

How we studied the horseshoe bat craziness - (FORMAL TITLE to be agreed on)

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Abstract

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Potential titles

1. CF bats do not show changes in echolocation calls in the presence of conspecifics
2. Echolocation remains unaltered in the presence of conspecifics in CF bats
3. Conspecifics do not affect echolocation call structure in CF bats

Notes on journal formats

RSocOpenSci : 200 words abstract, all data and code to be uploaded online and the link in the MS

Introduction (BROAD DRAFT, OTHERS CHIP IN!)

- Bats are known to echolocate and fly under complex conditions. They show responses in the presence of conspecifics, playbacks and clutter.

- There is a general FM bat bias in the study of how bats respond to adverse acoustic conditions, with little attention given to CF bats. Even in the CF bat literature, there is a strong focus on lab based studies.
- Lab based studies are powerful in that they can shed clearer light into the contributions of the manipulated variables and conditions. However, at the same time, the animals are in a new environment, and the environment itself can be a strong manipulating variable. Studying animals in natural conditions allows quantifying the day-to-day effect sizes as seen in the wild as the animal behaves in its natural environment.
- A common issue plaguing many acoustical studies, especially in bat echolocation is the use of manual measurements to segment and quantify the different parts of an echolocation call (CF, FM). These are known to lead to biased or inconsistent measurement. We overcome these issues with the use of an automated workflow. Our approach is thus more reproducible in the long-term.
- We observed and compared the behaviour of free-flying bats as they echolocated alone and in the presence of congeners emitting echolocation calls in a common frequency band. Our observations of free-flying bats show that changes in echolocation may not be as dramatic as observed in previous studies, perhaps due to the fact that the animals are flying in a familiar environment. Bats may be even less affected by so-called jamming in their native habitats.

Methods

Study species

Two species of rhinolophid bats *Rhinolophus mehelyi* and *R. euryale* were observed with video and audio recordings as they echolocated in their natural environment. Both species emit CF-FM calls (Tian and Schnitzler 1997) with peak frequencies between 102-112 kHz, and are not acoustically distinguishable due to the overlap of their call characteristics. While phylogenetically different species, for the purposes of this study we treat them as a single group of bats that may face the problem of acoustic jamming due to the major overlap in CF frequencies and similar spectro-temporal call structure.

Recordings were done in a dome-shaped cave (Figure 1) next to the main entrance of the Orlova Chuka cave system, Bulgaria. The dome was **X,Y,Z** (HxBXD) metres in dimension. The cave had only one opening with a roosting site on the opposite side that most bats flew towards and from.

Experimental setup

Three Avisoft CM16 microphones (Avisoft Bioacoustics, Germany) were connected to an Avisoft 416H (Avisoft Bioacoustics, Germany) recording at 250kHz sampling rate. Horseshoe bat calls are known to be directional (Matsuta et al. 2013), and the mics were placed at different positions to increase the number of on-axis calls captured. Microphones were placed in the same location with an estimated +/- 10cm error in the cave across multiple nights. The fourth channel of the Avisoft 416H was used to record the audio sync signal described in the section below. Audio was recorded continuously through the night in the form of consecutive multichannel files of 1 minute length. Our audio recordings showed that the dome was visited by multiple species of bats aside from our two main study species, and we only analysed audio data with *R. euryale* and/or *R. mehelyi* calls in it.

Two consumer grade CCTV cameras were connected to a digital video recorder to record the flight of bats as they flew in and out of the cave. The system recorded video mostly at 22 Hz, however there was frame rate variation between 18-27 Hz. The video stream of the two cameras was not frame-synchronised, however, we were still able to view the same bat flight on both cameras due to the common timestamps burnt-in on each frame. The two cameras were placed in approximately the same position on every recording night. The cameras were so placed to maximise the total cave area recorded while also capturing the video-sync signal in the form of a blinking LED light. Portions of the video files with stable camera positions were analysed.

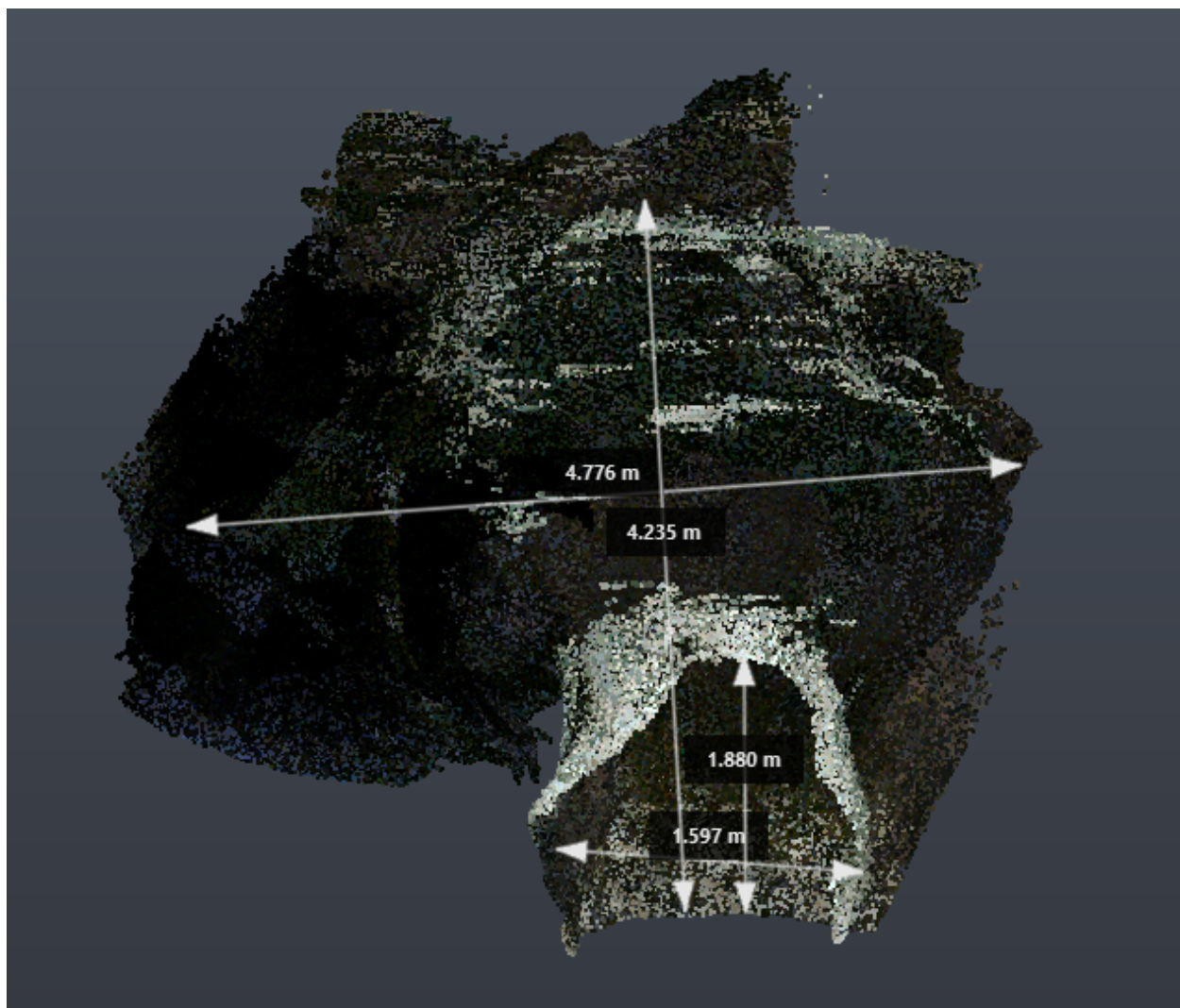


Figure 1: Schematic of how the three microphones and two cameras were placed in the recording volume/Klaus will send a more processed version OR Neetash to make a better one? 3D scanning by Klaus Hochradel, UMIT Tirol

Video was recorded continuously through the night and resulted in two video files (one per camera) for each recorded hour.

The audio and video feeds were synchronised using the low-cost method described in (Laurijssen et al. 2018). Briefly, ON-OFF signals between 0.08-0.5 seconds was generated by a portable computer (Raspberry Pi 3). The voltage signal was directly fed into the fourth audio channel of the USG 416H and also used to drive the blinking of an LED from the I/O pins of the Raspberry Pi (See Supplementary Information for signal generation script, electronic circuit and associated notes).

Identifying single and multi bat occurrences

Bat activity in the cave was recorded for a total of about 18 hours over four nights in the cave. Bats flew into the cave, and either headed straight for the roosting site or performed circling flights within the cave and exited. Bats also flew from the roosting site out of the cave. The start and end of all bat flight bouts in each video were manually annotated by an observer following a series of pre-defined criteria to ensure repeatability (See Supplementary Information). Each flight bout annotation recorded the number of flying bats as seen in the two camera views.

Video-audio synchronisation

For each video annotation, we attempted to match a corresponding region of recorded audio. This was done by cross-correlating the blinking LED signal over the video annotation window with the recorded ON/OFF voltage signal in the fourth audio channel. We managed to find successful audio matches for 1181 annotations, (55% of all video annotations). The low match rate is primarily due to the fluctuating nature of the camera frame rates, and the fact that many of the matched audio files had non-target bat species. For each successfully matched video annotation, we created a separate audio file. From all of the bat activity video annotations ($N_{annotations}=2132$), we extracted the final set of audio files screened for the presence of one or both of the target *Rhinolophus* species. This resulted in audio files varying in duration between 0.08-62.08 seconds ($N_{files}=1181$, median duration \pm 95%ile range: 1.04, 0.5-8.54s)

Acoustic analysis

We performed two complementary acoustic analyses to determine whether horseshoe bats changed their echolocation call parameters in the presence of conspecifics. The first analysis is the ‘individual call’ analysis, where we isolated one horseshoe bat call in each synchronised audio file, and performed measurements on the chosen call. The second analysis is the ‘whole audio’ analysis, where we measured the acoustic parameters of 50ms chunks from a whole audio file with one or more echolocation calls in it. The advantage of the single-call analysis is that the measurements made on the calls are directly interpretable. The disadvantage of the single-call analysis is that especially in multi-bat audio clips, it can be difficult to find non-overlapping calls. The advantages of the whole-audio analysis is that it allows a broader scale characterisation of echolocation behaviour across group sizes, and thus allowing analysis of audio data even with overlapping calls. Whole-audio analysis also allows a kind of null-hypothesis testing where ‘virtual’ multi-bat audio files can be created by adding multiple single bat audio files. Ultimately, using two analytical approaches simultaneously allows us to combine the results and form a robust conclusion.

Using the two acoustic analyses below we attempted to answer if bats alter their echolocation behaviour in the presence of conspecifics. Additionally, from a series of comparisons based only on individual call analysis we attempted to quantify the difference between call-components emitted in single and multi bat contexts.

Audio pre-processing and selection

All raw audio was first forward-backward high-passed filtered at 70 kHz were performed. Even though audio was recorded from three microphones simultaneously, later inspection showed that the first microphone, (placed slightly above the ground facing the single entrance/exit) provided call recordings with the highest signal-to-noise ratio. All analysed audio data were thus taken from the first recorded channel. The first channel microphone was also ideally located to record the calls of both incoming and exiting bats.

Multiple species were seen in the audio files as during video annotation it was not possible to distinguish bat species solely by their flight behaviour. The other observed bat species were *R. ferrumequinum* and other vespertionid and miniopterid FM bats, all of which are known to occur in the main Orlova Chuka cave system (Ivanova 2005). Even though most of our audio recordings had *R. mehelyi* and *R. euryale* calls, there were also recordings with a target and one or more non-target species. Any recordings with non-target species were not analysed.

Individual call measurements

Individual calls which were not overlapped by other calls and with sufficient signal-to-noise ratio (Figure 2) were manually chosen through a random search protocol (Supp. Info.). Briefly, an experimenter began searching from a randomly chosen time point in an audio file for an individual call. From this point in the file, the experimenter randomly began searching to the left or right until a suitable horseshoebat call could be identified. The start and end time of this call in the audio file were noted. We were able to find a total of 355 individual calls ($N_{single\ bat\ context}$: 261, $N_{multi\ bat\ context}$: 94) across all the synchronised audio files.

The FM and CF parts of the call were segmented automatically and acoustic parameters were measured using the *itsFM* package [UPLOAD TO BIORXIV NOWWWW, *Insert hyperlink to readthedocs page*]. Calls were automatically segmented into their corresponding parts (iFM, tFM or CF) as per the terminology of (Tian and Schnitzler 1997) (Figure 2). Most approaches to date focus on indirectly segmenting CF-FM calls into their components by high/low pass filtering near the peak frequency of the call (Siemers et al. 2005; Schuchmann, Puechmaille, and Siemers 2012; Tian and Schnitzler 1997; Lu, Zhang, and Luo 2020; Schoeppler, Schnitzler, and Denzinger 2018). For an accurate estimate of the peak frequency, this approach requires an on-axis recording of the call with a prominent CF component in the audio. While suitable for laboratory studies, this peak-frequency based filtering fails in the analysis CF-FM calls recorded in the field with a variety of recording conditions eg. loud FM, faint CF calls. Additionally, peak-frequency based methods inherently assume the presence of one CF region with two FM regions of lower frequency content. *itsFM* overcomes these limitations by segmenting calls into FM or CF regions based directly on the frequency modulation over the call, and is able to handle the segmentation tasks even for other types of sounds, eg. bird calls.

For each segmented call region the following measurements were performed 1) peak amplitude 2) root-mean-square(RMS) 3) Lower frequency (from -10 dB peak frequency). In addition, the following parameters were also calculated 4) relative iFM-CF levels (dB rms) and 5) relative tFM-CF levels. Peak amplitude, RMS and their relative levels were chosen as horseshoe bats are known to increase the source level of different parts of the calls independently in a context specific manner (Tian and Schnitzler 1997; Lu, Zhang, and Luo 2020). The peak frequency was chosen to see if bats showed variation in their CF frequency across group size and in noise, this has been a parameter of investigation in previous studies (Habersetzer 1981; Jones, Sripathi, and Waters 1994; Fawcett et al. 2015; Lu, Zhang, and Luo 2020). The -10dB peak lowest frequency was chosen to understand if bats showed an alteration in the FM bandwidth of their calls in the presence of conspecifics. An alteration in FM bandwidth has been shown to occur in at least one previous study (Fawcett et al. 2015). The end output of this analysis is a series of detailed measurements for each part of the CF-FM call.

Whole audio measurements

Entire audio files were analysed to quantify how different call sequences were across single and multiple bat contexts. Each audio file was split into consecutive windows of 50ms. Splitting began from the start to the

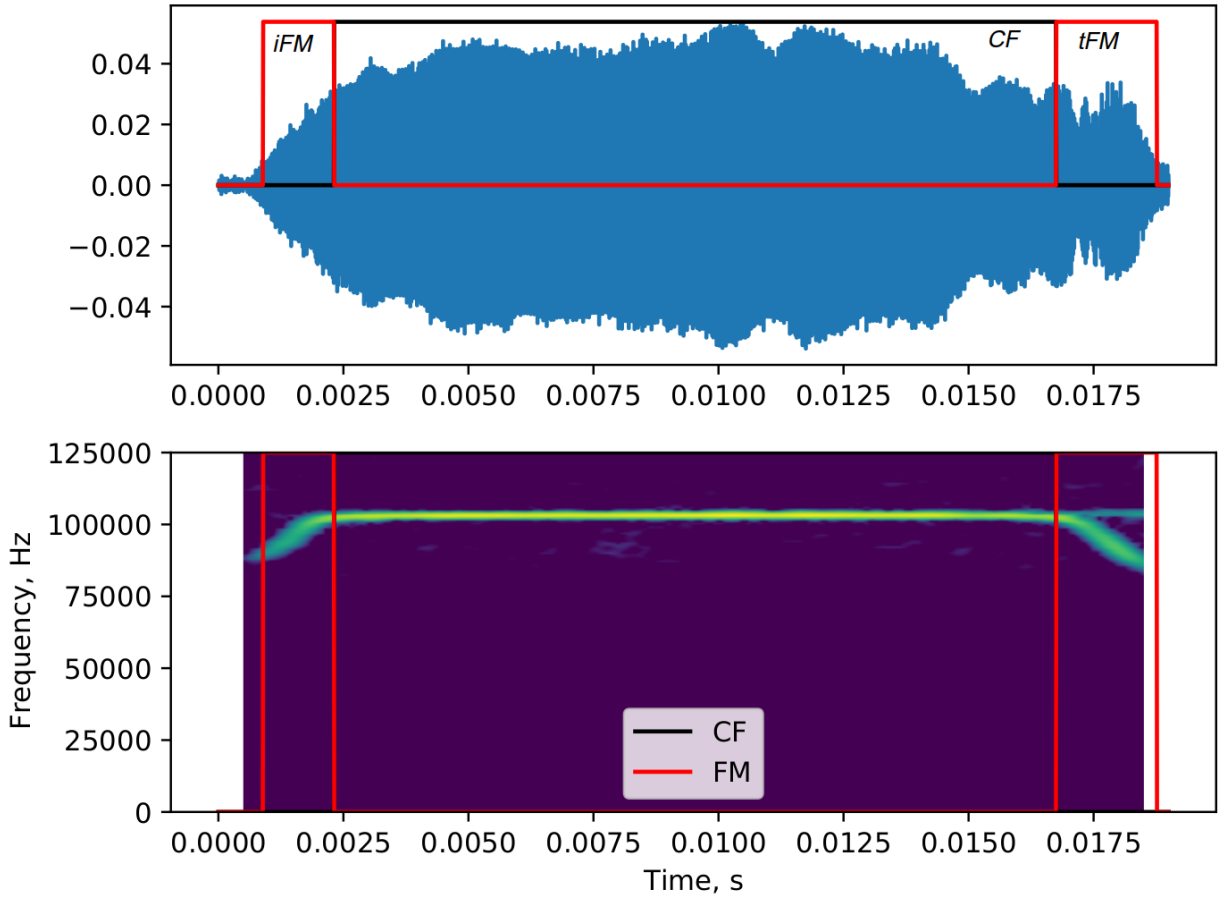


Figure 2: Example of a single CF-FM call with automatically segmented iFM, CF and tFM regions. The raw data is a manually selected audio segment, which is then automatically segmented by the **itsFM** package based on frequency modulation across the call. The **itsFM** package allows accurate segmentation into call parts under challenging recording conditions

end of the audio file. Any windows that were less than 45ms in length at the end of the file were discarded to maintain a standardised temporal and spectral resolution. The majority of windows generated were thus 50ms long. 50ms was chosen as it was estimated to be about twice the duration of a horseshoe bat call in our data, and also matched the longest call durations observed from initial observations. This ensured that there were at least 1-2 horseshoe bat calls in a given 50ms window, and provided high enough spectral resolution (20Hz for 12500 samples at 250kHz sampling rate) to distinguish multiple CF components that may be in it.

Over the course of an audio file, there may be multiple windows without calls or very faint calls in them. These ‘silent’ windows were removed from the analysis, and only the ‘non-silent’ windows with bat calls in them were analysed. Non-silent windows were defined as those that were 20 dB RMS more than manually annotated silent audio segments (Supp. Info.). On each non-silent window, the following acoustic measurements were performed: 1) peak amplitude, 2) RMS, 3) dominant frequencies 4) FM terminal frequencies. Dominant frequencies here are defined as frequency peaks in the smoothed power spectrum that are within 14 dB of the peak frequency’s power. Dominant frequencies are extracted from the various peaks of the power spectrum and are thus a proxy measurement for the CF frequencies of calls in a window. In a window with one bat call, there are likely to be a few dominant frequencies comprising of the direct call incidence and fainter Doppler shifted reflections of the same call. A window with many bat calls are likely to have more dominant frequencies due to the higher number of direct call incidences and echoes recorded by the microphone (Supp. Info.). FM terminal frequencies were determined by a spectrogram based method which identified FM regions and chose the lowest frequency in each FM region of a given audio window (Supp Info.). All measurements chosen in the whole audio analysis were done to be analogous to the measurements performed in the individual call analyses. The end output of this analysis is a series of measurements for each window in an audio file.

One advantage of the whole audio analysis is the possibility to make ‘virtual multi-bat’ data (Fawcett and Ratcliffe 2015; Ratcliffe et al. 2004) by combining observed single bat data. We created virtual multi-bat audio files by adding duration and group size matched single bat files together (Supp. Info.). This allowed us to create a ‘null’ dataset where multiple bats were echolocating, but not responding to each other’s presence. The virtual multi-bat audio was analysed in the same way as the observed single and multi bat audio data.

Statistical analysis

All of our data stemmed from observations done on a single population of unmarked wild bats done in a single field site. We thus performed a series of non-parametric analyses to compare the call parameters between single and multi bat contexts. We did not attempt to quantify the variation due to the effect of time of day or date of recording as we believe they are very unlikely to alter echolocation behaviour.

Quantifying CF and dominant frequency similarity Bats may choose to alter their CF peak frequencies in multiple ways in the presence of conspecifics. An overall ‘widening’, ‘narrowing’ or no change in the CF frequency range may be observed in the presence of conspecifics. A widening or narrowing in the CF frequency range can be inferred by an overall decrease in similarity between the CF frequency distribution that bats emit when alone in comparison to the frequency distribution in the presence of a conspecific. The same comparisons made for CF peak frequencies can also be applied to dominant frequency distributions.

We compared the similarity between single and multi bat distributions using the Hellinger distance between the two distributions. The underlying probability distribution function of the data through kernel density estimates, and the Hellinger distance between the two probability distribution function were calculated. The Hellinger distance is a distance measure that lies between 0-1. A Hellinger distance of zero implies complete overlap, and a distance of 1 implies no overlap.

Individual call measurements

Identifying the difference between single and multi bat calls The bootstrap median difference (Δ median) for the measured call parameters of single and multi bat calls were calculated. To estimate the similarity in CF peak frequencies, we first calculated the observed Hellinger distance in single and multi bat calls. A series of shuffled datasets were then generated, where the CF peak frequency values were shuffled across the single and multi bat groups. The observed Hellinger distance was then compared to the shuffled data’s Hellinger distances.

Whole audio measurements

To assess if bats in groups showed different acoustic properties in the chosen windows than those echolocating alone we calculated the bootstrapped difference in medians for two pairs of (single-multi, virtual-multi). The comparisons were performed for each measured parameter. The data for each measured parameter consisted of measurements arising from the multiple windows in each audio file. To reduce the extent of pseudo-replication in the dataset, we performed a bootstrapping in the following manner:

1. Begin bootstrapping round
2. For each audio file in the dataset choose measurement value from a single window
3. Split data into groups according to the number of bats (single/multi/virtual-multi)
4. Subtract the median values of the two datasets of interest (single-multi and multi-virtual multi)
5. Store the difference in median values and proceed to 1.

To estimate the similarity in dominant frequencies, we first calculated the Hellinger distance between observed pairs (single-multi , multi-virtual multi) to generate a distribution of the observed data. We then generated bootstrap shuffled datasets where the dominant frequencies were shuffled across the pairs to generate the shuffled data.

Software packages used in this paper

This paper was enabled by a series of open-source packages. Signal analysis, data manipulation and visualisation were done in Python (Van Rossum and Drake Jr 1995) through its scientific ecosystem: the scipy, numpy, matplotlib, soundfile and pandas packages (Virtanen et al. 2020; Oliphant 2006; Hunter 2007; Bechtold and Geier 2019; McKinney and others 2010). Reproducible analysis, documentation and presentation were enabled by the Jupyter Notebook and rmarkdown projects (Kluyver et al. 2016; Xie, Allaire, and Golemund 2018). Audio visualisation, preliminary measurements and single call annotations were done with Audacity (Audacity-Team 2019).

Results

Individual call analysis

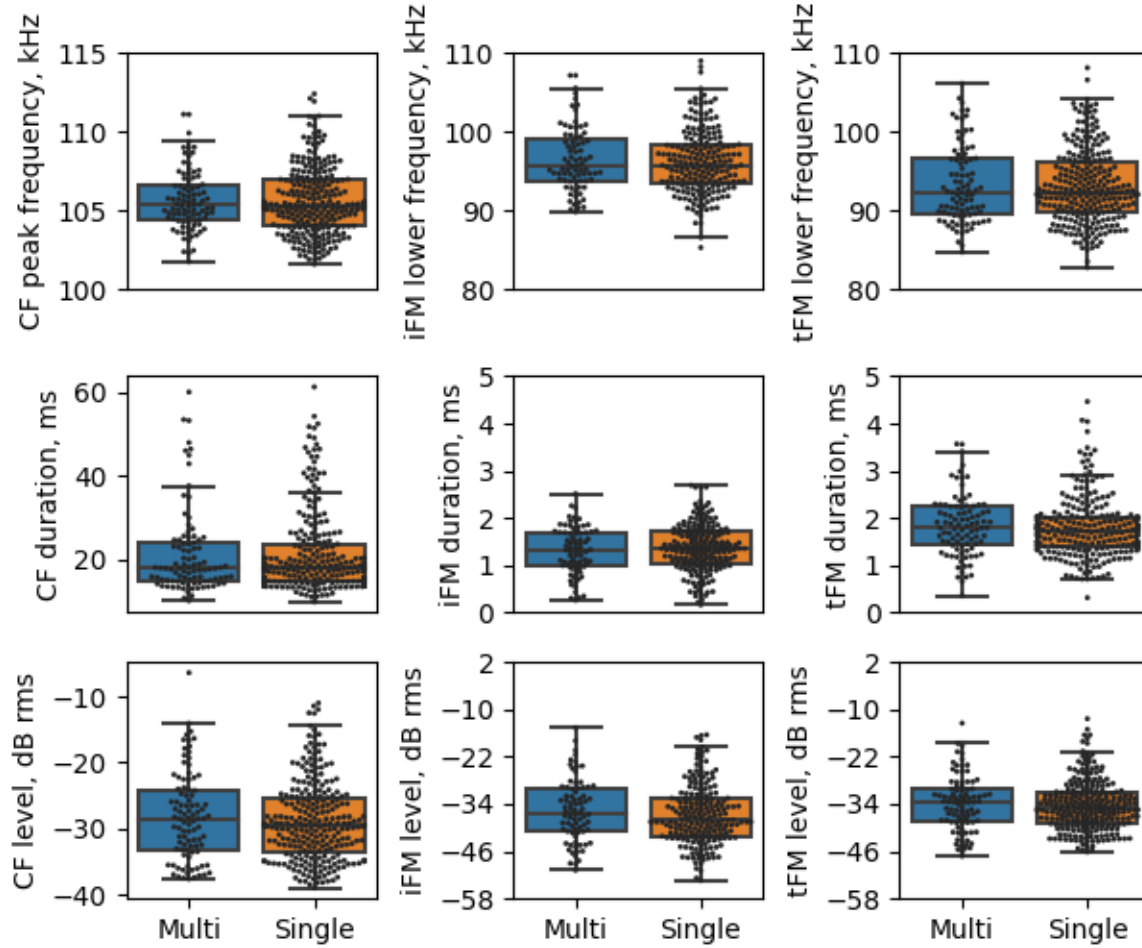


Figure 3: Measured acoustic parameters for the CF, iFM and tFM components of the calls emitted under single and multi bat conditions.

All measured call parameters (Figure 3) appear to be very similar across single and multi bat contexts. The 95 percentile range of the bootstrapped difference of medians for all measured parameters (Figure 4 A-H) include zero, which strongly suggests that the call parameters originate from one distribution. The observed Hellinger distance between single and multi bat calls is positioned in the 93rd of the shuffled Hellinger distances (Figure 4 I). The observed overlap's location is within the 95 percentile range (2.5-97.5), indicating that the observed overlap is indistinguishable from a scenario where there is no change in CF peak frequency across single and multi bat contexts.

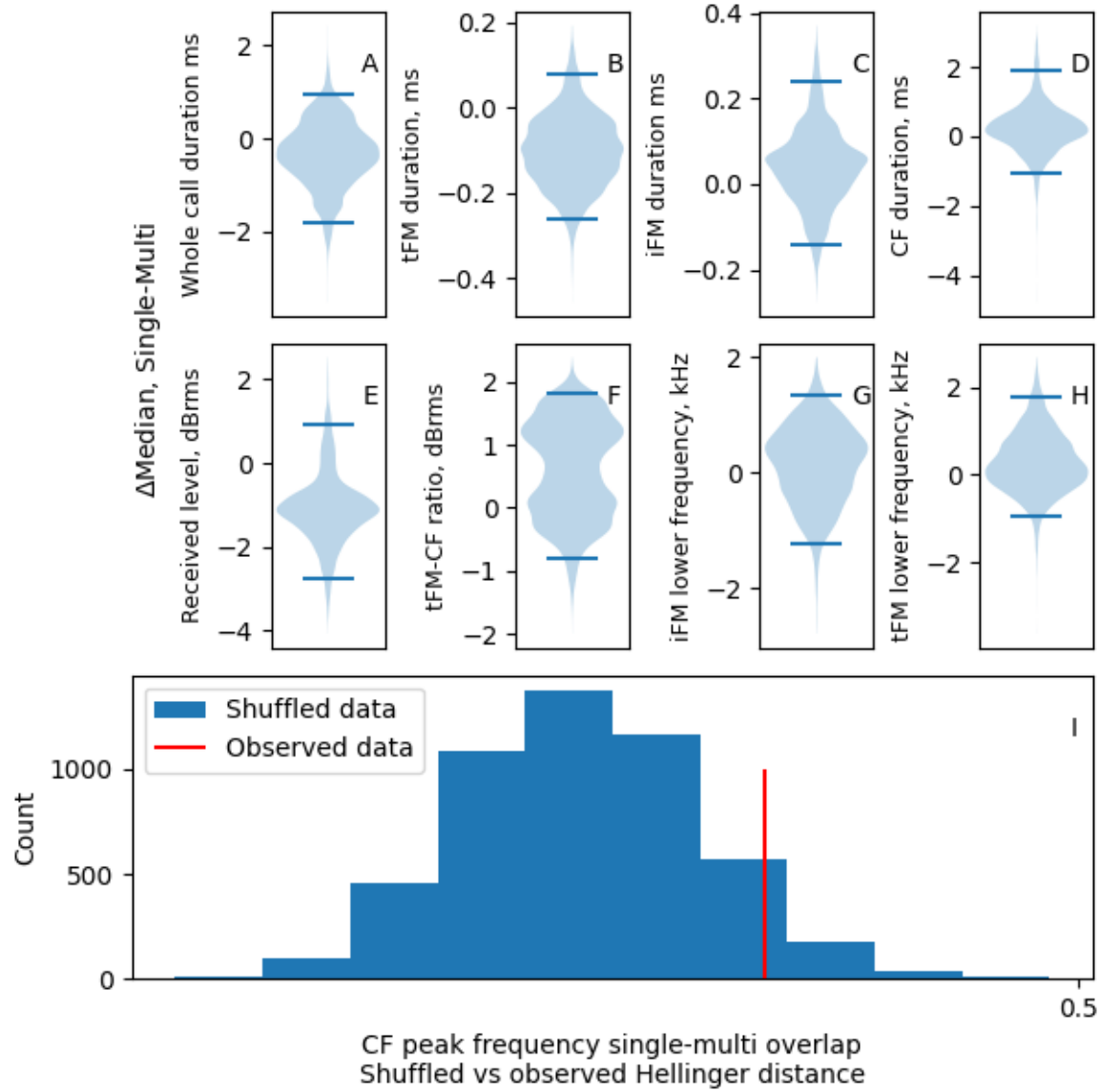


Figure 4: Comparison of various call parameters between single and multi bat context calls. A-H: The bootstrapped median difference of call parameters in calls recorded in single and multi bat contexts. The 95 percentile interval of the bootstrapped median for all variables contains 0, supporting the conclusion that call parameters from both groups belong to the same distribution. I: The observed Hellinger distance for CF peak frequency between single and multi bat contexts, in comparison to the distances generated from shuffled datasets. The observed Hellinger distance is placed at 93.3 percentile of the shuffled distribution, and is thus within the 95 percentile range of the shuffled data. This supports the possibility that the observed Hellinger distance is within the range of what would be expected if single and multi bat calls were from the same distribution

Whole audio analysis

All measured whole audio parameters (received level, dominant frequencies, terminal frequencies) showed no difference in either single-multi or multi-virtual multi audio comparisons (Figure 5). The bootstrapped median difference 95 percentile intervals for all comparisons and parameters contained zero in them.

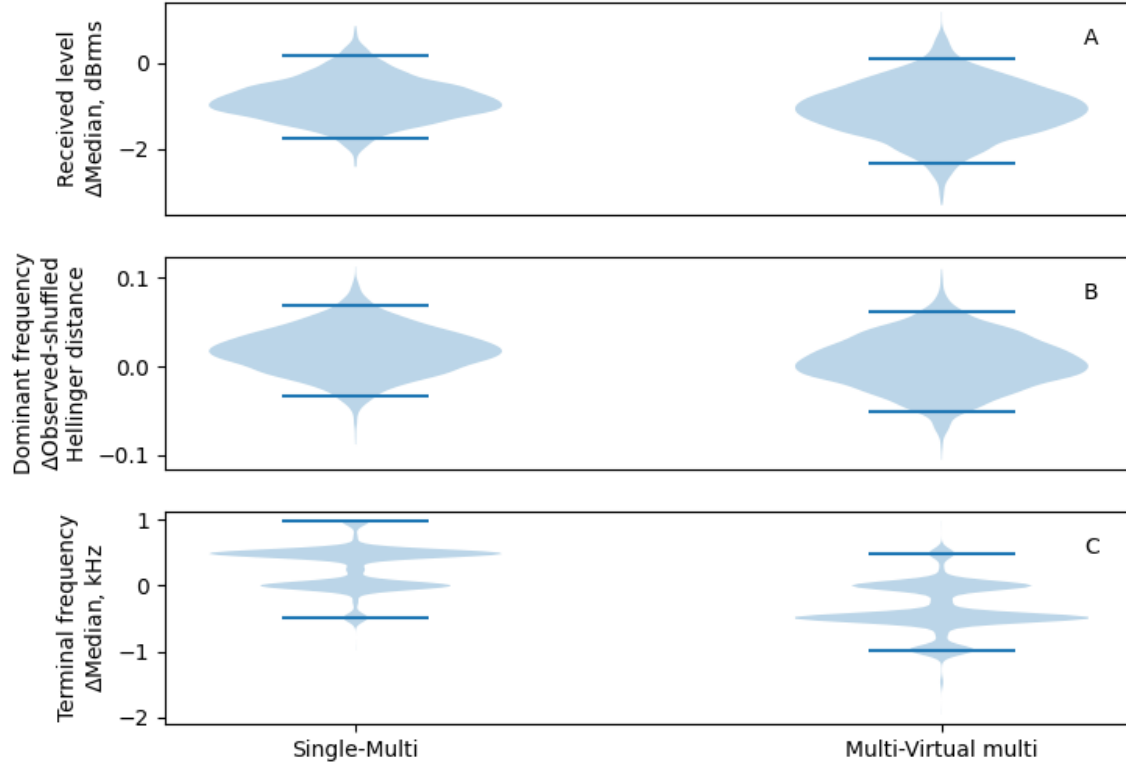


Figure 5: Comparisons of 50ms audio windows across audio with single and multi bat flights.

Discussion (BROAD DRAFT, OTHERS CHIP IN!)

1. **importance of field studies:** Bats may not show the same kinds of dramatic responses to conspecifics when studied in their natural habitat. Despite its challenging nature, we stress the importance of observing echolocation/behaviour in the wild.
2. We also present a method to assess differences in call behaviour with overlapping calls in the form of ‘windows’ than can incorporate a few calls.
3. One important aspect of the dataset missing in our study is the position of the bats as they called.
4. It maybe surprising that single and multi-bat audio windows didn’t seem to show very much difference. This does not mean that bats did not change their source level, and may be explained by a simple geometric consideration. The simplest factor is that when two sounds overlap, their dB received level is often dominated by the loudest sound. This means that in our case, when two bats fly past each other, one bat is always closer to the microphone - and its call is likely to dominate the measured received level (See Supplementary Information). Assessing source levels from the received levels requires knowledge of the bat positions. The source level calculations are in turn challenging due to the overlap of calls. One solution despite the presence of overlap is to exploit the slight interindividual difference in CF peak frequencies, and infer the individual call received levels from the power spectrum, and thus back calculate the source levels of the two overlapping calls.
5. Peak frequencies in individual calls and dominant frequencies in the audio windows did not show a systematic difference across single and multiple bat. This hints at the possibility that bats may not be

altering the CF portions of their calls very much, or at least, not in a uni-directional manner. Without knowledge of the exact speed and orientation of the bat’s flight while it emitted calls, the recorded calls may have had a Doppler shift of between ± 200 -600 Hz (Supplementary Information) as they flew towards and away from the microphone at an estimated speed of between 1-3 m/s. If the bats had indeed shown a unidirectional increase or decrease in their peak frequency when in the presence of others, then we would have been able to detect the change despite the Doppler shifts, which are both positive and negative in their effect.

6. An important reason we don’t see any difference between single and multi bat calls may also be because the bats are flying in a familiar natural setting. This may exclude the need for bats to ‘compensate’.
7. Our study has the advantage of wild bats flying in relatively small volumes. Unlike observational studies done in the wild, where it is difficult to assess how far away the bats may have been - we can be sure that the bats were flying at most $\pm X$ m away from each other.
8. Our measurement methods advance the state of the art a bit, but there is still a long way to go. All of our whole audio analysis methods include a lot of noise from echoes and reverberation. It would be good to be able to account/exclude such things.
9. WHAT WE DO NOT MEASURE — INTERPULSE INTERVAL ... THAT MAY HAVE A STRONG EFFECT - BUT THIS NEEDS MORE FANCY TECHNIQUES
10. ONE VERY IMPORTANT FACTOR TO CONSIDER – overlapping calls – the FM segments are relatively short (2-5ms), and at group sizes of 2-5, there’s very unlikely to be an issue with detecting objects in their surroundings. ref Beleyur & Goerlitz. Even though Fawcett et al. 2015 see a difference..

Data and code availability

All data and code used process data and generate the results and figures in the paper are available in the Zenodo repository [INSERT DOI HERE].

Acknowledgements

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Author Contributions

Study design and conception: TB,NMR Data collection: NMR, TB, AK, Audio and video annotation: AK,NM Audio-video synchronisation: TB Analysis: TB,NMR,HRG Interpretation of results: NMR, TB, HRG Manuscript preparation: NMR, TB, HRG. All authors read and approved the final draft of this paper

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