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<th>Journal:</th>
<th>Canadian Journal of Zoology</th>
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<tr>
<td>Manuscript ID</td>
<td>cjz-2017-0219.R2</td>
</tr>
<tr>
<td>Manuscript Type:</td>
<td>Invited Review</td>
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<tr>
<td>Date Submitted by the Author:</td>
<td>27-Sep-2017</td>
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<tr>
<td>Complete List of Authors:</td>
<td>Ratcliffe, John; University of Toronto at Mississauga, Department of Biology Jakobsen, Lasse; University of Southern Denmark, Department of Biology</td>
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<td>Keyword:</td>
<td>ECHOLOCATION &lt; Discipline, Bats, Recording, Signal fidelity, Microphones, Directionality</td>
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Don’t believe the mike: behavioural, directional, and environmental impacts on recorded bat echolocation call measures

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§ This review is one of a series of papers arising from “Learning to Listen — Second International Symposium on Bat Echolocation Research: Tools, Techniques, and Analysis” that was held in Tucson, Arizona, USA, 26 March – 1 April 2017. Invited speakers were encouraged to submit manuscripts based on their talks, which then went through the normal Canadian Journal of Zoology review process.
Abstract
Echolocation calls produced by bats in their larynges allow these flying, nocturnal mammals to orient and find food at night. The acoustic signals are not like bird song, and even individual bats exhibit great flexibility in call design and between-species overlap is common. As a result, identifying bats to species by their echolocation calls even in communities with few bat species can be difficult. Unfortunately, the situation is worse still. As a result of several factors – some to do with microphones, some with environment, some with bats and the calls themselves – acoustic information transmitted to- and transduced by microphones can be dramatically different from the actual signal produced by the bat and as would be recorded on axis, close to its mouth using ideal microphones under ideal conditions. We outline some of these pitfalls and discuss ways to make the best of a bad situation. However, overall we stress that many of these factors cannot be ignored and do impact our recordings.

Keywords: Echolocation, bats, recording, signal fidelity, microphones, directionality
Background and introduction

Currently, there are well over 1300 recognized species of bats making bats the second most species rich mammalian order after the rodents (Fenton and Simmons 2014). The estimate increases each year. Some of the largest bat communities – known to number more than 150 species (Fenton and Ratcliffe 2010) – are found in S. America and SE Asia, relatively understudied locations that are likely inhabited by even more as yet unidentified species. More than 1000 bat species are laryngeal echolocators and most, if not all, consistently produce echolocation calls whenever they are in flight. When foraging and in transit, bats are difficult to visually identify to species given the speed of flight, low light conditions, and their generally small size. However, an individual bat’s recorded echolocation calls not only yield valuable insight into the bat’s current behavioural context, call design can potentially provide reliable clues to a bat’s species identity. That said bat echolocation calls have been shaped by natural selection primarily to optimize perception, not as a means of communicating species identity and quality as a potential mate, as in species-specific bird song (Barclay 1999). As a result, even at the individual level, bats produce calls of different duration, peak frequency (frequency of maximum energy), and bandwidth depending on context and environment (Surlykkke and Moss 2000).

All non-echolocating or non-laryngeal echolocating bats belong to the family Pteropodidae (~200 species); all other bat species belong to one of the ~20 remaining chiropteran families (Fenton and Ratcliffe 2010). Based on acoustic recordings, some bats can be accurately assigned to their correct family based on unique suites of call characteristics and knowledge of what families are present at a given geographic location. For example, across the United Kingdom there are ~20 bat species, belonging to either the family Vespertilionidae or the family
Rhinolophidae (two species) (ter Hofstede et al. 2013). Vespertilionids all produce frequency-modulated (FM), downward sweeping calls, at low duty cycles (<30%) (Figure 1a). Rhinolophids produce longer, essentially constant frequency (CF) calls that are often bookended by very short, steep downward sweeps (Fenton et al. 2012; Figure 1b). No matter what the context, in the United Kingdom the chances of confusing a vesper bat’s echolocation calls with those emitted by a rhinolophid are vanishingly small (Figure 1) and because the two rhinolophid species found in Britain use very different peak frequencies in the CF portion of their calls (Greater horseshoe bat, *Rhinolophus ferrumequinum* (Schreber, 1774): ~80kHz; Lesser horseshoe bat, *Rhinolophus hipposideros* (Bechstein, 1800): ~110kHz) (Fenton et al. 2012), it is possible to assign each to species with confidence at any given location (ter Hofstede et al. 2013).

Roughly half of laryngeal echolocating bats belong to the superfamily Vespertilionoidea. Approximately 425 of these are vespsertilionids, ~100 of them are molossids, with the remaining 30 or so species found in the families Natalidae and Miniopteridae (Fenton and Simmons 2014). With respect to echolocation call design, bats from the superfamily Vespertilionoidea exhibit the greatest flexibility (Simmons et al. 1979; Neuweiler 1990). For a given individual of a given species, as the bat moves from open space to more cluttered space call duration decreases, peak frequency and bandwidth increases (Jensen and Miller 1999; Surlykke and Moss 2000). As a result of this vast number of species and the incredible extents of individual flexibility, sympatric species of similar size and foraging ecology often overlap in call design when in the same habitat (Obrist 1995; Biscardi et al. 2005). Worse still for species identification the calls of a larger vespertilionid species in clutter may look like those of a smaller species (e.g., Jakobsen et al. 2013). As these
bats approach airborne prey, they also decrease call duration and increase peak
frequency and bandwidth (Griffin et al. 1960; Surlykke and Moss 2000), however at
the terminal phase of attack this pattern ends: bats instead drop peak frequency by
an octave (Ratcliffe et al. 2013). These terminal buzz calls are highly conserved
across species and thus especially poorly suited for species identification (Ratcliffe et
al. 2013). These challenges are given fuller treatment in Russo et al. (this issue).

In addition to the above issues, all associated with the difficulty of assigning a
given call or series of calls to one species or another, the recording scenario (i.e. the
recording equipment and the bats location relative to the recording equipment) will
more often than not severely impact the recorded structure of the call, adding
substantially to the uncertainty involved in species recognition. Our purpose here in
this short paper is twofold: first to provide guidelines for call description that - while
not silver bullets - we believe will make the best of a bad situation and, second, to
make new researchers aware of the limits imposed on recorded call fidelity. We
essentially focus on a single echolocation call from the vespertiliionid Myotis
daubentoni (Kuhl, 1817) to illustrate that even a single call, produced by a single bat
can be transmitted and transduced under different conditions in very different ways,
and that this fact makes even describing a single call accurately with respect to
emitted structure difficult. Given this reality, assigning calls recorded in multi-species
bat communities to species automatically is a risky business.

Quantifying common call parameters

Laryngeal echolocating bats tend to produce calls well above our hearing
range; that is, most bats use call frequencies above 20 kHz. To listen to them they
must be artificially transposed to frequencies roughly 10 times lower than in reality
(Griffin 1958). For these and other reasons many bat researchers tend to inspect
echolocation call design and call emission rates visually. Ideally, using a combination
of spectrograms, oscillograms and power spectra (FFTs, fast Fourier Transforms)
(Figure 2). Spectrograms allow for rough visualization of call shape and frequency
content and an even rougher estimate of signal duration and, using a colour or grey
scale bar, energy distribution among the included frequencies. While they are often
used for much more, our recommendation is that spectrograms only be used to
distinguish echolocation calls from echoes and non-echolocation call sounds and for
species identification in bat communities where the time-frequency structure clearly
separates species, as in the previous example of the horseshoe bats in the United
Kingdom. With respect to environmental influence, a spectrogram of a vespertilionid
bat echolocation call that has travelled along a single path to the microphone (i.e. not
containing any reflections) looks like a smooth downward sweep (Figure 1a, Figure
2a). Calls that have instead travelled along multiple paths as a result of reflections off
vegetation and/or water surfaces will appear distorted (Figure 2b), often containing
nulls (i.e. wave cancellations) that are specific to the time-delay between the direct
path and the longer path of the reflection(s).

With respect to computational influence, obtaining quantitative measurements
from spectrograms such as call duration, bandwidth and peak frequency is also
prone to errors because of the inherent trade-off between accuracy in the time and
frequency domains of the spectrogram. That is, call duration will be overestimated on
most if not all spectrograms (Figure 3), while call peak frequency and bandwidth
obtained from spectrograms are typically just as unreliable. Our strong
recommendation is to always measure call duration on the oscillogram and frequency
parameters on the power spectrum using standardized repeatable measures. For
further details on the pitfalls of spectrogram measurements we recommend Zollinger et al. (2012) and Brumm et al. (2017). Commonly measured frequency parameters are peak frequency (pF), minimum frequency \(F_{\text{min}}\), maximum frequency \(F_{\text{max}}\), and bandwidth (BW). Peak frequency is the frequency containing the most energy, i.e. the highest value on the power spectrum. Bandwidth, \(F_{\text{min}}\) and \(F_{\text{max}}\) are less straightforward parameters, as simply measuring where the call appears to start and end is highly subjective and very sensitive to the signal-to-noise ratio of the call. Instead, bandwidth, \(F_{\text{min}}\) and \(F_{\text{max}}\) are usually defined relative to the peak-level of the power spectrum as \(X\) dB below the peak level where \(X\) dB is commonly 6 dB, 10 dB, 15 dB, or 20 dB below pF (Figure 3). Bandwidth is then simply \(F_{\text{max}}\) minus \(F_{\text{min}}\). The selected bandwidth dB-value varies between studies and is usually chosen based on the signal-to-noise ratio of the recordings. This measure of bandwidth based on the overall signal tells us much about sensory ecology of the bat. However, measuring bandwidth from the power spectrum can make it difficult to measure the frequency content of the individual harmonics and, if taking such measures is also desired, there are options available to separate the harmonics and then still use a power spectrum to quantify the frequency content of individual harmonics (see Surlykke et al. 2009 for more information). Signal duration appears as an easy parameter to measure and is in fact often eyeballed based on an observer’s judgement, but standardized measures should be applied here as well. Common methods for duration measures are energy content of a given time section containing the call or, similar to the bandwidth measures, \(X\) dB down from the peak of the signal’s envelope (see Madsen and Wahlberg 2007 for more information).

So in summary, we recommend that spectrograms only be used to verify the signal as a clean, clear bat echolocation call, and in large bat communities to assign
the call to one or a subset of plausible bat species or bat families. Oscillograms should be used to measure signal duration and other time parameter such as the time elapsed between one signal and the next. Power spectra should be used to measure frequency parameters such as peak frequency and bandwidth, and for all measures one should use standardized methods for all recordings to ensure reliability and repeatability. Although uncommonly used in studies of bat echolocation, an alternative means of visualizing the time-frequency structure of echolocation calls is with sparse time analysis, which produces a visualization of call design much more accurately with respect to both time and frequency than do spectrograms (for further information see Gardner et al. 2006, for examples see Elemans et al. 2011).

**Implications of the recording scenario**

The recording scenario will have profound implications for the recorded call, such that a recording of a given call will vary dramatically depending on the specific microphone, the direction of the microphone relative to the bat, the distance between the microphone and the bat and the direction the bat is calling relative to the microphone. Three microphone sizes are typically used for ultrasonic recordings, large ~1/2 inch microphones (such as Avisoft CM16 and Peterson DX1000), medium ~1/4 inch microphones (such as GRAS and B&K) and small microphones ~1/8 inch (such as Knowles FG series). As a general rule, microphone sensitivity increases with size, which means that a large microphone like the Avisoft CM16 is inherently much more sensitive than the much smaller Knowles microphone and that the larger microphone also has a lower noise-floor than the small microphone, meaning it can
Directionality refers to the fact that a microphone has a varied response to incoming sound depending on the angular incidence upon the membrane (Figure 4). In other words, the measured sound pressure will decrease as the off-axis angle increases. Directionality depends on the relationship between the size of the microphone and the frequency of the incoming signal. This means that a large microphone is more directional than a small microphone at any given frequency, and any microphone becomes more directional with increasing frequencies. This also means that even the small Knowles microphones are directional at high enough frequencies, although for most bat echolocation calls they are essentially omni-directional. The gold standard is B&K or GRAS 1/4 inch condenser free-field microphones (but note also the ~1/8 inch versions, which are seldom used due to their low overall sensitivity). These ~1/4 inch microphones have a flat frequency response between 4 Hz and 100 kHz (±2dB GRAS 46BF-1), meaning that they are equally sensitive to all frequencies within this range along the acoustic axis. This is extraordinary. Most microphones do not have a flat frequency response, which also needs to be accounted for when reporting call frequency content even when calls are recorded on axis (for an example see Ratcliffe et al. 2005).

The distance between the bat and the microphone has important implications as well. Sound attenuates with distance as a product of spherical spreading loss and atmospheric attenuation. On the one hand, spherical spreading loss is frequency independent and reduces sound pressure by $20\times\log_{10}(R/R_0)$ where $R$ is the distance between the bat and the microphone and $R_0$ is the reference distance (0.1 meter is commonly used for bats, but 1 meter is the standard distance in acoustics). As a rule
of thumb, this equates to a halving of the sound pressure (-6dB) per doubling of the distance from the sound source. Atmospheric attenuation, on the other hand, is highly frequency dependent, and higher frequencies will attenuate more so than lower frequencies. Thus, a given call’s maximum frequency will appear to be lower when recorded at a microphone further away from the bat than when recorded at a microphone closer to the bat (Figure 5). In addition atmospheric attenuation increases as a linear function of distance (X dB/m), so that while the effects of spherical spreading diminish with distance, those of atmospheric attenuation do not (Griffin 1958, 1971; Lawrence and Simmons 1982).

The direction the bat emits its call and the breadth of the sonar beam also impact recordings. Bats emit their echolocation calls directionally, that is they emit the highest sound pressure in the forward direction (the acoustic axis) and sound pressure reduces with increasing off-axis angle (Figure 4). As discussed for microphones, echolocation call directionality depends on the relationship between the size of the emitter (likely the size of the open mouth for mouth-emitting bats) and the frequency emitted. For example, in the downward sweeping, frequency modulated echolocation calls of a typical vesper bat the biosonar beam produced at the start of the call i.e. at high frequencies is much narrower than the beam produced at the tail end of the call i.e. the lower frequencies. This means that unless the bat is directing its echolocation call directly at the microphone, the recorded call will be effectively low-pass filtered relative to the directly emitted call meaning that the recorded call will have much less energy in the higher frequencies than the emitted call had (compare traces on Figure 5).

Taken together the limitations discussed above mean that most bat recordings are low-pass filtered to a lesser or greater degree, which will be reflected in the
measured parameters irrespective of the selected measurement criteria. Even at relatively short distances the combination of microphone directionality, bat directionality, atmospheric attenuation and spherical spreading loss can result in a profound difference between the recorded call and what the bat actually emitted (Figure 5). Even by utilizing systematic repeatable measures for call duration, peak frequency and bandwidth, the distance and angle between bat and microphone can have dramatic effects on call characteristics as transduced by even the most flat and almost omnidirectional microphones available. Add to this the fact that the bats under some conditions may well detect the microphones themselves and as a result will decrease call duration and call intensity (Nørum et al. 2012). Thus it is clear that even under controlled conditions call design as emitted by the bat is not reliably transduced by microphones. And the situation only deteriorates in the wild. While multi microphone arrays and computational calibration and correction can go a long way in reconstructing echolocation calls including emitted intensity, these technologies are neither economically viable nor practical for most researchers. This does not mean we should throw our hands in the air and give up, but we should be aware of the limits of single microphone recordings and the environmental impacts of long appreciated acoustic principles of sound.

In closing, the above is both brief and conservative and we by no means suggest you should “just take our word for it”. For those new to the bat echolocation, the “magic well” has long been and will always be Donald Griffin’s (1958) *Listening in the Dark*. We cannot recommend this classic book enough. Some of our favourite papers on bat echolocation call design and bat behaviour include Obrist (1995), Schnitzler and Kalko (2001), and Surlykke and Moss (2000). Pye’s (1993) short paper on similar topics to those we consider above is excellent; the chapters on
sound and hearing in Bradbury and Vehrencamp’s (1998) Animal Communication cover a lot of ground, providing a thorough introduction to bioacoustics. Finally, while there are more recent reviews on bat echolocation and neurobiology, in our opinion Neuweiler’s (1990) publication in Physiological Reviews remains among the best.

Acknowledgments

We thank Mark Brigham and Brock Fenton for inviting us to contribute to this special issue and Holger Goerlitz and one anonymous reviewer for constructive comments on an earlier version of the manuscript. The Natural Sciences and Engineering Research Council (NSERC) of Canada and the Danish Research Council (FNU) have funded our research.

References


Figures and figure legends

Figure 1. Spectrograms of bat echolocation calls. (a) Daubentons’s bat *Myotis daubentonii* (family Vespertilionidae) and (b) the lesser horseshoe bat, *Rhinolophus hipposideros* (family Rhinolophidae). Rhinolophid echolocation call file courtesy of M. Brock Fenton.

Figure 2. Oscillogram, spectrogram and power spectrum of an echolocation call from *Myotis daubentonii*. a shows the call recorded directly in front of the bat with no reflections from nearby surfaces. b shows the same call with a reflection generated artificially by addition of the same call with a delay of 80 µsec, the delay can be computed by the nulls in the power spectrum, frequency separation = 12.5 kHz, time separation = 1/12.5 kHz = 80 µsec.

Figure 3. Oscillogram, spectrogram and power spectrum of the same echolocation call (*M. daubentonii*) visualized using different FFT-sizes for the spectrograms. The duration estimate is based on the 99% energy content of the shown time segment measured from the oscillogram and the bandwidth is the -20 dB bandwidth measured from the spectrum. The indicated duration and bandwidth (dashed line) illustrates the trade-off between time and frequency accuracy of the spectrogram depending on the window size.
**Figure 4.** Directionality of a GRAS 40 BF ¼” microphone (left panel) and of a bat emitting sound as a piston with a 3.5 mm radius (right panel, see Strother and Mogus 1970 for details). Top right panel shows the emitted directionality at the listed frequencies, bottom right panels shows the relative spectrum of the emitted sound at the indicated angles.

**Figure 5.** Combined effects of distance and echolocation beam-direction for the frequency content of the recorded echolocation call (*M. daubentoni*), the illustrated off-axis angle (red and purple) is 40°. The illustrated scenario has no effect of microphone directionality, i.e. the microphone is pointing directly at the bat.