlap. Knowing the mix of species in your geographic area will help narrow the possibilities and consider who the "look-alikes" are.

The second approach is quantitative and relies on measuring spectral and temporal variables of echolocation calls to make an identification. The learning process may be divided as follows:

a) Learn the basics of acoustics (e.g., frequency and sound pressure level, sound propagation, and atmospheric attenuation). The theoretical details of these topics may prove daunting at first, but it is important to grasp the basic concepts even if you are not familiar with the mathematics behind them.

b) Digitize high-quality recordings of bat calls. Examine them with a sound analysis package and become familiar with sound processing. Learn the meaning of digitizing sound, the consequences of adopting different sampling rates, and the information provided by different sound representations (e.g., spectrograms, oscillograms, and power spectra). Many beginners generate spectrograms without being aware of key factors like the role of the fast Fourier transform algorithm or the effects of analysis window type, size, and overlap. Do not let your software generate spectrograms automatically without choosing the settings and testing the effects of changes to them.

c) Learn how to measure call variables. Most sound analysis software extracts the main call variables automatically, but it is instructive to learn how to measure the fundamental variables manually (e.g., start, end, and peak frequency; duration; inter-pulse interval). Changing the amplitude threshold in your spectrogram settings will substantially change variables measured manually.

d) Become familiar with the shape of call spectrograms and classify them into broad categories (e.g., Frequency Modulated (FM) calls, Frequency Modulated-Quasi Constant Frequency (FM-QCF) calls, Constant Frequency (CF) calls). More importantly, learn why bats use different call shapes and what this means for sensory ecology. Although there is a wealth of literature on these topics, get firsthand experience for your area. Make your own recordings of different species and examine them to recognize the features about which you have read.

e) Once you are familiar with the basic aspects of bat calls, explore the nature of call variation (see the following). The calls of a single individual can change dramatically.

f) To identify species, you can compare your spectrogram shapes with published ones. Furthermore, you can compare the values of some key variables measured from an unknown call with reference calls. Inter-specific convergence in call design and within-species variation lead to overlap in call characteristics among species, so there is no "diagnostic key" for all species. Some species are obvious; others are difficult, and the remaining are simply impossible to discriminate! No information is better than misinformation, so **resist** the temptation to identify every call.

Automated identification of bat calls

Automated identification software is increasingly being used to identify call sequences from the large amounts of data recorded by modern detectors. Software typically identifies calls using probabilistic algorithms (e.g., multinomial logistic regression, artificial neural networks, classification trees, discriminant function analysis, support vector machines), but calls may be identified using any method that can interpret measured parameters and divide calls based on those characteristics (e.g., a dichotomous key or decision tree). Identification algorithms may use both call- and file-level quantitative characteristics. Accuracy of identification algorithms is dependent on the quality of the training data set used to generate the algorithm. Training data sets used to develop algorithms that identify call sequences to species typically include reference calls from all species within an area, with reference calls representing the most variation in the echolocation calls of each species. Note that identification algorithms do not have to identify calls to species and that species identities do not necessarily need to be known to use an automated identification algorithm. For example, call sequences may be classified to a phonic group, sonotype, or acoustic guild.

Building an automated identification algorithm is straightforward if a high-quality training data set exists (i.e., echolocation data have been detected and parameterized in recordings for which the recorded species is definitively known), but the assumptions of statistical methodologies must be met for an identification algorithm to perform well. A unique consideration for bat acoustic identification algorithms is how to classify files that are bats but not identifiable any further. These files may be challenging to categorize because unidentifiable calls from different species may have highly dissimilar characteristics yet should all be included in a single "unidentifiable" pool. When building an automated identification algorithm, divide the reference call library used to build the algorithm into two sets — a training library to develop the algorithm and a testing library to validate algorithm performance. Bootstrapping the algorithm development, i.e., iteratively dividing the data into randomized sets for training and validation, is an effective way to maximize algorithm performance and to assess algorithm identification accuracy. If desired, determination of whether species are present with a measure of likelihood of misclassification of presence can be performed using a likelihood-ratio test of species absence. This likelihood-ratio test can be developed from the species/group accuracy estimation table (i.e., classified versus actual) and maximum likelihood estimation of the relative frequency of each species in the data (Britzke et al. 2002).

When multiple automated identification software programs are available, it often is of interest to compare software results. Such comparisons typically are performed using pair-wise agreement rates from cross-classification tables constructed from the file-level classifications of each program (Lemen et al. 2015; Nocera et al. 2019); when more than two programs are compared, multiple cross-classification tables must be used. These allow researchers to compare the outcomes of automated classification software or to theoretically establish greater certainty in species identifications and/or nightly presence. When performed for such purposes, a common assumption is that supposedly accurate software programs should have high levels of agreement (Lemen et al. 2015). Although this may intuitively seem to be the case, the expected rate of agreement between any two programs actually is a function of the relative proportion of each species considered in the data set and the correct classification rates and misclassification rates of each program. The expected rate of agreement between two automated identification software programs for species n is:

$$\frac{\sum_{i=1}^{n} r_n \times p\left(A_{nj} \cap B_{nj}\right)}{\sum_{i=1}^{n} r_n \times p\left(A_{nj}\right)}$$

where r_n is the true proportion of species n in the data set; $p\left(A_{nj} \cap B_{nj}\right)$ is the joint probability of classification of species j as species n by both program A and program B; A and B are the independent true cross-classification accuracy tables of program A and program B (i.e., $A = \left[a_{ij}\right]$ and $B = \left[b_{ij}\right]$); and $p\left(A_{nj}\right)$ is the cross classification accuracy rate of species n. More colloquially, the expected rate of agreement between two programs for any species n is the sum of the proportion of files classified as species n by both programs divided by the proportion of files classified as species n by one program.

Note that the expected rate of agreement is not symmetrical between programs (i.e., the agreement rate between A and B for species n is not equal to the agreement between B and A for species n). This is because the denominator in the previous formula is defined by the cross-classification accuracy of one program. Thus, program A may often agree with program B that species n is present, but program B may not often agree with program A that species n is present. Perhaps counterintuitively, two programs with high levels of accuracy, both overall and for species n, will not necessarily have high rates of agreement in presence of species n. As suggested by the equation, this is particularly likely to occur when species n is rare, and thus the joint probability of both programs misclassifying *other* species as species n on a file-by-file level is low; this phenomenon is demonstrated in Figure 4-6.

Given these factors, comparison of agreement rates between software programs without calculation of expected rates of agreement is unlikely to be highly informative with respect to program accuracy. This also applies to comparisons of human classifications to program classifications; in general, accuracy rates of human classifiers are unknown. Furthermore, using agreement between programs to assign higher confidence in species identifications should be done with caution, as the relative proportion of the species within the data set and their misclassification rates has a significant effect on the joint probabilities of misclassification. When the goal of comparing program-automated identifications is to understand program disagreement better, false-positive occupancy models (Austin et al. 2019) may be more informative. Similarly, when the

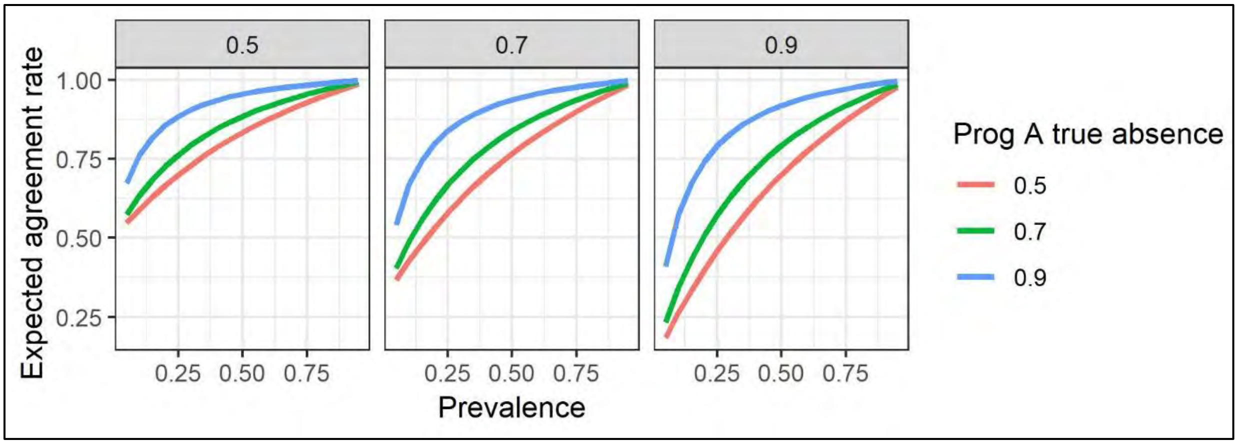

Figure 4-6. Factors affecting identification agreement among software packages. *The relative prevalence of species n has a strong effect on the expected rate of agreement in species n identifications between two classification programs. Lines show the expected rate of agreement in species n classification between hypothetical program A and hypothetical program B under different false-positive classification rates for species n when true positive classification rate for species n is perfect. False-positive classification rates for program B are denoted by values within gray headers, and false-positive classification accuracy rates for program A are denoted by line color. Observe that low levels of false-positive classifications actually results in lower levels of agreement than high levels of false-positive classifications. This is because the joint probability of misclassification increases under low accuracy conditions, which in turn increases the rate of program agreement.*

objective is to understand how selection of an individual program may influence understanding of habitat use, behavior, distribution, etc., direct comparison of the outcomes of using each software program may be more informative (Nocera et al. 2019); such comparisons may be performed by comparing model selection tables and model estimates.

Intra-specific variation in echolocation calls

One of the most difficult, and sometimes frustrating, components of studying bat echolocation is the intra-specific variation in echolocation call structure. The same individual recorded under different environmental or social conditions may use vastly different calls. This makes it particularly difficult to identify species; however, large call libraries, standardized recording procedures, and advanced algorithms for identification may reduce the problems associated with intra-specific variation. It is crucial to understand the major sources of variation in call structure, both within species and within individuals. This information is important to ensure you reduce unnecessary variation in your recordings (e.g., recording voucher calls in habitats of differing clutter levels) and that you understand any spatial or temporal differences in call structure.

Intra-specific variation in echolocation call structure can be partitioned into two categories. The first includes the “personal” information of an individual (e.g., demographic and reproductive condition; reviewed in Jones and Siemers 2011; Gillam and Fenton 2016). The variation attributed to personal information is expected to remain stable over time (e.g., sex) or change slowly (e.g., age). The second category of variation includes the ecological or behavioral conditions of the individual, which can change rapidly. Conditions that can elicit rapid changes in echolocation call structure include structural complexity of the foraging habitat (Kalko and Schnitzler 1993; Obrist 1995), presence of conspecifics (Ulanovsky et al.

2004; Gillam et al. 2007; Cvikel et al. 2015), and sources of noise in the surrounding area (Bunkley et al. 2015), as well as detection of and distance to potential prey (Griffin 1958). In the following, we examine both categories of intra-specific variation in more detail and discuss which of these factors are most likely to be problematic in terms of manual and automated species identification.

Personal information can be encoded into the echolocation calls of bats and is a source of variation in call structure within a species. Personal variables affecting calls include age, sex, reproductive condition, body size/condition, individual identity, and group identity. Individuals may transition between classes for some of these variables (e.g., juvenile to adult), but this is expected to happen over long timescales (i.e., not seconds or minutes). A table in Bohn and Gillam (2018) summarizes the literature about personal information signatures in the echolocation calls of bats.

Behavioral state, also referred to as "activity information," refers to changes in the surrounding behavioral or ecological conditions of an individual that can lead to large shifts in echolocation call structure over short periods. In insectivorous bats, stereotypical shifts in call structure occur as an individual transitions from search phase (i.e., searching for prey) to approach phase (i.e., prey detected at a distance) to terminal phase (i.e., calls emitted immediately before prey capture; Griffin 1958). Calls during these three phases are characterized by different spectro-temporal structures, which can be seen clearly in Brazilian free-tailed bats (*Tadarida brasiliensis;* Figure 4-7 A–C). These rapid shifts in call structure are not limited to bats while foraging. When *T. brasiliensis* are exposed to a conspecific call that overlaps with their own, they shift call frequencies upwards in less than 200 ms (Gillam et al. 2007). Furthermore, *T. brasiliensis* exhibits different calls when flying alone compared to flying in the dense conditions associated with mass emergence from a cave (Gillam et al. 2010; Figure 4-7A, D–F). Ecologically, changes in the

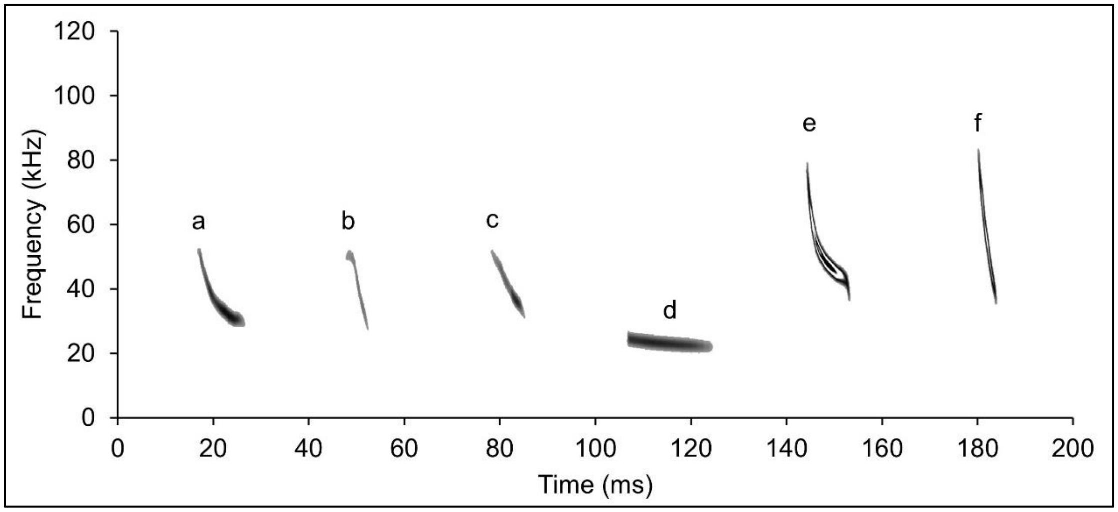

Figure 4-7. Intraspecific variation in echolocation call structure. *As illustrated by Brazilian free-tailed bats* (Tadarida brasiliensis)*, intra-specific echolocation call structure may vary substantially when the bats are flying (A–C) with conspecifics during mass emergence or (D) alone. Further variation occurs during the various stages of capturing prey ((D) search phase, (E) approach phase, and (F) terminal phase).*

structural complexity of the surrounding habitat can also drive rapid changes in echolocation. In many taxa, bats produce short, broadband calls in the presence of dense vegetative clutter and comparatively long, narrowband calls in open areas (Obrist 1995; Kalko and Schnitzler 1993). Echolocation differences owing to an individual's personal information are likely to be minor in comparison with variation caused by changes in behavioral state. Although personal variation in echolocation is interesting from a communication perspective (i.e., bats may advertise reproductive condition to eavesdropping conspecifics), variation between sexes and reproductive classes within the sexes are generally small and limited to only one or two call variables. Thus, this variation should not prohibit identifying species using automated programs. Alternatively, the potential for relatively large changes in various call parameters over short periods means that variation attributable to behavioral state is likely to be a more significant barrier to accurate species identification.

Call Libraries

Identifying calls to family, genus, or species, requires a reference library of "known calls" (i.e., calls recorded from bats of a known species). Many publicly available call libraries exist and can easily be accessed (Table 4-3). All were developed by different researchers with different criteria, so caution is required before applying any one library to a study system. For researchers working in an area where the bat community has received little study, building a call library may be one of the first steps in developing an acoustic research or monitoring program. Case Study 5 ("Bats in the Ghats: Building a call library to study the impacts of agriculture on bats in a biodiversity hot spot,") at the end of this Handbook, provides an example of this.

Call libraries may be useful for many purposes, including as a reference for other researchers who are manually identifying calls and as training data sets for algorithms that identify calls from quantitatively measured parameters in individual calls or call sequences. The ultimate use of a call library is an important consideration, because what constitutes a good library depends on whether it will be used for manual or automated identification. We provide guidance on both. Regardless of final use, **calls from free-flying bats identified subjectively should not be included in a library because they may make the reference collection unreliable.**

A call library of known bats is essential for proper acoustic identification. These may be acquired by recording bats emerging from known-species colonies, recording bats hand-released after capture, or sometimes recording echolocation sequences identified by the presence of species-specific social calls. Recording calls made by a bat in the hand or otherwise confined is not recommended, because these calls are not representative of search-phase echolocation calls. Recording a many calls from a single species is necessary to capture the full range of intra-specific variation, leading to increased confidence in correct identification (e.g., Figure 4-7).

The process of recording search-phase calls of known-species identity can be difficult for some species. In addition, bats of the same species exhibit an enormous amount of

Table 4-3. Echolocation call reference libraries currently available. *Recording method abbreviations are as follows: H=heterodyne; FD=Frequency Division; TE=time expansion; RT=real time. Reprinted from Walters et al. (2013) with permission © Springer Science+Business Media, New York.*

Library name	No. of species	No. of records	Recording method	Source
Bat Conservation Trust Sound Library	15	27	H	http://www.bats.org.uk
Southeastern Australian Bat Call Library	9	31	FD	http://www.csu.edu.au/batcall/batcall.html
Pacific Northwest Bat Call Library	10	33	FD	http://www.depts.washington.edu/sdwasm/pnwbat/batcall/html
Wyoming Bat Call Library	14	73	FD	http://www.uwyo.edu/wyndd/data-dissemination/priority-data-comp/wyoming-bat-call-library/index.html
BatCall-Museum of Southwestern Biology	22	3821	FD	http://www.msb.unm.edu/mammals/batcall
Batcalls.com	26	60	TE	http://www.batcalls.com
Cornell Lab of Ornithology-Macaulay Library	29	258	TE	http://macaulaylibrary.org
BatCalls.org	42	91	TE	http://www.batcalls.org
British Library-British Sound Archive	139	~700	TE	http://www.bl.uk/soundarchive
EchoBank	297	3531	TE and RT	Collen (2012)

variation in their echolocation calls. These two factors make the development of a comprehensive known call library a time-consuming and difficult endeavor. When constructing a call library, it is important to collect accompanying relevant metadata (e.g., species, location, date, recording environment, microphone used, bat species, bat behavior, person making the recording, etc.) to be able to make sense later of the variation recorded.

Call libraries as a reference for manual ID

A call library is beneficial to those learning how to use bat detectors as they begin navigating the complex world of call classification and is also useful as a resource for experienced researchers. Using a call library means that recordings from unidentified free-flying bats can be compared to pre-identified reference calls. Many publications provide images of call spectrograms and values of echolocation call variables for multiple species. However, by creating and using your own library, you can generate your own spectrogram, vary the amplitude threshold to determine the effects on spectrogram visualization, or replay the recording at your leisure. One of the advantages of setting up your own library is that you can focus on local populations. The calls from local populations might differ from those of conspecifics from populations found elsewhere, and furthermore, you can include examples to illustrate intra-specific call variation and relate this to recording conditions.

In many cases, known call collection efforts should focus on bats that are behaving normally and when their calls are most characteristics of the species. Although it may be easy to get recordings of bats as they exit roosts or immediately after hand release, these conditions commonly fail to produce search-phase calls that are consistent in structure and inter-pulse interval. Thus, instead of trying to obtain the entire echolocation repertoire of a species for a call library, researchers should instead focus on recording the call repertoire of bats under conditions in which they can be identified (i.e., free-flying, not in highly cluttered environments, away from roost emergences). Given this approach, researchers must then acknowledge the limitations of their call library and consider those limitations when sampling and conducting call analysis. Accepting the limitation of lacking a complete call repertoire of a species minimizes the effort needed to acquire a suitable call library, while providing for sufficient call variation for species identification.

When collecting calls for a call library, record metadata such as species identity, individual characteristics, recording conditions, and habitat structure. These factors may influence call structure, and you will quickly learn to appreciate the variation caused by different personal, behavioral, and ecological states. Remember to include social calls, as they are often species-specific and can greatly aid identification. Finally, limit the number of recordings made available by colleagues, as you will get the maximum benefit from the experience of preparing and using your own!

Call libraries for machine learning and automated classifiers

Call libraries are essential to build automated classifiers. The first attempts to train machines in classifying bat calls were limited by the paucity of available reference recordings. Moreover, reference recordings were previously collected for human learning and were biased towards good-quality recordings (i.e., high signal-to-noise ratio). This bias limited the efficiency of automatic identification, especially for omni-directional recordings made when bats were far from the microphone or in noisy environments.

For these reasons, recent efforts to train machines in identifying calls have focused on building large call libraries. Humans are still considerably smarter than machines, which need hundreds of independent reference recordings per species to identify bats. For machine-learning call libraries, reference recordings should always include a range of individual behaviors including commuting and foraging flights, feeding and drinking buzzes, and a diversity of social calls. However, social calls recorded inside roosts are quite different from those emitted on foraging grounds and may confuse software. Include a large assortment of recording environments, especially those with structures producing echoes that influence call features. These include smooth structures, like rocks and buildings that produce a small number of distinct echoes and complex vegetation structures that produce multiple echoes.

Incorporate calls with a wide range of signal-to-noise ratio, including the faintest possible calls, especially if you are interested in species with low detectability. Most importantly, add a diversity of sonic events that are not bat calls (e.g., insects, wind, rain, and mechanical and electronic noise). Recording equipment also influences the measurements made by software, so automated classifiers typically perform best when applied to recordings made with similar equipment used for training the classifier.

The two most important features of recording equipment that can confuse an automated classifier are the directionality of the microphone and the use of microphone capsules — the part that is responsible for converting sound waves to a microphone signal — that influence the frequency response and background noise patterns. Automated classifiers used to analyze long passive recordings can benefit from training with large numbers of recordings made with omni-directional microphones because these microphones more faithfully document ambient noise conditions than the narrower focus of a directional microphone. Recording of ambient noise in calls used to train classifiers therefore improves the ability of classifiers to differentiate between true signals and ambient noise.

The labeling of call libraries for machine learning should be more precise than those used for human learning. The reference labels (i.e., species or behavior) should be placed on a sound file and each single call with clear frequency and time delimitation. This will help classifier accuracy by removing any other sound event that could be associated with the label.

Finally, in addition to training automated classifiers, reference calls can be used to test or benchmark them. This process can be useful so long as the training sets of reference calls are independent from test sets. Training and test recordings should occur at different sites, so there is a low probability that calls from the same individual occur in both sets. One way to ensure this is to split your reference database into two random sets of recording sites; however, this method sacrifices an important part of your training set and decreases the predictive power of your classifier. Analytical methods that use bootstrap sampling to create an ensemble of different realizations of the classifier, such as the random forest technique, are particularly effective for minimizing loss of predictive power in a classifier when data sets are partitioned for training and classification (López-Baucells et al. 2019; Prasad et al. 2006; Brieman 2001). Note that ensemble model realizations can be created for many machine-learning techniques.

A suggestion for managers: Develop call analysis guidelines that are specific to the various regions in your area

Using acoustic techniques to determine whether a bat species is present in a region can be done with varying levels of confidence, depending on the call characteristics of the species in question, as well as the composition of the local bat community. Some species have extremely distinctive call characteristics, whereas others may be notoriously flexible in the structure of their calls. A species that can be easily identified based on its unique call characteristics in one region may have one or several look-alike conspecifics in another region that make species distinctions almost impossible.

Developing guidelines that rate the difficulty level of identifying individual species in different regions, as well as providing region-specific lists of possibly confusing species, can provide a useful framework for practitioners conducting acoustic work. Furthermore, it can provide you with a consistent set of expectations for when species identifications can be taken at face value and when they should be validated by a local expert. For example, the Swiss Bat Bioacoustics Group has developed a series of guidelines for bat researchers working in Switzerland. A generalized version of these (Table 4-2) illustrates one potential format for clearly communicating call analysis guidelines to researchers in your area.

Summary

Echolocation call analysis to identify species is an extremely important and complex aspect of using acoustic techniques to study bat communities, and there is no widespread consensus on best practices for conducting these analyses. Analysis is complicated by significant intra-specific variation and inter-specific overlap in call structure. No identification process is perfect and there will always be unidentified recordings.

The call or call-sequence identification comprises three processes: detecting calls, parameterizing them, and assigning an identification based on those parameters. Any of these steps may be conducted manually or automatically. The use of manual and/or automatic techniques to conduct call analyses is contentious. Regardless of the chosen technique, a strong understanding of acoustics in general, and bat echolocation call structure specifically, are required for users to analyze their data with confidence. In all cases, acoustic identification efforts can be optimized by creating the highest-quality recordings possible. See some of the best practices on detector deployment in Chapter 3 ("Bat detector choice and deployment") for ideas on how to achieve top-quality recordings. For both automatic and manual identification, the presence of an extensive call library is important to act as a known comparator.

Some additional suggestions

1. Do not attempt to identify every recording to species and do not blindly rely on automated software to separate similar species.

Not every recording, especially from passively deployed detectors, can (or should) be confidently identified to species. Identifying every call will result in questionable publications, theses, reports, and presentations. Distance and clutter affect the quality of recorded echolocation calls. Some recordings can be identified as a bat, and maybe to a specific super-family, or even genus, but not all can be confidently identified to species.

2. Spend enough time in the field actively recording bats and learn how to think like a bat.

The quickest growing demographic of students fascinated by bats are those who are interested in acoustic surveys. Unfortunately, most of these students have never had a bat in the hand and may be unfamiliar with natural history and how different species evolved to colonize various habitats. The insights gained through using a heterodyne detector while directly observing bats in their element are invaluable and can help you to think like a bat! This will be useful when you consider where to set up your passive recorder or transect.

3. Do not skip the basics

Many new students or researchers have no idea how bats echolocate, how high-frequency sound behaves in air, or the physical properties of ultrasound. This severely hampers the ability to collect, analyze, and correctly interpret acoustic survey data. Hit the books and learn the basics, this will help you to build a strong foundation on which to interpret your data.

A pygmy fruit-eating bat (*Artibeus phaeotis*) in flight. © Bruce Taubert/Bat Conservation International.

Chapter 5. Data, Analysis, and Inference

Introduction

The results of many acoustic studies include enormous quantities of data, both primary and derived, which must be appropriately stored, organized, and ultimately analyzed. In this final chapter, we begin with a brief discussion about the utility of databases for organizing acoustic data sets and then describe a number of analytical approaches that may be used. The nature of acoustic data — typically recordings that cannot be attributed to individual animals and so are not traditional count data — means that many analytical approaches that may be used on other types of survey data must be re-evaluated when applied to acoustic data sets. When necessary, we have specifically addressed how commonly used analytical techniques may be modified so that they can be appropriately applied to acoustic data sets. We provide a discussion of analytical techniques that may be used with data collected for each of the study types described in Chapter 2 ("Acoustic survey design") and, for ease of reading, have presented them in the same order as in that chapter.

Data

Databases

Modern acoustic detectors have changed bat monitoring and research projects by increasing data volume and complexity. As data sets grow and change, our need for reliable storage and streamlined data management grow as well. The data from a small or short-term project that records only acoustic calls may be adequately managed in a single table in a spreadsheet program like Microsoft Excel (i.e., “flat” data). However, a project that records calls and site conditions would most effectively store data in two interrelated tables that are linked by common fields such as site name and date (i.e., “relational” data). A measured variable at a detector site consists of a single record per point (e.g., elevation or clutter), but several acoustic files may be associated with that point. In a flat table, the site variables would be replicated for each acoustic file, and in a relational database, each record exists only once. However, because the relationship between the two data types is defined, site-specific information may be quickly associated with acoustic files without duplicating data. The management of relational data in a spreadsheet program is inefficient and error prone. A database program (e.g., Microsoft Access) provides a simpler and more reliable solution.

In a database, data are organized into multiple tables that look like spreadsheets but are designed for complex querying in relation to other tables. Interrelated tables are linked together by common factors that you can specify (Figure 5-1). Using these established relationships among data tables, you can create queries and generate reports that compile and synthesize data from multiple tables. Structured Query Language (SQL) is the set of instructions used to interact with a database. Structured Query Language allows you to ask questions and perform commands on data in a non-analytical way, like selecting values that match search criteria, updating records in bulk, or finding duplicate values. Databases do contain some capability for calculations and analysis but are more appropriate for keeping data organized. This allows for rapid search and retrieval of data, which can then be analyzed in a statistical program. The initial set up of a database requires some planning and expertise, but once established, they are easy to operate and maintain. When selecting or building a database, it is crucial to identify the type of information to be saved and then to determine the relationships among those data.

Using a database

Observations by experts as well as laypeople offer a powerful tool to aid conservation efforts. Data may be reported in various ways (e.g., through web interfaces or applications on mobile devices). For bat records, depending on the study question, data formats can differ (e.g., detection of droppings, visual sightings, roost discovery, acoustic records). Acoustic records comprise large data sets rarely submitted as records. However, changes in storage technology and network bandwidths may change this in the future. This makes adapted data flow processes necessary.

Metadata

In addition to raw and processed acoustic data and site information, it is often important to record and maintain metadata. Metadata means “data about data.” It is information about a data set that is intended to help researchers organize, summarize, describe, or otherwise aid in their use of the data set. Loosely, it is a short explanation of what the data are. For example, a digital image may include metadata that details the file type, size, creation date, resolution, and geolocation. The metadata associated with a text document

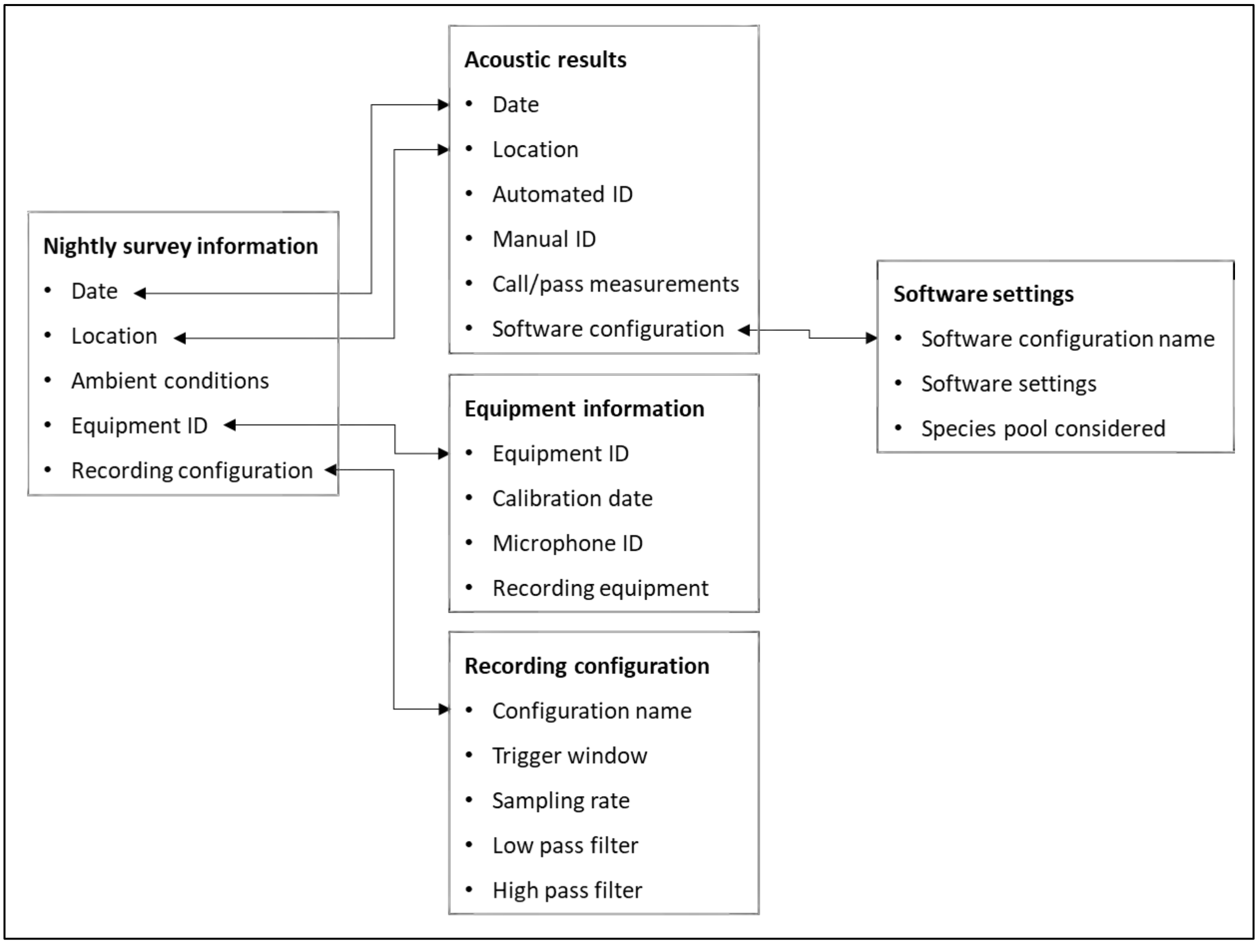

Figure 5-1. Example database structure for storage of acoustic survey information. *Diagram of potential relationships among data tables in a database of acoustic survey information. Individual boxes are data tables, bullets are fields, and arrows show the relationship between fields across tables. This design could be used to query call or pass measurements made under specific ambient conditions using specific recording and software settings, pulling information from four separate tables. Note that this is a hypothetical example only*

may include the author name, number of words or pages, and total editing time.

For ecological and environmental projects, metadata can document the "who, what, where, when, why, and how" of data collection. This typically includes the individual, institution or organization that collected the data, the data type(s) and format(s), the study location and time period, the reason for data collection, and the methodology employed in data collection and storage. Providing metadata ensures that each user can understand the data set's organization and structure, even when data sets are accessed by multiple individuals or over a span of time. Metadata also helps support the archiving and preservation of data sets, which are essential for the maintenance of long-term data sets and data provenance and may be encouraged or even required by publishers as well.

There are many different metadata schemes that propose standards, often discipline specific. Ecological Metadata Language is the metadata standard for ecology that was developed to allow documentation of digital data sets in the ecological sciences (Jones et al.

Advantages of storing and managing data in a relational database include:

a) *Quality control.* A database provides numerous tools to ensure data quality and integrity. Data tables can be designed with validation parameters that dictate the structure and format of data, which helps prevent things like typographical errors, data format issues (e.g., text versus number), and missing values. Validation criteria also apply when importing records in bulk from another spreadsheet or text file. Data entry forms are customizable, user-friendly interfaces to data tables that include the validation parameters inherent in the table. Forms can be developed with convenient tools like pull-down menus, which save time and prevent mistakes. Databases also enforce referential integrity, meaning that new records in one table are required to have a corresponding record in a related table. You could specify that each record in the acoustic call table should contain a site name that corresponds with a record in the site conditions table.

b) *Automated processes.* Queries and reports are powerful functions that allow for quickly selecting and summarizing data, whether the data are contained in one table or many. The SQL instruction sequences that make up queries and reports can be saved and repeatedly applied, even as datasets grow. This makes databases powerful for projects that record data regularly and require repeated selection or summaries (e.g., annual or monthly data reports). Automating frequently performed actions saves time and reduces mistakes.

c) *Multiuser capability.* A database stored on a shared server can be opened and edited by multiple people simultaneously. Only records currently being edited are locked, so others can edit different records without conflict. This allows everyone to access the most up-to-date file at any time which is particularly useful when multiple teams are collecting data in separate locations.

2019). Darwin Core is a body of standards used in biological sciences for recording and sharing information on species occurrence, distribution, and related information (Wieczorek et al. 2012). For bat acoustic studies, the Grand Unified Acoustic Notation Ontology for Bats (GUANO) metadata format is an increasingly popular standard that has been incorporated into a variety of acoustic programs (https://guano-md.org/). The GUANO metadata format was designed specifically for acoustic studies and provides metadata fields suitable for acoustic studies of many formats. Note, however, that it is always possible to record additional metadata beyond the specifications of any format. In particular, databases allow excellent collection and storage of additional metadata.

Data analysis

Concurrent with advances in bat detectors and echolocation-processing software, advances in statistical methodology and computer-processing power have provided previously unparalleled ability to analyze and document patterns in bat acoustic data and enabled innovative new experimental designs. Although matching study design and statistical methodology is critical, there is no single correct answer for what method(s) should be used to analyze acoustic data. Planning and undertaking statistical analysis can be daunting and challenging. However, you should view the selection of an appropriate statistical analysis as natural extension of your question of interest and part of the study design process (Chapter 2, "Acoustic survey design"). When considered as part of the study design process, selecting a statistical analysis or analyses becomes part of the process of ensuring that the data you collect provide valid answers to the question(s) of interest. It is best practice to select appropriate statistical methods based on study design, with consideration given to both study design and analysis prior to data collection. When study design and statistical methodology are selected in conjunction *a priori*, prospective power analysis can be conducted to help determine appropriate sampling intensity for the desired level of statistical power, as referenced in Chapter 2.

Many study designs are intended to be used with specific analytical frameworks, making selection of appropriate statistical methods straightforward. Appropriate statistical techniques for common study designs (i.e., before-after-control-impact) are described in the literature where the study design is presented. Reviewing study designs and literature regarding a chosen design before data collection in the field and analysis after data collection is highly recommended and supports stronger inference than post hoc selection of statistical methods following data collection with no formal study design.

Not all data are collected under a pre-planned experimental design. For example, it may be of interest to opportunistically collect pilot data while performing other studies to design a future study, aggregate data across multiple studies, assess historical data, or simply to explore an interesting feature of the data that previously had not been considered or observed. Finally, it is unfortunate but not uncommon for study designs to entirely or partially unravel because of extrinsic factors such as weather (e.g., typhoon or drought), logistics (e.g., field vehicle or equipment break), or disease outbreaks (human or wildlife). When analyzing data not collected under a strict or specific study design you must first determine if an analytical method of interest matches the limitations of the data. Indeed, even when using a well-known study design with a matched statistical framework, it is beneficial to consider what makes a statistical analysis valid.

As a highly generalized process, when determining whether an analysis is appropriate, consider the following three items. First, are measured and response variables categorical and/or continuous? Some analyses can only be performed on specific types of variables and identifying incompatibilities between variables and analytical methods is an effective way to reduce the number of analytical methods you are considering quickly. Second, what is the structure of the sampling protocol? If there are treatment groups, consider if they are blocked (e.g., male/female, elevation gradient), and if the number of readings for each blocking groups is equal. Finally, are repeated measurements (i.e., multiple reading from a single individual) taken at any point? Repeated measures designs are available for most common statistical methods, but proper selection of repeated measures analyses requires careful thought. Finally, because it is not uncommon in field studies, particularly those conducted over the long-term, for sampling sites to “drop out”, it is important to consider whether the prospective analytical method will be able to address such drop outs. Once you have determined that an analytical method is appropriate, you need to check that the data do not violate any assumptions of the analysis.

All statistical methods have a series of underlying assumptions. While study design is important in leading to valid inference, statistical assumptions identify the conditions under which a given statistical method will lead to valid estimates (and thus influence inference). Deviations from statistical assumptions can lead to incorrect results and false inferences from an otherwise valid study design. Unfortunately, bat acoustic data often violate several general statistical assumptions, most commonly arising from measurement error and independence, sometimes conflated with one another.

Acoustic methods are unable to differentiate between individual bats (Chapter 2, “Acoustic survey design”) and, in many cases, bat species (Chapter 4, “Echolocation call identification”). Therefore, you cannot argue logically that activity levels or even species presence have been assessed without error. Whereas most statistical methods assume that variables are measured with no error, it is common in acoustic studies to assume that activity patterns are measured imperfectly, with errors attributed to both false-positives and false-negatives. Of the two errors, false-negatives are easier to address when the species of interest is present and presence or absence can be distinguished reliably for any individual or set of site visits and/or measurement periods. Since individuals can’t be everywhere within their home range at once, it is invalid to assume that species presence or absence may be assessed without false-negatives (Gu and Swihart 2004; MacKenzie 2005). However, for false-negatives related to detection, occupancy models account for the measurement error of detection/non-detection (i.e., presence/absence) by using the pattern of detections within sites to estimate the probability of detection and the probability of presence for the species of interest separately (see below; MacKenzie et al. 2002; Bailey et al. 2014).

After imperfect detection, the second most commonly violated assumption is independence among samples. Most statistical methods assume that measurements are independent (i.e., unrelated to other measurements) at the same sampling location and/or other sampling sites. Given bats’ ability to cover large distances in a single night, independence among sampling sites is difficult to assess, particularly when studies occur at small spatial scales. Similarly, independence among activity measurements at an individual sampling site is difficult to ascertain. For example, bat activity from one minute to the next is likely to be correlated, as is activity hour to hour, and night to night. This poses a problem as classical repeated measures techniques, such as repeated measures analysis of variance, are unable to accommodate this autocorrelation. However, many statistical techniques, particularly those related to generalized linear models, have extensions that address this issue by directly modeling the nature and structure of the autocorrelation. Additionally, supplemental techniques, such as principal coordinate analysis of neighbor matrices (Dray et al. 2006), independently model autocorrelation and produce a representation of the pattern that is suitable for analysis using classical statistical tests. Broadly, the best practice is to assess your data for patterns of covariance among sites and autocorrelation between activity or presence on the temporal scale of interest, prior to statistical modeling.

Despite the potential negative consequences, violations of measurement error are commonly ignored and many analyses incorporate data or designs that violate assumptions of their statistical methods. In these cases, the conclusions drawn from the data should be given with caveats or re-interpreted relative to the violation of the assumptions.

Proper study design, including considering statistical techniques while designing studies can help avoid and minimize violations of statistical assumptions. When study design and statistical methodology are selected in conjunction *a priori*, prospective power analysis can be conducted to help determine appropriate sampling intensity for the desired level of statistical power (Chapter 2, “Acoustic survey design”). Below, we discuss various lines of study inquiry, the commonly associated statistical methods, and the unique considerations that bat acoustic studies may require. We also provide some general guidance for analyzing acoustic data.

Species diversity

Quantifying biodiversity may be problematic as it can be measured in many ways, but species richness remains the most frequently used measure. However, comparisons of species richness among sampling sites may be biased if the sampling effort (e.g., number of nights surveyed, number of detectors deployed) differs among sites. Species accumulation curves (i.e., the cumulative number of species on the *y*-axis and the sampling effort on the *x*-axis) are a good way of standardizing comparisons, because species richness can be estimated using the asymptote of the curve (Moreno and Halffter 2000). Species accumulation curves provide other advantages such as an evaluation of survey completeness and calculation of minimum sampling effort required to assess species richness.

The use of species richness has been criticized because the relative abundance of species is not taken into account. Without considering abundance, rare species will have the same weights as common ones. Thus, Shannon's (H) and Simpson's (D) diversity indices — the two commonly used measures that consider evenness among species — are usually calculated alongside species richness. These three indices have been unified by Hill numbers that summarize them as a single expression (Chao et al. 2014; Hsieh et al. 2016). Using Hill numbers has numerous advantages over other diversity indices because Hill numbers all have the same unit (effective number of species), and it is now possible to conduct rarefaction (interpolation) and extrapolation (prediction) with them (Chao et al. 2014; Hsieh et al. 2016). Like species accumulation curves, this approach enables standardized comparisons of the three indices between sampling units.

Although not traditionally taken into account, correcting for detection probabilities of different species may improve estimates of diversity (Stoner et al. 2011).

In the context of community composition, researchers are usually interested in investigating spatial and temporal patterns in species composition, examining changes in community composition in response to environmental factors, and identifying which taxa are likely drivers of the patterns observed. These approaches require use of multivariate analyses (multiple response variables) that fall into three categories: eigenanalysis-based, distance-based, and linear model-based methods.

Eigenanalysis-based analyses use unconstrained ordination techniques, such as principal component analysis (PCA) and correspondence analysis (CA). These analyses also use constrained (canonical) ordination techniques, like redundancy analysis (RDA) and canonical correspondence analysis (CCA) to assess whether the patterns observed are associated with environmental gradients. RDA and CCA are the constrained form of PCA and CA, respectively. The principle consists of associating the species data matrix to the environmental factor matrices. A full description of the methods and associated R scripts are given by Borcard et al. (2011) and Ramette (2007).

Distance-based methods like permutational multivariate analysis of variance (PERMANOVA), analysis of similarities (ANOSIM), and Mantel tests are mainly used to test for statistical differences between two or more groups of multivariate units (Anderson and Walsh 2013). Bray-Curtis is the most frequently chosen distance/dissimilarity measure, but others may be more suitable in some circumstances (Borcard et al. 2011). Data exploration can be performed using non-metric multidimensional scaling (NMDS) or principal coordinates analysis (PCoA).

Finally, the multi-species linear model-based approach consists of fitting a specified generalized linear model to each species (many GLMs) and drawing community-level inferences using a resampling method. This technique provides many advantages and is more robust than distance-based ones (see Warton et al. 2012). Wang et al. (2012) provide useful information about the different steps to follow.

Species distribution, and presence/absence

Species distribution models (SDMs) generally seek to show where a species occurs by describing the relationship between the presence of a species of interest relative to measured environmental variables. These models are used when the question of interest relates to the distribution of a species at a broader landscape scale (e.g., geographic region), whereas species presence/absence models (PAMs) describe whether a species is present at a finer landscape scale (e.g., specific forest block). Statistically, there is little or no difference in the analytical methods used to construct SDMs and PAMs, and most statistical methods that can predict event occurrence based on combinations of variables can be used for SDMs and PAMs. Some of these methods include generalized linear and generalized linear mixed models, classification and regression trees, neural networks, support vector machines, occupancy models, and maximum entropy models. Although these approaches are all distinguished by their approach to the use of data and underlying assumptions, it is easiest to separate models into those that use both presence and absence/non-detection (or background) data vs. those using presence-only data.

To date, maximum entropy models have been the most widely used presence-only SDM approach (Baldwin 2009; Merow et al. 2013; Barnhart and Gillam 2016), although newly developed methods using maximum likelihood are increasingly popular (Royle et al. 2012; Merow and Silander 2014). Presence-only models are relatively robust to small sample sizes and may be of particular use for rare species that are detected infrequently. Presence-only modeling is robust to filtering data, which may be useful in acoustic studies that model species distribution and only use detections with a high level of confidence for species identification. This type of presence-only modeling relies on definite detections, excludes possible or probable detections, and partially circumvents the issues of species detection probability by avoiding the assumptions associated with non-detections. However, it is important to consider that by not using non-detection sites or not modeling detection probability the results of your SDMs may predict low probability of presence due to biased data, rather than avoidance by the species of interest.

Although various model types were historically used to create SDMs and PAMs, models that incorporate detection probability, most commonly occupancy models, are increasingly popular due to their ability to separate the processes related to likelihood of detection from species presence (i.e., occupancy). Occupancy models use the pattern of detections across multiple sampling occasions at each site to assess detection probability, while occupancy is assessed using the pattern of detections across sites. Importantly, these occupancy estimates are adjusted for the imperfect detection process.

Single season occupancy models were originally designed to model the presence of a single species under imperfect detection during a closed time period. These models assume that 1) sites are closed to changes in occupancy state between sampling locations, 2) the detection process is independent among sites, and 3) the probability of occupancy and detection could be explained by covariates or is consistent across sites (MacKenzie et al. 2002). Since their initial development, occupancy models have been designed to match an array of study designs that address nuances in the relationships among occupancy, detection, and abundance. Further, these models allow open populations (i.e., changing occupancy status), incorporate spatial correlation, and can integrate false-positive detections (Popescu et al. 2012; Bailey et al. 2014; Chambert et al. 2015). Moreover, particularly with Bayesian statistical methods, it is possible to develop new estimators accommodating additional designs and considerations (Royle and Kéry 2007; Mordecai et al. 2011; Aing et al. 2011).

The great variety of occupancy models makes it difficult to provide guidance on their use in specific situations. However, to analyze acoustic data using a simple single season occupancy model, the basic assumptions that must be met are independence of detection among sites, detection and occupancy probability are explained by covariates, and no uncertain detections. Independence of detection among sites may be difficult to verify as many bat species exhibit social behaviors, form large aggregations, or travel long distances regularly. Lack of independence among sites can affect both occupancy and detection estimates, and therefore, it is critical to consider the distance between your sampling sites. In theory, the detection and occupancy probabilities of bats are related to measurable parameters. In practice, modeling detection is difficult as detection and occupancy probabilities may be impacted by variables such as humidity, three-dimensional structures at the sampling site, and other factors that are difficult to quantify and often go unmeasured. For example, it has been widely reported from mist-netting studies that insect hatches attract and concentrate insectivorous bats into areas scarcely used at other times. There are no definitive and universally applicable answers to how these issues may be avoided; however, by carefully considering study design and detector placement relative to the ecology of the species of interest in the planning stage of your project, you can begin to identify potential issues and determine how best to overcome them.

Perhaps the biggest challenge for the analysis of acoustic data in general is uncertain detections that include both false-positive and false-negative detections. Although occupancy models account for false-negative detections, they must be related to measurable, typically environmental, parameters. False-negatives associated with uncertainty in call species identity and false-positive detections are not typically incorporated into occupancy models (Figure 5-2). However, the issues related to false-positive and false-negative detections in wildlife have led to the development of occupancy models that incorporate them, provided that detection data can be coded into groups of high and uncertain reliability (Chambert et al. 2015; Clement 2016). To date, false-positive occupancy models have rarely been used in bat acoustic studies, but Clement et al. (2014) paired acoustic data with capture data to categorize acoustic detections for use in this class of model. False-positive occupancy models estimate parameters for occupancy, false-negative detection, false-positive detection, and true positive detection, so it is important to be aware that they require considerable amounts of data. Despite limited use to date, the ability to model likelihood of false-positive and true positive detection in bat acoustic data foreshadows exciting possibilities. For example, with proper design and covariates, it may be possible to assess differences in automated acoustic identification software, qualitative call analysts, and the effect of other species presence, among many other factors.

Despite the staggering number of occupancy models designed for different situations, you may find that occupancy models are impractical or unsuitable. One of the first considerations for whether to use occupancy models should be how many site visits will occur. Due to finite time and funding, there is always a tradeoff between number of sites sampled and length/number of times any individual site is sampled. If multiple sampling periods are infeasible or undesirable, other binary methods for assessing presence/absence may be more appropriate. Commonly used binary methods for PAMs include logistic regression, logistic mixed regression (i.e., logistic regression using random effects), and machine-learning techniques like classification trees. Despite their inability to model detection probability, these alternative methods are not without some advantages. Logistic regression, for example, is widely used and produces models that are simple to fit and evaluate. Logistic mixed models are also easy to fit and evaluate but allow for complex study designs with hierarchical effects and otherwise nested designs. Machine-learning techniques, particularly classification trees, allow modeling of non-linear relationships using

***Figure 5-2. Analytical approaches to false-positive and false-negative identifications.** The search phase echolocation calls of (a) big brown bats (*Eptesicus fuscus*) and (b) silver-haired bats (*Lasionycteris noctivagans*) are very similar and may easily be confused. An effective bat occupancy model needs to incorporate the potential for false-positives created when calls are incorrectly attributed to one of these species when it is not present, as well as the false-negatives that may result from that same misidentification if the true species is never detected. © Michael Durham/Minden Pictures, Bat Conservation International.*

thresholds and can be useful in assessing patterns when there are no particular *a priori* hypotheses.

Activity patterns

In principle, any analytical technique relating a continuous response variable to continuous and/or categorical predictors may be used to model bat activity data, and the appropriate analysis depends largely on the structure of the data.

Activity data are commonly recorded as counts of calls or call sequences at individual sites within a sampling period but can also be condensed at an individual sampling location into a mean or median value. This collapses repeated sampling at individual sites into a smaller number of observations, which is useful when intragroup variability is high relative to intergroup variability (as is often the case in acoustic studies), and when the rate of call sequences is the parameter of interest. From an analytical perspective, these data are not true counts and are not truly linear, since the observed values cannot go below zero. Therefore, be aware that the assumptions of linear and multiple linear regression models will be violated, and that some parameter estimates may result in predicted values less than zero. Additionally, condensing data to mean, median, or other aggregate values does reduce the overall usable data, relative to other statistical techniques, like mixed-effects models with random effects structures around individual sites. The extent of the reduction of data is related to the number of sampling occasions at an individual site; when few visits are made (generally less than 5), averaging values may be preferable to using mixed-effects models as these do not work well with few repeated measurements. As discussed elsewhere in this chapter, species distribution, presence/absence, population monitoring, occupancy, and N-mixture models make use of repeated site visits to calculate detection probability values, which are a useful way of addressing imperfect species detection. To date, no version of either model family has been developed to analyze activity patterns such as those collected for bats. Techniques to model abundance of unmarked animals based on repeated counts (Royle and Nichols 2003; Royle 2004), as discussed above in the context of population monitoring, are generally unsuitable for modeling activity patterns of bats due to violations of model assumptions.

If data are treated as counts, linear regression and mixed linear regression generally are inappropriate analytical methods due to the impossibility of negative counts of call sequences as noted above, but also because count data generally do not follow a normal distribution. Count data are typically modeled using generalized linear models or mixed models with a Poisson link function. Perhaps the greatest challenge in modeling activity levels of bats and one that has a significant influence on the analytical approach is how to deal with an excess of zeros (i.e., overdispersion). An excess of zeros is a common difficulty in modeling counts related to wild animals. In these cases, the Poisson link function is insufficient for modeling activity levels, and the negative binomial distribution, zero-inflated, or a model combining the two is necessary. Overdispersion is evident if the variance of the response is greater than the mean. You can determine overdispersion with a histogram of the response (i.e. activity data); if there is a clear abundance of zeros and the distribution does not approximate a typical Poisson distribution, data are likely overdispersed. In some cases, it may be beneficial to fit Poisson, negative binomial, and zero inflated models using identical predictors and compare model information criterion values (such as Akaike's Information Criterion; AIC), and select the best supported link function for use in further modeling.

Machine learning methods also may be useful in modeling activity data but these have not been widely used to assess bat activity. Nonetheless, machine learning provides several benefits as it is not constrained by the assumptions of generalized linear model. For block designs, nonparametric tests may be useful. Nonparametric tests are typically used when distributional assumptions cannot be met using parametric tests, or when outliers are problematic. An additional common challenge imposed by acoustic data, though not a violation of statistical assumptions *per se*, is high intrasample variability relative to intersample variability in treatment or group block design studies. In such cases, it may be necessary to reduce the number of categorical groups.

If activity is to be modeled over a continuous period (e.g., across hours after sunset), temporal autocorrelation (TAC) may occur. You can test for TAC using the Durbin-Watson statistic, which assesses presence of autocorrelation at lag intervals using the residuals from a regression analysis. When temporal autocorrelation in activity is present, it may be necessary to consider time series analytical methods, including moving average models and autoregressive models.

Analysis of sounds for behavioral studies

Once a sound of interest has been recorded, a researcher must decide what to do with it. With an understanding of the vocal repertoire of different bats, you should measure and classify different signals according to their temporal and spectral characteristics. You may also include an identification of individual and group signatures, or measures of the temporal and spatial changes of these signals. By estimating temporal changes, you can assess how ontogeny and/or learning influences call design (Knörnschild 2014, Engler et al. 2017). Measuring spatial differences in call parameters may allow inferences about the effect of ecological selection, sexual selection, and genetic drift on call design and vocal repertoires (Wilkins et al. 2013).

The most commonly measured acoustic parameters include duration, mean peak, minimum and maximum frequency, bandwidth, and entropy (Fernandez and Knörnschild 2017). Acoustic parameters are typically measured for syllables (i.e., the smallest acoustic unit of a vocalization), and calls (i.e., the simplest emission of a vocalization; Kanwal et al. 1994, Bohn et al. 2008). Further, for each call and syllable, you can create frequency contours by measuring minimum frequency at regular intervals (e.g., dividing the call in sections). From these contours, you can calculate values of call slope as

$$\frac{(freq\ at\ t_1 - freq\ at\ t_0)}{(t_1 - t_0)}$$

and concavity as

$$\frac{(slope\ at\ t_1 - slope\ at\ t_0)}{(t_1 - t_0)}$$

where t_0 is the start time of a given section and t_1 is the start time of the following section (Gillam and Chaverri 2012). You may also measure temporal distribution to determine if calls are monosyllabic or multisyllabic (Bohn et al. 2008). If calls are monosyllabic, you can extract call parameters for the entire signal, whereas if calls are multisyllabic or if syllables may be clearly divided in distinct sections, you should take separate measures for each syllable and section (Gillam and Chaverri 2012, Fernandez and Knörnschild 2017). After all this, you could end up with several call parameters that are likely important in explaining call variation but are auto correlated. At this point you may reduce variable dimensionality using PCA.

To determine if social calls have individual signatures or to measure other trends, like ontogenetic changes, you could use the reduced number of call parameters and compare them among individuals and time periods. Several studies have used discriminant function analysis to determine if vocalizations have individual and/or group signatures, and which call parameters may allow for discrimination between individuals using acoustic signals (Gillam and Chaverri 2012, Eckenweber and Knörnschild 2013, Knörnschild et al. 2013, Engler et al. 2017, Fernandez and Knörnschild 2017). By separating recordings from different periods during pup development, you can assess which call parameters change with development (Fernandez and Knörnschild

2017). Alternatively, linear mixed models may be used for estimating how the slopes of separate call parameters change during ontogeny (Engler et al. 2017).

Population monitoring

As previously described, it is virtually impossible to generate counts of individual bats using stationary acoustic studies. Consequently, it is common to model populations using metapopulation techniques that assess the turnover of sites (i.e., changes in site occupancy status). In this case, dynamic occupancy models may be particularly useful as they can provide estimates of turnover in site condition and can relate turnover to measured parameters (MacKenzie et al. 2003). However, the basic dynamic occupancy model may not be applicable in all cases, and modifications to the estimator may be necessary. For these cases, a Bayesian modeling framework is particularly useful (Royle and Kéry 2007), because this approach is relatively accommodating of modifications to estimators (Clark 2005). Bayesian modeling can also incorporate *priors,* which are probability distributions that express a belief about a quantity before data are assessed. When modeling populations, priors may be used to express beliefs about the population behavior before sampling.

When population data are counts in which call sequences represent individual bats and sampling is repeated (Royle and Nichols 2003; Royle 2004), N-mixture models for estimating abundance from repeated counts may be used to generate population estimates within years. Like occupancy models, these models allow estimation of detection probability using repeated site visits. When repeated site visits are conducted within years and sites are monitored for multiple years, open population versions of these models should be considered (Kéry et al. 2009; Dail and Madsen 2011). When count data obtained during population monitoring are measurements of activity at stationary points where activity cannot be attributed to individual bats, refer to analysis of activity patterns (above).

Summary

Selecting the most complicated statistical analysis should never be the goal. Often, a simple statistical analysis violating some assumptions will provide answers consistent with much more complicated statistical analyses with equal or greater violation of statistical assumptions. As with all statistical models, violations of the underlying assumptions does not mean that models produce uninformative results. In many cases, numerical estimates will be correct, but must be interpreted carefully regarding the nature of the violations and what they imply. Finally, when considering statistical techniques, always consider the statistical methods of recently published studies with similar objectives, including for unrelated taxa, a well as biostatistical journals to assess modern analyses in action and to stay abreast of ongoing developments.

Some additional suggestions

1. Document detector "up time" to quantify survey effort.

Nearly all bat detectors designed for passive use (e.g., stationary, unattended deployments) record a "log file" that documents when detectors are armed, triggered, recording, and/or writing files. New researchers often assume that detectors behave flawlessly and dependably. Indeed, there are a myriad of reasons for passive detectors to fail to record for hours or even nights at a time. By learning how to interpret your log-files you can confidently determine the “up-time”, which will influence your conclusions, especially if your goal is to infer relative activity levels or species occurrence.

2. In auto-classification, remember to account for the ramifications of recordings containing multiple bats in a file, or bats performing atypical behavior

Auto-classification software is a popular tool for reviewing long-term acoustic data and for analyzing large amounts of data from complex surveys involving multiple monitoring locations, sites, and nights. Unfortunately, current software is not sophisticated enough to identify recordings that have multiple individuals and/or have non-typical search-phase echolocation call types. Both of these conditions can lead to invalid assumptions about bat activity (i.e., one recording does not equal one bat pass) and species identification. In some cases, 10% to 25% of recordings include files with more than 1 bat pass and another 3-5% of recordings include non-search phase echolocation calls.

3. Become well versed in different types of software

It is difficult to develop acoustic identification skills using only one type of software. Bat calls look different in different software, due to a number of factors. The default y-axis scale may differ between logarithmic, which allows you to see more call body detail and makes calls look ‘shorter’ compared to linear scales that emphasize bandwidth. Software may also differ in displaying compressed vs. true time (e.g., compressed mode in KaleidoscopePro generally drops pulses out of full spectrum sequences), levels of zoom, and full spectrum vs. zero-crossed pulses that look different due to the fundamentally different way they present frequency data.

4. Collect metadata

Metadata are crucial for acoustic monitoring as a recording of a bat call is almost useless without some degree of contextual information. This information is important for identifying the species that made the call but it also for broader questions like distribution or seasonal activity of the species. Newer software, like the open source ‘GUANO’, is now common across most equipment/software and available in various coding languages, including R, reducing the learning curve and making it easier to record metadata.

A little brown myotis (*Myotis lucifugus*) chasing a moth. © Michael Durham/Minden Pictures, Bat Conservation International.

Chapter 6. Case Studies

Introduction

The main objective of the Handbook to this point has been to summarize current relevant information about hardware, software, and best practices for acoustic monitoring of bat populations. Our goal has been to create a brief but comprehensive guide for practitioners with varying levels of experience that is particularly accessible to novices.

The objective of this final section is to provide concrete examples of the concepts discussed in Chapters 1–5. This last chapter contains five short descriptions of what we believe to be well-designed and executed studies that used acoustics as the principal method. We want to be very quick to point out that these examples are certainly NOT the only good studies that exist; we only mean that they are good examples. We choose them to represent a diversity of research questions, choices of detector and call ID software, and geographic areas. Although there is a North American bias in the studies that are included, the goal for this chapter, as well as for the Handbook in general, is to be global in scope. We thank the authors for summarizing the details of their work and allowing themselves to be exposed to the detailed acoustic imaging systems of readers! We are also grateful to the numerous colleagues who offered their own examples of fine work that could just as easily have been used.

Case study 1: Acoustic Surveys at Fort Drum Military Installation – the Value of Long-term Monitoring

Mark W. Ford, Christopher A. Dobony, David S. Jachowski, Laci S. Coleman, Tomas Nocera and Eric. R. Britzke.

Prior to the advent of white-nose syndrome (WNS), most bat conservation in the eastern United States consisted of one issue: the known or suspected presence of the endangered Indiana bat (*Myotis sodalis*). The National Environmental Policy Act and the Endangered Species Act requires Department of Defense land managers to prioritize identification, monitoring, and conservation of Indiana bat day-roost areas, foraging habitat during the maternity season, and pre-hibernation swarming sites during autumn.

The presence of Indiana bats requires modification to the extent and timing of use of military areas and forest management that could be disruptive for mission needs or other stewardship actions. Following the discovery of active Indiana bat maternity colonies near Fort Drum in northwestern New York in the early 2000s, U.S. Army biologists set out to determine the extent to which Indiana bats used the 44,000-ha installation and the environmental correlates linked to their presence.

By confirming presence and spatiotemporal habitat use by Indiana bats, management could be targeted, habitat enhanced, and training and stewardship allowed to proceed fairly unhindered. We recognized that mist-netting was inefficient without significant data to guide surveys and incorporated acoustic surveys to identify locations and habitat types with high relative activity levels. Since 2003, we conducted annual passive acoustic recordings with zero-crossing detectors in a habitat-specific stratified random design to survey > 250 locations. Many surveys were repeated within and among years, leading to a database of 10,382 “detector-nights”. Early surveys helped determine locations where activity occurred, from which we selected mist-netting sites to maximize capture success. Telemetry led to landscape-, stand- and tree-scale examinations of maternity day-roosts and foraging habitat that led to conclusions about the response of populations of Indiana bats to management in the Northeast (Jachowski et al. 2014b, 2016).

In 2008, WNS arrived at Fort Drum. With 5 years of pre-disease acoustic data, we were able to detect declines in the relative activity of *Myotis* spp. congruent with mortality at WNS-impacted hibernacula in the Northeast (Ford et al. 2011, Coleman et al. 2014c). Moreover, the pre-disease data suggested that, in addition to declines in bat numbers returning from hibernacula, rates of juvenile recruitment must also have declined (Ford et al. 2011). This provided impetus for failed recruitment assessments at other locations in the Northeast and mid-Atlantic (Francl et al. 2012, Reynolds et al. 2016). However, the news was not all bad! Based on assessments of annual survivorship and immigration from collapsing colonies, we postulated that little brown myotis (*M. lucifugus*) populations at Fort Drum might stabilize, albeit at lower numbers, and acoustic data support this contention (Dobony and Johnson 2018; Figure 1).

By analyzing changes in relative foraging activity levels between riparian and wetland habitats on an hourly basis we determined that, prior to WNS, little brown myotis occurred in large numbers at Fort

Drum associated with open riparian and wetland habitats. In these locations, they predominated over big brown bats (*Eptesicus fuscus*) and eastern red bats (*Lasiurus borealis*; Ford et al. 2011; Jachowski et al. 2014). However, after the WNS-related decline of little brown myotis, both big brown bats and eastern red bats increased foraging activity in these habitats, suggesting a disease-mediated niche change.

Following declines from WNS, the efficacy of mist-netting as a survey tool has declined due to low capture success. The likelihood of false-negatives is greater for mist-netting than acoustic monitoring. To determine the necessary acoustic sampling effort needed to assess presence or absence in an occupancy framework at high levels of probability, Niver et al. (2014) used pre- and post-disease acoustic data from Fort Drum to calculate the spatial and temporal variation in detection probability of Indiana bats and the threatened northern myotis (*M. septentrionalis*).

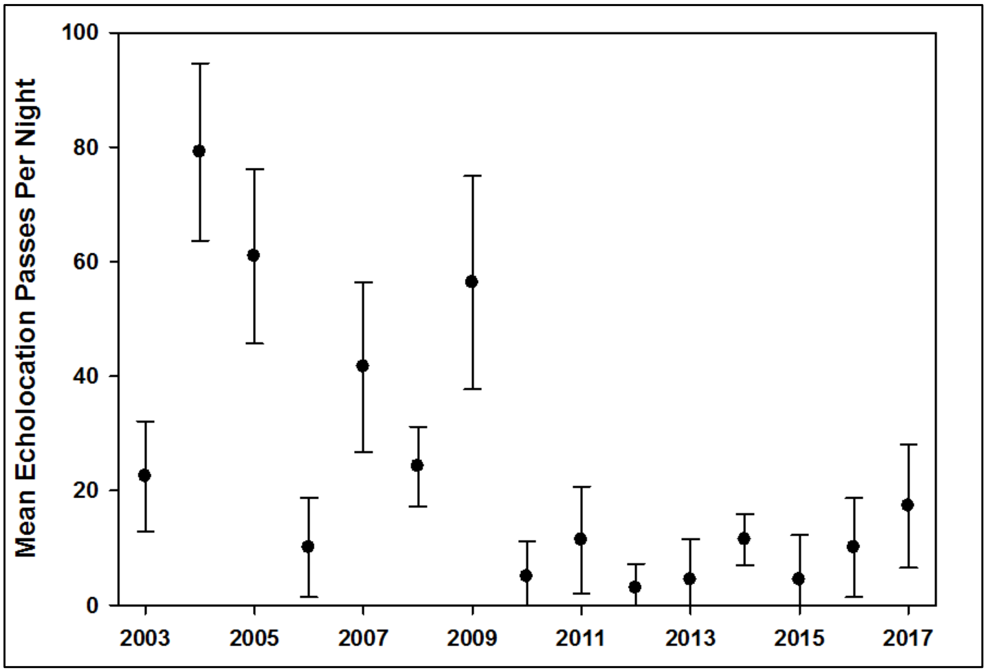

*Figure 1. Long-term acoustical monitoring trends during the summer maternity season (June-August) at Fort Drum Military Installation, New York, U.S.A., for the little brown myotis (*Myotis lucifugus*). White-nose Syndrome impacts began locally in 2008.*

As the impact of WNS continues and the number of species at risk increases, our focus has changed from just Indiana bats to a wider species assessment. Accordingly, we have adopted acoustic approaches to assess the spatiotemporal use of military installations by all bat species. One such approach used acoustic data from Fort Drum to create species-specific sampling protocols to maximize detection probability and showed how detector arrangement and spacing can address species-specific or entire bat community monitoring needs (Coleman et al. 2014a, 2014c). Additionally, our acoustic data on habitat association mirrored the results of a congruent radio-telemetry survey, which gives confidence in using acoustics to describe foraging habitat use (Coleman et al. 2014b).

Ongoing analyses are using Fort Drum data to determine the spatiotemporal scales at which relative activity and occupancy provide similar patterns of distribution on the landscape. Moreover, we are using the acoustic dataset to compare output from the automated bat identification functions of the software packages currently approved by the U.S. Fish and Wildlife Service with seven years (2003–2010) of visually vetted call identification (Ford et al. 2011). For this purpose, the visually-vetted call information serves as a call library that can be used to critically assess the automated identification functions. In summary, our work at Fort Drum highlights the benefits of maintaining a multiyear acoustic survey and showcases the intended, and sometimes serendipitous, value of acoustic data as a research and management tool. *Ed. Note*: "For further information on generating a call library for use by automated identification software, please see the section in this Handbook on creating call libraries. Note that the authors of the call libraries section suggest that, under ideal circumstances, calls being used in call libraries should be collected from known individual bats."

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Case study 2: Using ultrasonic surveys to inform management of floodplain forests for Australian bats

Rachel V. Blakey, Bradley S. Law and Richard Kingsford.

Floodplains are globally threatened ecosystems that host diverse aquatic and terrestrial communities (Kingsford 2015). The Murray-Darling basin in Australia (> 1 million km^2) supports extensive floodplains, which are threatened by river regulation and floodplain development (Kingsford 2000). Managing populations that inhabit floodplains is challenging, but bat communities are a diverse and important group within floodplains and their management should be a priority (Blakey et al. 2018). Acoustic surveys allow for an efficient and simultaneous census of bats at numerous, widely separated sites within a wetland and provide a measure of habitat use for more species than trapping. We used acoustic surveys to investigate two broad management questions about bats in floodplains: 1) how important are floodplain habitats for bats compared to the surrounding dominant dry environments (Blakey et al. 2017a) and 2) how does forest thinning impact bats in floodplain forest (Blakey et al. 2016)?

We conducted acoustic surveys during the spring-summer lactation period, when maintenance of an individual's energy and water balance is presumed to be most challenging. We restricted our surveys to nights without precipitation and with overnight temperatures > 15°C, and bats were surveyed over multiple nights at each site, as nightly differences in activity can account for significant variation at the site level (Fischer et al. 2009).

We assessed the use of water by bats because one species (large-footed myotis, *Myotis macropus,* common name as listed on the IUCN Red List, https://www.iucnredlist.org/species/136697/4328885) specializes in foraging over water surfaces. We compared activity levels among habitats, but not among species, due to variation in species-specific call detectability. The habitats in which we recorded represented a decreasing frequency of flooding along a floodplain mosaic/gradient. We classified habitats as river, lake, vegetated wetland, floodplain forest and floodplain woodland. We also compared two dry habitats classified as dry vegetation and agricultural. We replicated these habitats in each of six floodplain systems, traversing climatic and hydrological gradients.

In our second study, we compared the activity of 11 bat taxa from six guilds across four forest thinning categories. These categories included unthinned regrowth, forest thinned recently (0–4 years), thinned in a medium term (5–10 years), and reference forest (mature open forest; Figure 1). We evaluated differences in vegetation attenuation between our thinning categories (e.g., dense regrowth, recently and medium-term thinned, and reference forest) using "call quality" (i.e., percentage of calls that were successfully assigned to bat taxa) as an index of how well detectors recorded bat calls.

Both studies used Anabat detectors (Anabat II, Anabat SD1, Anabat SD2, Titley Scientific, Brendale, QLD, Australia), which were calibrated to detect a constant 40 kHz sound emitted by a bat chirper

(Nevada Bat Technology, Las Vegas, NV, USA). The attenuation of sound by vegetation is an important confounding variable (O'Keefe et al. 2014), and to increase the quality of the recordings and directionality of the weather-proof detectors, we placed the ultrasonic microphones into S-bend PVC pipes pointed vertically at a 45° angle. When using zero-crossings recording, loud insect noise can mask soft bat calls during the same period and can continuously trigger recordings that drain battery power. To lessen attenuation of sound and insect noise, we raised detectors 1 m from the ground and pointed them into vegetation gaps.

*Figure 1. A comparison of highly cluttered (left) and open reference (right) floodplain forest, with inland broad-nosed bat (*Scotorepens balstoni*, common name as listed on the IUCN Red List, https://www.iucnredlist.org/species/14942/4481710) in center.*

We used *Anascheme*, an automated call identification software developed in Australia (Adams et al. 2010). This python-based software relies on classifiers built and tested with regional call libraries. We used existing local call libraries and gathered bat reference calls from across the Murray-Darling basin to construct the regional classifiers and, after testing with independent reference calls, achieved a misclassification rate of < 2 %. We manually verified any unexpected species identifications (range extensions), as well as difficult-to-separate species, such as the large-footed myotis (*M. macropus*), which can only be distinguished from long-eared bats (*Nyctophilus* spp.) by experienced observers. Since *Anascheme* analyzes calls on a pulse-by-pulse basis, we used a filter within the software to separate the calls of Gould's wattled bats (*Chalinolobus gouldii*) and little pied bats (*C. picatus*), which often contain consecutive pulses that alternate in frequency. We used an additional filter to separate feeding buzzes, all of which were checked manually by listening and visual observation to remove steep "clutter calls". These were assigned to species when possible.

How important are floodplain habitats for bats compared to the surrounding dominant dry environments?

Rivers and lakes with open water and riparian trees had greater total activity (5 times), foraging activity (14 times), and bat richness (1.5 times) than dry vegetation. The activity of all mesic bat species, as well as some widespread and arid-adapted species, were positively associated with floodplain habitats compared to dry vegetation. Lowest overall activity, foraging activity, and richness were observed in dry agricultural (cropping, grazing, and fallow) habitats, with two of six threatened species in our study area never recorded in these habitats.

Recording over water can be problematic due to echoes from the water surface confounding call identification and the presence of several bat species, the latter of which leads to multiple species in one recording potential call identification issues. Additionally, including water as a habitat confounds the quantification of foraging activity by feeding buzzes, because bats also emit a "buzz" when drinking (Griffiths 2013). Despite these challenges, we were able to identify 58% of calls made over water to species. We were careful in our interpretation of feeding buzzes and drinking buzzes and hope that future research will elucidate the acoustic differences between these activities.

How does forest thinning impact bats in floodplain forest?

Total activity was 60% less and foraging activity was 80% less in unthinned regrowth compared to reference sites. Further, activity levels were similar between thinned and reference sites, despite greater average prey availability in unthinned sites (Blakey et al. 2017a). We also found that foraging strategy (i.e., open-space, above-canopy, edge-space, closed-space) underpinned the relationship between bats and forest structure (Blakey et al. 2017b).

Call quality did not vary significantly among thinning categories (unthinned: 29 ± 2, recently thinned: 31 ± 2, medium-term thinned: 35 ± 2, reference: 31 ± 2 % identified; $X^2 = 1.95$, $P = 0.58$). Overall, the quality of these recordings was lower than our floodplain study, likely due to larger open spaces for recording and higher detector sensitivity. Long-eared bats (*Nyctophilus* spp.) are quiet-calling bats that are best adapted to clutter and were present within the floodplain bat community. Not surprisingly, long-eared bats were most active in the dense regrowth. To quantify call attenuation within different habitat types before conducting acoustic surveys, we recommend using a bat chirper, or even better, broadcasting recorded bat calls and determining the range at which they can be detected.

Recording bats flying below the canopy and within the vegetation, as opposed to individuals flying above the canopy or along an edge, was challenging. To minimize the number of bats that were recorded above the canopy, we reduced the sensitivity of our detectors; however, our recordings of open-space adapted bats over cluttered sites indicated that we still recorded some of these species. Where possible, we recommend setting up multiple vertical microphones to study both the below-canopy and above canopy space as per Adams et al. (2009) and Müller et al. (2013).

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Case Study 3: Going, going, gone: Declining bat activity in summer following the arrival of white-nose syndrome in upper New York State

Yvonne Dzal

From 2007 to 2009, we examined the effects of historical contamination by polychlorinated biphenyls (PCB) in the Hudson River (NY) on bat activity and foraging behavior (Hooton et al. 2016). During this time, bat mortality linked to a fungal disease, white-nose syndrome (WNS), was first reported from a cave less than 100 km from our study sites (Veilleux 2008; Reeder and Turner 2008; Turner and Reeder 2009) (Figure 1). Ten years later, the subsequent outcome of WNS is all too well known (Frick et al. 2010).

Shortly following the first documented case of WNS in North America, many studies reported substantial bat die-offs in overwintering caves (e.g. Turner et al. 2011). We were in the unique position of having access to an extensive multiyear acoustic dataset that examined summer bat activity in an area where WNS was first recorded. Furthermore, this acoustic dataset coincided with the discovery and spread of WNS in the area. Thus, we used these data opportunistically to determine how bat mortality linked to WNS at overwintering caves affected activity and species composition in their summer range (Dzal et al. 2010).

*Figure 1. Little brown myotis (*Myotis lucifugus*) with white-nose syndrome. © Michael Schirmacher, Bat Conservation International.*

To collect our data, we used a four-microphone array, with microphones arranged in a tetrahedron, 1 m from one another. This microphone arrangement allowed us to capitalize on intensity differences between simultaneously recording microphones, enabling multiple individuals to be distinguished from one another, but also allowed us to pick up calls that may have gone undetected had we used a single-microphone to record bat echolocation calls (Koblitz 2018). Furthermore, we placed our microphone array on a boat. This allowed us to: 1) sample activity over a larger area in one evening than if we had remained stationary, as is normally done; 2) record echolocation calls along a large body of water, a prime foraging location for many species; and 3) avoid the tedious paperwork often associated with sampling on private and/or public land. We monitored activity acoustically at six sites and 48 sampling stations along a 40 km stretch of the Hudson River. We began recording after confirming the presence of the first bat and continued to record for 10 minutes before moving to the next sampling station. Bats were sampled at only one site on any given night.

We identified species present at our study sites by specific parameters in their echolocation calls. Specifically, we measured call duration, inter-pulse intervals, minimum and maximum frequencies, frequency with most energy, and the presence of harmonics. We analyzed call sequences using callViewer, automated detection software, which was designed for analysis of echolocation recordings (Skowronski and Fenton 2008). The automated detection software allowed us to analyze large quantities of data using consistent detection criteria. Results generated by the automated detector were graphically displayed in spectrogram view, allowing for a visual assessment of accuracy. These call parameters were then compared with literature values for bat species present in New York State. If detection errors in the automated process were identified in review, acoustic measurements were manually recalculated.

To assess activity, we counted the number of search-phase call sequences present in each 10-minute file. Search-phase call sequences consist of a series of individual calls and are a commonly used metric for bat activity. Finally, to minimize the chances of repeatedly sampling the same individual, we chose a maximum of two call sequences within 1 min of recording, with a minimum 10 s separation between sequences. The benefits of acoustic monitoring are numerous, but users must be aware of limitations and potential biases. For example, although we used bat activity to make inferences about the relative abundance of the little brown myotis (*Myotis lucifigus*) during the spread of WNS in North America, our data do not allow for an estimate of population size.

From our acoustic data, we concluded that there was a 78% decline in summer activity by the little brown myotis, coinciding with the arrival and spread of WNS. Interestingly, we found that summer activity of a bat species not known to be affected by WNS (the hoary bat, *Lasiurus cinereus*) remained constant from 2007 to 2009. Collectively, our data indicated that WNS-linked mortality at overwintering caves was reflected in reduced summer activity, suggesting that WNS affects entire populations and not just individuals in hibernacula. More importantly, our study provided us with insight into the health of bat populations in upstate New York, and the potential effects of WNS on summer activity of the little brown myotis that, prior to WNS, was likely the most common and widespread bat in North America.

In summary, our study provides an example of how existing acoustic data sets may be used for assessing long-term changes related to disease outbreak, providing insights into population and ecosystem health.

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Case Study 4: NABat acoustic monitoring allows inferences about bat populations at multiple scales

Brian E. Reichert, Thomas J. Rodhouse, Susan Loeb, and Jason Rae

North American bats face unprecedented risks from continuing and emerging threats including habitat loss, white-nose syndrome (WNS), and wind-energy development. Indeed, many species are experiencing unparalleled population declines (O'Shea et al. 2016). The North American Bat Monitoring Program (NABat) was conceived to elucidate the ecological consequences of these large-scale population declines (Loeb et al. 2015). To improve our knowledge about the 47 species of bats shared by Canada, United States, and Mexico, NABat imposes standardized protocols and a unified sample design that allows a multi-agency, multinational, collaborative monitoring effort. A key element of NABat is cross-boundary partner coordination and the sharing of limited resources for collecting acoustic monitoring data. These data are obtained by continuous passive recording using stationary acoustic detectors, as well as mobile transect surveys. Using data from stationary acoustic surveys undertaken by multiple partners, NABat generates data on species distributions via "site occupancy models" (MacKenzie 2002) and assesses changes to distributions over time via "dynamic occupancy models" (Mackenzie et al. 2003; e.g., Rodhouse et al. 2015). Data from mobile transects provide an index of relative abundance or activity (Loeb et al. 2015). Here we provide three examples of how this program provides a convenient framework for using acoustic data to assess the potential impacts of current and future threats to North American bats across multiple spatial scales.

Using the NABat sampling design, partner organizations can address local research objectives, while still contributing to analyses of trends at regional, landscape, and continental scales. The foundation of NABat is a probabilistic sampling design that integrates a master sample approach with a 10 x 10 km grid-based frame. Sampling priorities have been assigned to each of these 100-km^2 grid cells within the continental sampling frame, using the generalized random-tessellation stratified (GRTS) survey design algorithm (Stevens and Olsen 2003). Importantly, this sampling method ensures spatial balance and randomization for any jurisdictional subset of the NABat master sample. As a result, jurisdictional subsets (e.g., all grid cells on Forest Service land in Arizona and New Mexico) can be used to meet agency-specific inventory and monitoring needs, while the data collected are still useful for continental scale status and trend analyses. Similarly, data subsets may also be used to determine the potential drivers of bat distributions at the jurisdiction level (e.g., Li et al. 2018) or potentially smaller scales (e.g., counties or national parks). Some partners may also be interested in testing for potential effects of processes affecting bat populations at finer spatial scales than can be captured at the scale of the 100-km^2 grid cells (e.g., forest management practices). In these cases, partners can develop experimental study designs to test for potential management effects, while still contributing to the broader goal of monitoring populations at spatial scales ranging from local to continental.

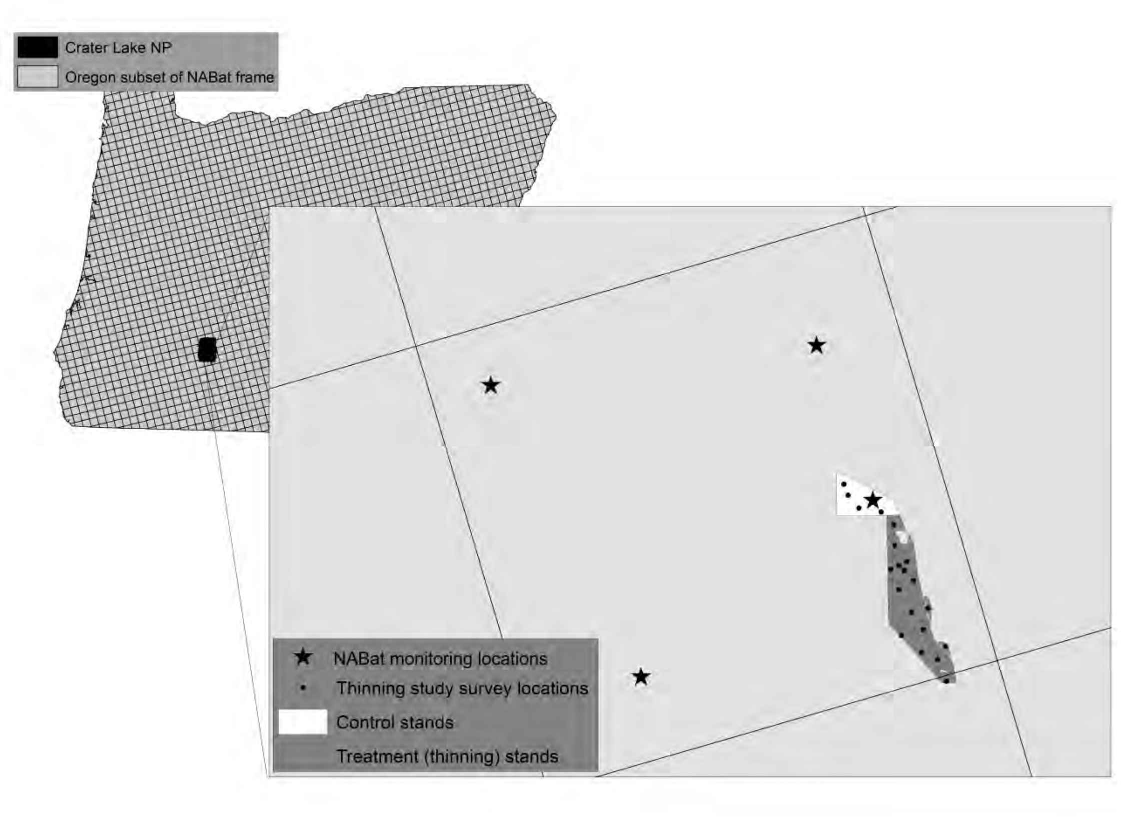

Figure 1. Nested study design for Crater Lake National Park, Oregon. The local-scale acoustic surveys of bats have been made compatible with NABat methodology and programmatic requirements, and are nested within the NABat grid-based sampling frame. This example illustrates a "scaling-up" and "scaling-down" strategy to motivate local-scale relevancy and engagement in regional NABat efforts.

Example 1. Effects of forest thinning on bats in Crater Lake NP

For the results of any acoustic survey to be used to make inferences and conclusions, the survey must have have been conducted at the the relevant geographic scales, grain, and resolution of study design. For NABat, the goals and objectives and subsequent design and inference decisions were optimized for regional to range-wide geographic scales with coarse-grain architecture. How then to incorporate local-scale relevancy and motivate busy people to participate in such a coarse-grained endeavor? One strategy for bridging the gap between local and regional relevancy was to nest fine-grain projects within the coarser NABat grid-based sampling frame. If the methods are compatible, then some or all of the data collected to meet local-scale objectives are also useful to the NABat program.

To evaluate the impacts of thinning for reducing fuels for forest fires, a 200-ha portion of Crater Lake National Park, Oregon, is being surveyed over time with stationary detectors (Figure 1). The study area fits within the southeast quadrant of a single NABat grid cell and was subdivided into treatment and control stands, which were each surveyed annually before and after treatment, as a replicated before-after control-impact experiment (Underwood 1994, Smith 2002). Sub-sampling of the study area is more intensive than required by NABat so, of four stationary sites, a single stationary detector in one of the control stands serves as the long-term NABat monitoring site (Figure 1).

Example 2. Developing long-term bat monitoring protocols in South Carolina

In 2015, the South Carolina Department of Natural Resources, Clemson University, and the USDA Forest Service, Southern Research Station, cooperated to implement NABat across South Carolina. The objective was to establish long-term bat monitoring for the state, while contributing data to NABat for regional and range-wide trend analyses. Following the GRTS sampling priority, stationary survey points and/or mobile transect routes were conducted in 38 cells from mid-May to late July 2015–2017. The research team detected all species known from the state, except Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), a "whispering bat" that is difficult to record acoustically. Using occupancy models with the acoustic data, the research team developed statewide distribution maps for seven species (or species groups) incorporating land cover, landscape, and regional variables.

This success stemmed from key partnerships. First, the state agency and Clemson University supported a student, who developed the monitoring design, which included placement of stationary acoustic detectors and identification of routes for mobile transects. Several state and federal agency personnel, as well as private citizens, adopted routes and points within grid cells for stationary acoustic monitoring, which they continue to survey. Next, partnerships with private citizens, municipalities, and state and federal agencies were critical for acquiring access to monitoring sites, as only 12% of land in South Carolina is publicly owned. As a result, mobile transect routes were chosen because these can be relatively easier to establish (30 of 38 cells had mobile transects) and typically do not require landowner permission.

Example 3. Bat population status prior to the arrival of WNS in British Columbia

Wildlife Conservation Society Canada implemented the NABat program in British Columbia, Canada, in 2016. The program served two primary objectives: (1 to provide data on bat species diversity and distribution at a local/provincial level prior to the arrival of WNS and (2 to provide reliable data to NABat to inform conservation efforts that support long-term viability of populations on a continental scale. Acoustic detectors were deployed following NABat sampling priority in grid cells across the province by a collaborative group of biologists, natural resource managers, and naturalists. At the local scale, the data were useful to answer simple questions such as "what species are using the land that we manage?" or "what species occur in the region"? As with many parts of North America, much of British Columbia has not been surveyed for bats. However, simply cataloguing species diversity in each location will allow local managers to identify and manage critical habitat within their jurisdictions more effectively. Indeed, NABat data from 2016 provided additional evidence to support the contention that Brazilian free-tailed bats (*Tadarida brasiliensis*) are now a common visitor to British Columbia (Ommundsen et al. 2017).

At the provincial scale, NABat data are crucial to assess species diversity and distribution across the province. Long-term data will be important for examining fine-scale habitat associations to inform land conservation and management actions. These data are particularly valuable in advance of the impending ingress of WNS that, in the spring of 2016, was confirmed just south of British Columbia, in Washington State. In the future, NABat monitoring will provide an indication of where the first signs of WNS appear, which species are most affected, and help guide mitigation and management efforts to maximize their effect on reducing WNS-related mortality across the province.

The future

Understanding and predicting responses of populations to ongoing and future threats requires active participation by multiple stakeholders following a standardized protocol to collect data. With more data, NABat will enable rigorous analyses of status and trends, document changes in species distributions, focus conservation efforts on threatened populations, and evaluate conservation and adaptive management actions. NABat can help maximize sampling efficiency and minimize redundancy of efforts by providing the operational framework for landscape-level conservation science, while concurrently meeting the widespread need for smaller-scale, jurisdictional research and monitoring. To address state/provincial, regional, and range-wide objectives of the partners, NABat will provide on-demand reporting for resource and management agencies, mapping applications to improve decision-making for WNS surveillance, and data products such as dynamic distribution maps and a “State of North American Bats” report every five years.

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Case Study 5: Bats in the Ghats: Building a call library to study the impacts of agriculture on bats in a biodiversity hot spot

Claire F.R. Wordley

Inadvertently causing a bomb scare was one of the least consequential problems I had while studying bats in India. Some of these problems were caused by my inexperience as a young Ph.D. student, working without a bat expert to help me, in a country that was not my own. Other problems were inherent to working in a tropical mountain range where bats had barely been studied. Despite experiencing (and causing) a fair degree of trouble, I managed to create a workable acoustic library in a biodiversity hot spot, the Anamalai Hills in the Western Ghats of India (Wordley et al. 2014), and use that library to understand how agricultural systems affected those bats (Wordley et al. 2015, 2017, 2018). I hope my work will encourage further development of call libraries across the world, as they are invaluable for studying bat ecology.

Working out how to work

The goals of my work were to compare bat abundance, diversity, and functional diversity among tea and coffee plantations, forest fragments, and protected forests, along with riparian versions of those habitats (Wordley et al. 2017, 2018). I planned to use both acoustic data and captures to complete this work, and also wanted to understand the relative detection properties of these two methods better (Wordley 2018).

When we began the study in 2010, little was known about bats at the study site—or indeed across much of India. A master's student had undertaken some acoustic transects and netting in the Anamalais; however, most calls I recorded on transects were initially unidentifiable, so my first step was to build a call library. I began by catching bats in caves and tunnels to build the library, but this did not yield many new species. I concluded that I would have to start gathering data on the bat assemblages in different habitats, while simultaneously building my call library, meaning that at first I could not identify the bats in the acoustic data I gathered.

To compound the difficulties of developing a study system from scratch, working at night in the area was a challenge. By far the biggest danger was elephants, and we always stayed in pairs, so one person could be on the lookout for them. This risk was compounded by my insistence that about half our sites were along rivers, where animals came to drink at night. This included bats, and we managed to catch species over rivers that we never caught elsewhere, but of course, it also included elephants, bison, and even the odd tiger.

Initially, we tried to quantify local bat activity by recording free-flying animals continuously while walking a kilometer-long transect within each habitat, an approach used by Ph.D. students in the U.K. This didn't work very well. First, the Anamalai Hills were so steep in places that we needed both hands to scramble up a slope. Second, the noise made by walking on the dead leaves in forests affected the recordings, making it hard to get clean recordings. Third, if we focused on walking and recording, it was easy to miss hazards such as snakes or holes in the ground. Fourth, some of the forest fragments were so small and had so few navigable areas, that we couldn't fit a long transect inside them. And finally, due to the risks posed by elephants in particular, I wanted to keep team members as close as possible.

The protocol I developed included a "transect" of five recording sessions of 15 minutes each per site, with recording locations 100 m apart (Wordley et al. 2017, 2018), and five mist nets about 100 m from the nearest stop on the acoustic transect. This was designed to minimize the risks. While two people manned the mist nets, two others detected bats using Pettersson D240X detectors in time-expansion mode set to record continuously, to try and pick up even the faintest calls. Despite sampling a smaller area with these multiple "stop points" than we would have on a longer, walked transect, I think it was the right approach.

To build habitat suitability models for bat species in the area, I walked an additional 18 longer (2 km) transects with shorter (3-minute) stop points (Wordley et al. 2015). These transects were designed to encompass a range of habitats, at different distances from the protected forest, whilst walking on easy terrain and not trying to catch bats simultaneously.

Additionally, we placed Pettersson D500X recorders overnight at each site, set to trigger with noise. We put them inside tough plastic cases, with a hole cut for the microphone, and chained them to trees – the advantage being that we could set them up and take them down in the relative safety of daylight. The first time we did this, when we came to pick up the recorder a crowd had gathered, worrying that it was a bomb. After profuse apologies, we collected the recorder and wrote a brief explanation of its purpose in English and Tamil on the outside. It was a useful reminder that communicating with local people is as important as the fieldwork itself.

Unfortunately, despite collecting thousands of hours of recordings from the D500X, I couldn't easily use these data. Insect noise meant the recorders were triggered constantly, generating thousands of 3-second files which needed to be scanned for bat calls. We could have increased the frequency at which the detectors were triggered, but we had some bats calling at the same frequency (10–20 kHz) as the insects, and I was convinced we would be able to automate the call identification later on. We tried using call identification software developed in our lab (Scott et al. 2012) and primed with my call library, to identify the bat calls automatically. Sadly, using the automated method, we could never distinguish between Horsfield's myotis (*Myotis horsfieldii*) and eastern bent-winged bats (*Miniopterus fuliginosus*), even though they were two of the most common species in the area and their calls were easy to tell apart by eye. In the end, I abandoned the D500X data, and relied on manual call classification of the recordings collected at the recording points and during transects.

Building the call library was slow, as it took time to catch all the species, but straightforward. One person released the bat in the direction of the other worker, who would "follow" the bat by moving a Petersson D240X and manually trigger the detector four seconds after release, to capture 3.4 seconds of the bat calling in 10x time expansion. Our recordings were usually clear, although FM bats used a very "steep" call on release compared to when they were recorded on acoustic transects, probably for rapid orientation as they set off into the unknown. This did not affect manual identification, but may have contributed to some of our later problems with automatic identification.

What we found

Using the call library, we could manually identify most bats recorded on our acoustic transects. Of course, there were some difficulties. Some bat species did not echolocate at all—if we relied just on acoustic data, we would not have realized that we had one of only two legally protected species in all of India at our site (Salim Ali's fruit bat, *Latidens salimalii;* Wordley et al. 2016). Also, several bats called so softly or at such high frequency that we never or almost never recorded them on transects (only when released near the detector) (Wordley et al. 2018). Other bat species had so much overlap in call frequency and type that, despite promising early results, when we had more release recordings from each species, we could only positively identify a few of the calls (Wordley et al. 2014, 2018). Yet despite this, we reliably detected more species with acoustic monitoring than through captures (Wordley et al. 2018).

We recorded calls from five species that had never been recorded before and also found species calling at different frequencies from other parts of their range, possibly indicating that they are cryptic species (Wordley et al. 2014). As this was such a little-studied site, we had surprises even after the call library was published. In late 2014, we caught a rufous horseshoe bat (*Rhinolophus rouxii*), which we had previously recorded acoustically but never confirmed with a capture. Luckily the echolocation calls of this species, along with its morphology and genetics, have been well studied (Chattopadhyay 2010, 2012), and we managed to incorporate this species into the publications of 2017 and 2018.

We found that bat abundance, diversity, species composition, and functional diversity in forest fragments and shade coffee plantations were similar to those in protected forests (Wordley et al. 2017, 2018). Often the diversity in protected forest was higher than the other habitats, but not significantly so; species accumulation curves indicated that more sampling per site (e.g., the inclusion of the D500X data) would probably have increased the probability of detecting significant differences (Wordley et al. 2018). By every metric, tea plantations were a significantly poorer habitat for bats. Similarly, the habitat suitability models found that percentage tea cover in the surrounding area reduced the likelihood of detecting several species (Wordley et al. 2015). The bats most vulnerable to the spread of tea plantations were frugivorous, large, had short broad wings, or made constant-frequency echolocation calls (Wordley et al. 2017).

The positive outcome was that bat abundance, diversity, and functional diversity were high, even in small forest fragments or riparian corridors within tea plantations, suggesting some land management approaches to maintain many species even within intensive agriculture (Wordley et al. 2015, 2017, 2018). Also, the relative richness of bat communities in coffee plantations grown under native tree cover supports this approach as a relatively eco-friendly land use possibility (Wordley et al. 2015, 2017, 2018).

My research—along with other call libraries from India (Raghuram et al. 2014) and even from far more diverse parts of the tropics (Zamora-Gutierrez et al. 2016)—shows that acoustic monitoring of bat populations is possible across the world. Acoustic monitoring is less stressful and invasive for bats than catching (although for the fullest picture, both methods should probably be combined), can be easier and safer, especially if using overnight dataloggers, and records more species that catching does.

The Anamalai Hills are the second wettest part of India, making them wonderfully diverse but sometimes challenging to work in. ©Claire F. R. Wordley.

*Lesser short-nosed fruit bat (*Cynopterus brachyotis*) sometimes became torpid if kept in bags for a while – we fed them bananas on release to boost their energy. © Claire F. R. Wordley.*

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Concluding Remarks

Doesn't that inspire you to go out and turn on an acoustic detector!

We really hope that having read this, we have met the main objective for the Handbook, namely to summarize current relevant information about hardware, software and best practices for acoustic monitoring of bats, especially for those with limited experience. If we were asked to summarize the take away messages, we think they would be as follows:

1. Carefully formulating your research or survey question is the key to designing and conducting an acoustic study, influencing everything from sampling design, detector selection, detector deployment, software choice and data analysis.

2. There is no one size fits all technical guidance for conducting acoustic studies. The community of bats in your area of interest, as well as the amount of information currently available, will play a significant role in determining how you go about your study.

3. Rapid developments in technology are enabling acoustics to answer questions previously not considered possible. Many of these developments are the result of consumer (researcher, land manager, public) interest.

4. Never hesitate to reach out to experienced practitioners.

5. Acoustics are but one of many powerful tools that can be employed to collect information useful for bat conservation.

In the mind of the senior (chronologically) editor of this volume, we are really not very far removed from the days of leak detectors, QMC minis, back-breaking RACAL Store 4-D tape recorders and portable (ha!) oscilloscopes. Fast forward to today. It has never been easier to gain access to the acoustic world of bats and it is easier than ever before to answer questions about them. It is hard to believe that the first paper describing supersonic sound detected using a "sonic amplifier" (in essence a heterodyne detector attached to a modified AM radio receiver to produce audio output) was only 80 years ago (Pierce and Griffin; 1938. J. Mamm. 19:454-5). The first "portable" bat detector that Donald Griffin assembled in 1951 required a station wagon to carry all the necessary apparatus. Griffin coined the term "echolocation" for the means by which bats use echoes to locate objects and prey in their environment. The rest of us have been ever so fortunate to have the privilege of trying to learn the secrets of how they do it ever since.

We challenge the manufacturers and inventors. What you have given us over the past 40 odd years is amazing but don't stop putting your minds and talents towards better, smaller, cheaper and more reliable devices. We will buy them, we will test them, we will drop them, we will use them and all the while we will continue to tell you to make them better and cheaper.

We hope that you the reader found the Handbook useful, but we also challenge you! Although much of what you have read comes from those with considerable experience, remember that it also comes with unintentional bias and baggage attached. So DO question what we have written here. DO try new things. DO challenge the inherent assumptions we make. DO understand that the detector systems and software have limitations. DO test the ideas and rationale. DO help yourself and those around you to be better. But, most of all, DO get out there and in the spirit of Donald Griffin, visit the magic well that is Echolocation, again and again.

We thank all of the contributors for their efforts.

Now get going, it's getting dark.

Erin Fraser
Alexander Silvis
Mark Brigham
Zenon Czenze
March 2020

Australian false vampire bat (Macroderma gigas). © *Matthias Breiter/Minden Pictures, Bat Conservation International.*

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