FORMAL TITLE to be agreed on

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Echocating bats emit loud calls and listen for returning echoes to detect their surroundings. When echolocating in groups, bats may not be able to detect their own returning echoes due to the loud calls coming from neighbours. Bats a show a variety of echolocation responses in the presence of such acoustically challenging conditions. To date however, most studies have been performed on low duty-cycle FM bats. High duty-cycle CF-FM bats remain understudied despite the higher chances of call-echo overlap during echolocation. Studying high duty-cycle CF-FM bats has also been hindered by a lack of methods to analyse overlapping calls and a predominance of flightroom and playback studies. We present methods to analyse and extract call parameters from audio with overlapping calls, and study the echolocation of a multiple CF-FM bats in the field. Our results show that bats do not seem to alter their call parameters even in the presence of conspecifics. This lack of response is in contradiction to a previous flightroom study. Our results highlight the robustness of bat echolocation, and the important of studying behaviour in a field setting.

## 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. Echolocation calls in the field remain unaltered even in groups of CF bats
4. Echolocation calls in the field remain unaltered in the presence of CF bats
5. Conspecifics do not affect echolocation call structure in CF bats

## 1.0 Introduction

Active sensing animals like echolocating bats face a sensory challenge when engaging in social behaviours like group emergence or foraging with conspecifics (Ulanovsky and Moss 2008; Gillam et al. 2010). Echolocating bats emit loud ultrasonic calls and detect their surroundings by listening for the echoes reflecting off objects around them (Griffin 1958). In groups however, a bat’s returning echoes can be overlapped by the calls and echoes from its neighbours, preventing detection of its surroundings. (Møhl and Surlykke 1989; Ulanovsky and Moss 2008). A combination of laboratory and field studies have shown the diverse responses bats show in groups and similar situations with loud sounds like noise or playbacks. Bats increase their call emission levels, alter temporal features such as call rate, duration and duty cycle (Amichai, Blumrosen, and Yovel 2015; Jarvis, Jackson, and Smotherman 2013; Lu, Zhang, and Luo 2020; Hage et al. 2013; Lin, Abaid, and Müller 2016), along with spectral properties such as bandwidth and terminal frequency (Hase et al. 2018; Cvikel et al. 2015; Götze et al. 2016; Fawcett and Ratcliffe 2015). Each of these responses however seem to be species specific, with different species showing seemingly opposite responses to similar situations (Ulanovsky et al. 2004; Amichai, Blumrosen, and Yovel 2015; Jarvis, Jackson, and Smotherman 2013; Adams, Davis, and Smotherman 2017). A wider variety of species need to be studied, to understand the myriad of echolocation responses in context of their ecology and auditory systems.

There are two broad groups of echolocating bats (Fenton, Faure, and Ratcliffe 2012) characterised by their duty cycle, or the fraction of time spent emitting calls. The first and major group of bats are low-duty cycle bats, which typically emit frequency-modulated (FM) calls. The second group is the high-duty cycle bats which typically emit calls with both FM and constant-frequency (CF) components in them, also called CF-FM calls. From a temporal perspective, low-duty cycle bats typically emit calls of a few milliseconds (1 to 20ms) duration at duty cycles between 5-20%. In contrast, high-duty cycle bats emit relatively longer calls (10 to 50ms), at much higher duty cycles upwards of 25%. Echolocation duty cycle is directly proportional to the probability of calls overlapping echoes (Beleyur and Goerlitz 2019). High-duty cycle bats such as rhinolophids and hipposiderids are thus likely to be more affected in group echolocation than low-duty cycle bats, making them a unique system to understand the sensory strategies echolocators use in challenging conditions.

A typical CF-FM call may consist of upto three call components consisting of an initial upwards FM sweep (iFM), leading to the CF segment (CF), and a terminal downward FM sweep (tFM) (*sensu* Tian and Schnitzler (1997)). The CF component is used for the flutter detection of prey wingbeats (Schnitzler and Denzinger 2011), and the auditory system of high-duty cycle bats shows a pronounced sensitivity to a narrow spectral band around the CF frequency component (Neuweiler 2000) called the acoustic fovea. Bats show inter-individual variation in the frequency tuning of their acoustic foveas (Schnitzler, Suga, and Simmons 1976), and compensate for flight-induced Doppler shifts to maintain the frequency of the CF component’s returning echo within their own acoustic fovea (Schnitzler 1973; Schoeppler, Schnitzler, and Denzinger 2018). Previous investigations (Jones, Sripathi, and Waters 1994; Jones et al. 1993; Furusawa et al. 2012) of group echolocation in CF-FM bats centred around whether CF-FM bats showed ‘jamming avoidance’ type responses (sensu Ulanovsky et al. 2004), where individual bats shift the spectral ranges of their calls to reduce overlap. Previous studies have not found support (Jones, Sripathi, and Waters 1994; Jones et al. 1993; Fawcett et al. 2015) for changes in CF frequencies. While the CF component is involved in prey detection, the tFM component is thought to be involved in target ranging (Tian and Schnitzler 1997; Neuweiler et al. 1987), and the role of the iFM remains ambiguous. CF-FM bats show rapid alterations in tFM bandwidth and duration based on the behavioural context at hand, eg. resting, landing or prey capture (Neuweiler et al. 1987; Schoeppler, Schnitzler, and Denzinger 2018; Tian and Schnitzler 1997). Due to the historical focus on the CF call component, alterations in the FM components in group flight have not been quantified in most studies. To our knowledge there is only one study (Fawcett et al. 2015) that has quantified FM components, and found an increased tFM duration and bandwidth in the presence of conspecifics. Given the tFM’s malleability and role in ranging , there is a strong need for its explicit quantification in multi-bat contexts. The tFM may show the same kinds of changes in multi-bat contexts as shown in low-duty cycle bats, which also use their FM calls primarily for ranging (Fawcett et al. 2015; Amichai, Blumrosen, and Yovel 2015; Hase et al. 2018).

A majority of studies on group echolocation have so far investigated low-duty cycle bats (Lin, Abaid, and Müller 2016; Fawcett and Ratcliffe 2015; Götze et al. 2016), likely due to ease of call analysis and their speciosity (only ~160/1428 bats (Fenton, Faure, and Ratcliffe 2012; Database 2020) are high-duty cycle species). Studying group echolocation in high-duty cycle bats entails analysing audio with overlapping calls. The analysis of recordings with overlapping calls is a nascent field (but see Izadi, Stevenson, and Kloepper 2019), and call parameter estimation has not been attempted before to the best of our knowledge. Even studies with multiple high-duty cycle bats have been limited to 2-3 bats in flightroom conditions (Fawcett et al. 2015; Jones, Sripathi, and Waters 1994; Jones et al. 1993). Flightrooms provide controlled conditions that can allow direct interpretation of results. However the echolocation of animals is also affected by familiarity (Merten and Siemers 2020; Chen et al. 2015; Yamada et al. 2020), and properties of the experimental room (Surlykke, Boel Pedersen, and Jakobsen 2009). Studying multi-bat echolocation in the wild provides a direct glimpse into the acoustic challenge animals face in a familiar environment and how they respond to changes in group size.

In our study we fill the gaps by 1) shedding light on the group echolocation in the understudied high-duty cycle bats 2) presenting a methodology to quantify echolocation parameters in the presence of overlapping calls and 3) studying group echolocation in the field.

## 2.0 Methods

### 2.1 Study species and site

Two species of rhinolophid bats *Rhinolophus mehelyi* and *R. euryale* were recorded in their natural environment. Both study species emit CF-FM calls with peak frequencies between 102-112 kHz, and are not acoustically distinguishable due to overlap in their call characteristics (Dietz and Kiefer 2016). 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 similarity in spectro-temporal call structure.

We used an audio-video recording setup positioned in a dome-shaped cave (Figure 1) next to the main entrance of the Orlova Chuka cave system, Bulgaria. The cave was 5x3x1.6m (lxbxh) in dimensions. The cave had only one opening with roosting sites on the inside where most bats flew in and out of through the night.

### 2.2 Experimental setup

The experimental setup consisted of an audio-video recording system made of three microphones and two infrared cameras. The audio and video feeds were synchronised using the low-cost method described in Laurijssen et al. 2018. ON-OFF signals between 0.08-0.5 s were generated by a portable computer (Raspberry Pi 3). The ON-OFF voltage signal was directly fed into one of the channels of the soundcard. The same voltage signal was also used to drive the blinking of an LED that was recorded by the two cameras. (See Supplementary Information (SI) 1.0 for signal generation script, electronic circuit and associated notes).

For the video recording, two consumer grade CCTV cameras with infrared lamps 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 volume recorded while also capturing the blinking LED light. Only sections of the video that had stable camera positions were analysed. Video was recorded continuously through the night and resulted in two video files (one per camera) for each recorded hour.

Three Avisoft CM16 microphones (Avisoft Bioacoustics, Germany) were connected to an Avisoft 416H (Avisoft Bioacoustics, Germany) soundcard running at 250kHz sampling rate. Horseshoe bat calls are known to be directional (Matsuta et al. 2013), and the three microphones were placed at different positions in the cave 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. 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.

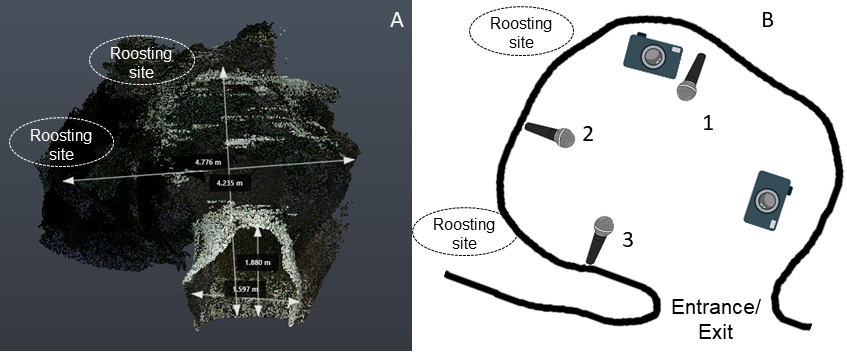


Figure 1: Scan of cave volume and schematic of microphone positions with reference to the entrance/exit and roosting sites of the cave. A) Point cloud scan of the cave as seen with the entrance/exit facing the viewer. (3D scanning by Klaus Hochradel, UMIT Tirol) B) Schematic of the microphone and video camera positions as seen from a top-view of the cave. The numbers next to the microphone icons are the corresponding channel numbers.

## 3. Data analysis

### 3.1 Video analysis to determine group sizes

Bat activity in the cave was recorded for a total of about 12 hours across four nights in the cave. Bats flew in and out of the cave often showing different flight behaviors such as circling, approaching and following. Sometimes however, bats spent time (few seconds to several minutes) in the roosting sites within the cave and then exited. The start and end of all bat flight bouts in the video was manually annotated following a series of pre-defined criteria to ensure repeatability (SI 2.0). Each flight bout annotation recorded the number of flying bats as seen in the two camera views.

### 3.2 Matching video annotation to obtain synchronised audio

For each video annotation of a bat flight bout, we attempted to match the corresponding region of recorded audio. For each successfully matched video annotation, we created a separate audio file. Audio matching was done by cross-correlating the blinking ON/OFF LED signal over the video annotation with the recorded ON/OFF voltage signal in the audio. We managed to successfully find audio matches for 1181 video annotations, ( i.e., 55% of all video annotations). The low match rate is primarily due to the fluctuating camera frame rates, and because many of the matched audio files had non-target bat species calls. Multiple species were seen in the audio files as during video annotation it was not possible to distinguish bat species by their flight behaviour. The other observed bat calls were from *R. ferrumequinum*, vespertilionid and miniopterid FM bats, all of which are known to occur in the Orlova Chuka cave system (Ivanova 2005). For the acoustic analysis we chose matched audio files that only had *R. euryale* and/or *R. meheyli* calls. The audio files varied in duration between 0.08-62.08 seconds (, median duration: 1.04s , 95%ile range: 0.5-8.54s).

## 4.0 Acoustic parameter analysis

All matched audio files were first forward-backward high-pass filtered at 70 kHz. For the analysis we used recordings from the first microphone, as it appeared to have consistently captured calls with the least reverberance of the three channels. The first microphone was located facing the cave opening, perhaps therefore capturing calls of both entering and exiting bats well.

We quantified frequency, duration and amplitude across different parts of the echolocation call (iFM,CF and tFM) using two complementary acoustic analyses. The first analysis is the ‘individual call’ analysis, where we measured parameters of one horseshoe bat call from each matched audio. The second analysis is the ‘window’ analysis. Each matched audio was split into 50ms windows. We then measured the acoustic parameters from all windows of a matched audio file. In recordings with multiple bats, the 50 ms windows could have overlapping calls.

The advantage of the individual call analysis is that the measurements made on the calls are directly interpretable as call component alterations reveal the sensory decisions of the bats. On the other hand, the disadvantage of the individual call analysis is that especially in multi-bat recordings, it can be difficult to find a non-overlapped call. The window analysis complements individual call analysis by enabling measurements even on audio with overlapping calls. Window analysis also allows a kind of null-hypothesis testing where the observed multi-bat audio can be compared with 1) single bat audio and 2) ‘virtual’ multi-bat audio files created by adding multiple single bat audio files. These ‘virtual’ multi-bat audio files recreate a scenario where two bats echolocate in the same volume without actively responding to each other’s presence. The disadvantage with window analysis is the lack of call-level measurements. Ultimately, using the two approaches simultaneously strengthens the interpretation of our results.

### 4.1 Individual call measurements

Individual calls that were not overlapped by other calls and with sufficient signal-to-noise ratio (Figure 2) were manually chosen through a random search protocol (SI 3.0). Briefly, an experimenter began searching from a randomly chosen time point in an audio file for a non-overlapped horseshoe bat 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 226 individual calls (: 177, : 49) across all the synchronised audio files. Calls were automatically segmented into their corresponding parts iFM, tFM or CF (Tian and Schnitzler 1997) (Figure 2) using the *itsfm* package [Beleyur (2020);*biorxivpaper*]. Most approaches to date focus on indirectly segmenting CF-FM calls into their components by high/low pass filtering around 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. While suitable for laboratory studies, filtering around the peak frequency fails in the analysis of CF-FM calls recorded in the field under a variety of conditions eg. calls with loud FM and faint CF components. *itsfm* overcomes these limitations by tracking the *change* in frequency over the call to segment it into FM and CF components.

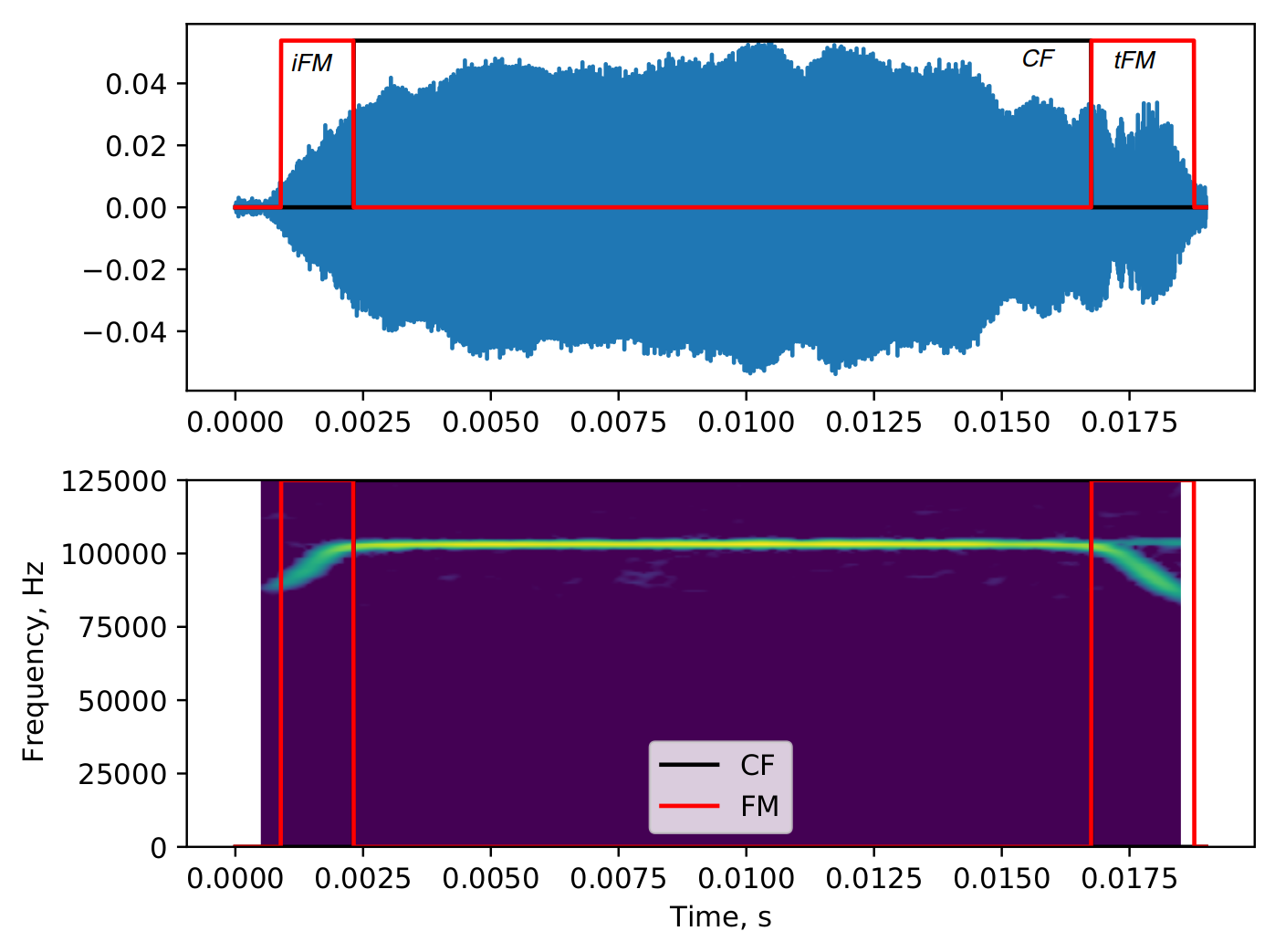


Figure 2: Example of a single CF-FM call with automatically segmented iFM, CF and tFM regions. The raw data is a manually selected audio segment, which is then automatically segmented by the itsfm package based on frequency modulation across the call. The itsfm package allows accurate segmentation into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

From the segmented CF and FM components we measured specific parameters. In the CF component, we measured the peak frequency, RMS amplitude and duration. The CF peak frequency was quantified as bats may shift their CF frequencies in the presence of conspecifics. ‘Jamming avoidance’ type reponses have been a parameter of investigation in previous studies (Habersetzer 1981; Jones, Sripathi, and Waters 1994; Jones et al. 1993; Fawcett et al. 2015; Lu, Zhang, and Luo 2020). From the FM components, we measured the lower frequency (-10 dB peak frequency of the FM audio segment), bandwidth (defined as difference between the CF peak frequency and the lower frequency of the FM segment), RMS amplitude and duration. The bandwidth is important for target ranging in CF-FM bats. An increase in bandwidth in the presence of conspecifics has been shown in at least one previous study (Fawcett et al. 2015). We also calculated the relative i/tFM-CF amplitude ratios (in dB). The relative call component measures were calculated as CF-FM bats are known to independently vary the level of call components in a context specific manner (Tian and Schnitzler 1997; Lu, Zhang, and Luo 2020).

### 4.2 Window measurements

Each audio file was split into consecutive 50ms windows (SI 4.0). The time window of 50ms was chosen as it provided high spectral resolution (20Hz for 12500 samples at 250kHz sampling rate) to distinguish multiple CF components that may be in it. Often in the multi bat recordings, the 50 ms windows consisted of one to many horseshoe bat calls. Initial observations showed that 50 ms was about the longest observed duration of a bat call in our data, and was also about twice the length of typical calls. We therefore chose a 50 ms duration as it could contain one long call or multiple short calls.

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 (SI 4.1). On each non-silent window, the following acoustic measurements were performed: 1) received level (dB RMS), 2) dominant frequencies and 3) FM terminal frequencies. Dominant frequencies here are defined as frequency peaks in the smoothed power spectrum that are within 14 dB of the window’s peak frequency. Dominant frequencies are extracted from the various peaks of the power spectrum and are thus a proxy measurement for the CF component frequencies of calls in a window (SI 4.2). 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 (SI 4.3). There could be multiple terminal and dominant frequency values for a single window, however only one received level measurement per window. All measurements chosen in the whole audio analysis were done to be analogous to the measurements performed in the individual call analyses. For instance, the dominant frequencies in the whole audio analysis complements the CF peak frequency measurements in the individual call analysis. The FM terminal frequencies and RMS measurements are again analogous to the bandwidth and RMS of the individual call analysis.

### 4.3 Virtual multi-bat audio

The advantage of the window analysis is the possibility to make ‘virtual multi-bat’ data (Fawcett et al. 2015; Ratcliffe et al. 2004) by combining observed single bat call measurements or sequences. We created virtual multi-bat audio files by combining single bat files that were of similar durations (SI 4.4). This allowed us to create a ‘null’ dataset where multiple bats were echolocating, but not responding to each other’s presence. Acoustic measurements were also performed on the virtual multi-bat audio using the window analysis described above.

## 5.0 Statistical analysis

We observed upto 1-4 bats flying in the cave at the same time. However, the sample sizes in group sizes 2 bats were low (SI 5.0), and we thus decided to combine all annotations with 2 bats into a ‘multi’ bat class. We thus performed comparisons of ‘single’ and ‘multi’ bat calls in the individual call analysis. To maintain consistency with individual call analysis we also performed comparisons of ‘single’,‘multi’ and ‘virtual-multi’ audio in the window analysis.

### 5.1 Individual call measurements

We calculated the median difference () between multi and single bat call parameters for all parameters except CF peak frequency. For CF peak frequencies, we calculated the range difference () of CF peak frequencies in multi bat and single calls. The range difference was calculated as ‘jamming avoidance’ type responses imply an alteration in the range of frequencies used. Bats may decide to shift their call frequencies in groups, leading to an increased range (Habersetzer 1981), or as has been experimentally observed, paradoxically converge (Furusawa et al. 2012). Permutation tests were performed to assess the significance of the observed median and range difference between the groups.

Our dataset has calls from a group of resident wild bats that may have visited the cave site multiple times over the course of a night. Moreover, bat activity over the course of a single night was relatively clustered in time, and flight annotations were thus fairly close to each other at <= 1 minute (median inter-annotation times was 36 s for annotations used in individual calls and 54 s for annotations used in window analysis). Due to the clustered nature of activity, our dataset may have had a disproportionate representation of a few individuals, leading to pseudo replication, and thus a lowering of variation in the data.

To account for the temporal pseudo-replication in our data, we repeated the median/range difference analysis by creating two subsets from our full dataset. We created the ‘clustered’ subset, where all calls from annotations that were 1 min from each other were taken together. The ‘isolated’ subset included all calls from annotations that were at least 1 minute away from another annotation. The ‘isolated’ and ‘clustered’ subsets had unique datapoints, with no overlap in the calls used. One minute was chosen as it was slightly larger than the observed median inter-annotation interval. Broadly speaking, we expect that if the results of our analysis are comparable across the isolated and clustered subsets, there is a common underlying effect that is independent of temporal clustering. However, if the results of the subset analysis do not corroborate each other, it hints at an effect due to temporal clustering/isolation in the dataset.

### 5.2 Window measurements

In analogy to CF peak frequency range in the individual call analysis, we calculated the dominant frequency range () across an audio file. Even in single bat audio files, we expect variation in recorded dominant frequency due to the combined effect of the bat’s active Doppler shift compensation and Doppler shift due to its flight past the microphone (SI 8.0). Multi-bat and virtual-multi bat audio files are expected to have an increased range due to presence of multiple bats. We performed a comparison of the median difference in dominant frequency range between multi-single and multi-virtual multi audio. A permutation test was performed to assess the significance of the observed difference. To understand the expected dominant frequency range from single and multi bat flights, (and thus the expected range difference) we also performed simulations quantifying Doppler shift and Doppler shift compensation parametrised by the observed data (SI 8.0). The dominant frequency range estimates from the simulations informed the interpretation of the observed data.

Unlike one value per file for the dominant frequency range measurement, there are multiple potentially correlated received level and terminal frequency measurements from each file. We accounted for this potential file-level pseudo-replication by resorting to repeated random subsampling and median difference calculation. To estimate the median difference between groups we randomly chose one measurement value per file for the single, multi and virtual-multi bat groups. The median difference between multi-single and multi-virtual multi groups were calculated and followed by the next subsampling round. We performed 10,000 such subsampling iterations, and report the 95 percentile range of median differences in received level and terminal frequency. No tests were run on the median difference estimates obtained for received level and terminal frequency.

To account for temporal pseudo-replication in our study, we also repeated the entire window analysis using clustered and isolated subsets as described in section 5.1.

### 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). Median difference and permutation tests were performed with dabest (Ho et al. 2019) while reproducible analysis, documentation and presentation were enabled by the Jupyter Notebook and Rmarkdown projects(Kluyver et al. 2016; Xie, Allaire, and Grolemund 2018). Audio visualisation, preliminary measurements and single call annotations were done with Audacity (Audacity-Team 2019).

## 6.0 Results

### 6.1 Individual call analysis

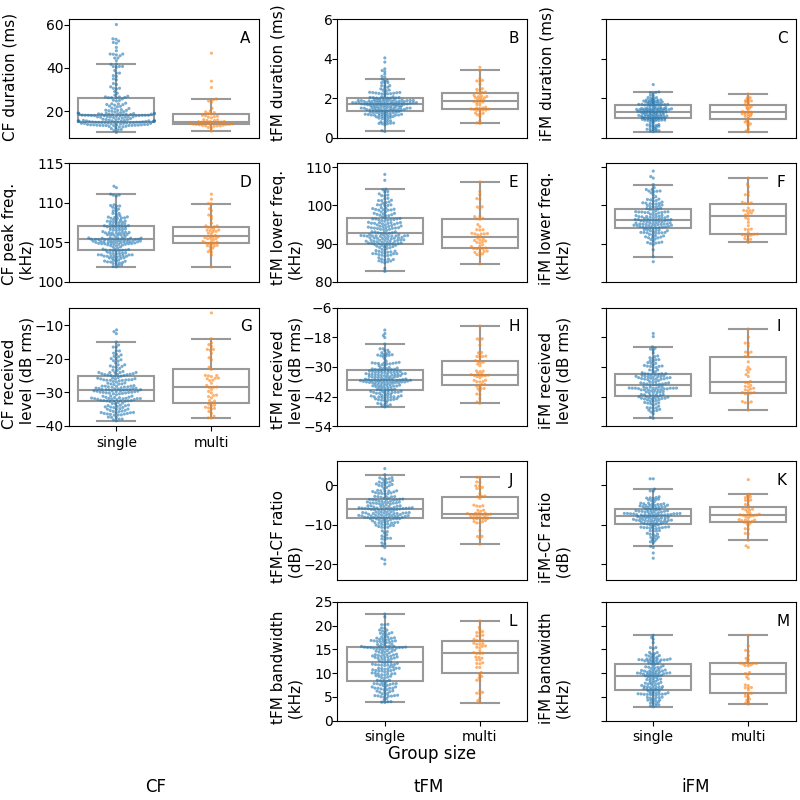


Figure 3: Measured acoustic parameters for the CF, iFM and tFM components of individual calls emitted under single and multi bat conditions. Each column shows the measurements on a call component, while each row shows a group of related measurements A-C) duration D-F) spectral measurements G-I) received level J-K) relative FM-CF ratios L-M) FM component bandwidths. 177 , = 49

The measured acoustic parameters of call components are shown in Figure 3. Call parameters showed little difference between multi and single bat groups (Table 1). Among the temporal parameters, median CF duration appeared to show a ~3ms decrease in multi-bat calls, indicating shorter calls. The iFM and tFM median durations seemed to differ between the groups by around 0.1 ms in opposite directions. Among the spectral parameters, CF peak frequency range, iFM and tFM lower frequencies all differed by around 1 kHz in different directions. Among the received level parameters, iFM and CF components showed a ~ 1.5 dB decrease, while tFM level showed a slightly larger ~-3 dB decrease in multi-bat calls. The i/tFM-CF level ratios however showed very slight differences of less than 1 dB magnitude. Median tFM bandwidth seemed to be slightly increased in multi-bat calls by 1.8 kHz, while iFM bandwidth did not show very much difference (~300 Hz). Our ‘whole dataset’ results broadly match with the results using the ‘clustered’ and ‘isolated’ subset data (SI 6.0). One complicating factor in the interpretation of the isolated subset is however the severe drop in sample sizes of the multi-bat calls in this subset. In the isolated subset, = 5 calls, in contrast to the much higher =53.

Table 1: *Difference between multi and single bat call parameters. The median difference is reported for all parameters except CF peak frequency, where the difference in range is reported.*

| Measurement | Difference (Multi-Single) | Permutation test p-value |
| --- | --- | --- |
| CF duration (median ms) | -2.95 | 0.003 |
| tFM duration (median ms) | 0.14 | 0.16 |
| iFM duration (median ms) | -0.04 | 0.7 |
| CF peak frequency (range kHz) | -1 | 0.18 |
| tFM lower frequency (median kHz) | -1.03 | 0.29 |
| iFM lower frequency (median kHz) | 1.07 | 0.24 |
| CF level (median dB RMS) | -1.48 | 0.2 |
| tFM level (median dB RMS) | -3.15 | 0.01 |
| iFM level (median dB RMS) | -1.66 | 0.32 |
| tFM-CF ratio (median dB) | -1.08 | 0.16 |
| iFM-CF ratio (median dB) | 0.25 | 0.75 |
| tFM bandwidth (median kHz) | 1.83 | 0.12 |
| iFM bandwidth (median kHz) | 0.27 | 0.82 |

### 6.2 Window analysis

Multi-single comparisons (Table 2) revealed an increased dominant frequency range in multi bat audio windows by around 2 kHz. The estimated median differences for received level and FM terminal frequency showed no systematic trend, indicating no relative increase or decrease. Subset analysis also revealed similar trends (SI 7.0).

Table 2: *Multi-single bat comparison of window parameters. For dominant frequency, the range difference was calculated along with running permutation test. Dominant frequency range is larger by 2.2 kHz in multi-bat windows as expected. 95 percentile estimated range for median difference are reported for received level and FM terminal frequency. Received levels and FM terminal frequency median differences indicate no systematic trend towards a relative increase or decrease in multi-bat audio windows.* = 233 87

| Parameter | Difference | Permutation test p-value | Median difference, 2.5%ile | Median difference, 97.5%ile |
| --- | --- | --- | --- | --- |
| Dominant frequency range (kHz) | 2.2 | 0 |  |  |
| Received level (dB rms) |  |  | -0.88 | 1.61 |
| Terminal FM frequency (kHz) |  |  | -1.46 | 0.98 |

Multi-virtual multi comparisons (Table 3) revealed a small increase in dominant frequency range of around 0.5 kHz in multi bat audio windows. Received level and FM terminal frequency median differences indicate no systematic trend towards a relative increase or decrease in multi-bat audio windows. Subset analysis also revealed similar trends (SI 7.0)

Table 3: *Multi-virtual multi bat comparison of window parameters. For dominant frequency, the range difference was calculated along with running permutation test. Dominant frequency range difference is small and hints at a scenario with no active change in CF frequencies. 95%ile estimated ranges are reported for received level and FM terminal frequency. Received levels and FM terminal frequency median differences indicate no trend towards a relative increase or decrease in multi-bat audio windows.* = 87 = 83

| Parameter | Difference | Permutation test p-value | Median difference, 2.5%ile | Median difference, 97.5%ile |
| --- | --- | --- | --- | --- |
| Dominant frequency range (kHz) | 0.48 | 0.16 |  |  |
| Received level (dB rms) |  |  | -0.72 | 2.10 |
| Terminal FM frequency (kHz) |  |  | -1.95 | 0.98 |

## Discussion

We quantified the difference in horseshoe bat echolocation calls when alone and with conspecifics in the field. Our results do not support a biologically meaningful difference in echolocation calls with reference to group size for all of the call parameters measured using two different approaches. This may seem somewhat unexpected, especially considering the fact that bats in our field site were flying in an enclosed reverberant volume - which would only amplify the problem of masking in multi-bat echolocation. We interpret our results below in more detail.

The idea that bats may alter their call frequencies to reduce spectral overlap in groups has been investigated with mixed results over many studies (Jones et al. 1993; Jones, Sripathi, and Waters 1994; Ulanovsky et al. 2004). Specifically in CF-FM bats the results do not support the idea that bats may alter their CF frequencies (Jones et al. 1993; Jones, Sripathi, and Waters 1994; Fawcett and Ratcliffe 2015; Pye 1972). Habersetzer (1981) seems to suggest CF frequency shifting in a quasi-CF bat, *Rhinopoma hardwickei* (but see Cvikel et al. (2015) for an alternative interpretation). However, the echolocation of *R. hardwickei* is not entirely comparable with those of the hipposiderids and rhinolophids in previous studies (Simmons, Kick, and Lawrence 1984). Hipposiderids and rhinolophids are more constrained in their echolocation as they show a marked individual-specific acoustic fovea that does not vary over short periods of time (Neuweiler 2000; Schnitzler, Suga, and Simmons 1976). CF-FM bats are thus constrained to emit calls so that the Doppler-shifted echoes arrive within their own acoustic fovea’s range. Our data (Figure 3, Tables 1,2,3)) also support previous studies showing an absence of active CF frequency shifting in the presence of conspecifics. If bats were to show ‘jamming avoidance’ type responses, one would expect an overall increase in the CF frequency range in groups, and thus an increased range difference between single and multi bat audio. If they were to show ‘convergence’ (eg. as in Furusawa et al. 2012), we expect a reduction in range. The observed CF and dominant frequency range differences of around 2 kHz between single and multi bats falls within the expected magnitude seen when bats do not show any special responses to each other (SI 8.0). More convincingly however, the low difference in dominant frequency range between multi and virtual multi audio shows that even when bats are indeed flying together they are not actively altering their CF frequencies to reduce or increase overlap. Our simulations (SI 8.0) and experimental data show that a receiver (eg. a microphone or another bat) placed in the proximity of a flying CF-FM bat may hear a series of CF frequencies that vary by upto 3 kHz from the emitted frequency. This relatively large variation in the received frequency thus decreases the extent of spectral overlaps during multi-bat echolocation. The combination of individual specific acoustic foveas and Doppler-shift driven variation in received CF frequency make it unlikely that the CF component would be masked effectively even in groups.

The tFM call component may also be expected to undergo alterations in groups. Fawcett et al. (2015) found an average of 5 kHz tFM minimum frequency (-10 dB call peak frequency) increase in pairs. We failed to find effects that matched their results, with a drop in tFM lower frequency (-10 dB tFM peak frequency) of around 1 kHz at most, and an increase in tFM bandwidth of at most 1.8 kHz. Our window analysis revealed no systematic differences in terminal frequency estimates between single and multi bat windows. Alterations to duration are also known to occur in calls in the presence of conspecifics and noise (Fawcett et al. 2015; Lu, Zhang, and Luo 2020). Fawcett et al. (2015) found an average increase in tFM duration by 1.8 ms in pairs, while we find a slight median increase by about 0.1 ms in multi-bat calls. In another study with artifical playbacks, Lu, Zhang, and Luo (2020) found an increase of 0.6ms in comparison to calls in silence. Compared to previous studies, our effects are small, and unlikely to have biological significance. We also found a median decrease in CF component duration by around 3 ms in multi-bat calls. This decrease matches a similar finding of Fawcett et al. (2015) where average call duration decreases by around 1.2 ms in pairs. However, whether our observed decrease in CF duration is a result of an increased call duty cycle or an artifact of our individual call selection protocol is difficult to tell apart. Our individual call selection protocol specifically looked for non-overlapping calls, meaning that it may have favoured the selection of shorter calls.

Bats are known to increase their call levels in the presence of experimental playbacks (Hage et al. 2013, 2014; Lu, Zhang, and Luo 2020). In our study, we did not have access to the source level of the calls as we did not track the bats’ position in 3D space. We only had access to the *received* level at the microphone, which is modulated broadly by 1) the bat-microphone distance, and 2) source level of the call. With these caveats in mind, we discuss our results. Aside from the 3dB median drop in tFM received level, the multi-single difference in other call components were smaller (~1.5dB) in the individual call analysis. Window analysis revealed no systematic alteration in received level in multi-single and multi-virtual multi comparisons. The relative iFM-CF and tFM-CF ratios were at most 1 dB. Why was there no major difference in received levels even in the window analysis, where overlapping calls are expected to lead to a higher received level? The similarity in received levels of multi and single bat windows can be explained by the inequal contribution the nearest bat’s call makes to the received level. Due to the spherical spreading of sound, the received level at the microphone primarily reflects that of the bat calling closest to the microphone. Thus, even when there are multiple bats - the nearest bats’ call dominates the received level measurements. This nearest-bat dominance means we typically measure the received level of one bat’s call even when the audio has overlapping calls. Multi and virtual-multi bat audio-segments having similar received levels thus indirectly suggests there is no change in source level even in the presence of another bat. However, the tFM received level showed a drop of around 3dB that we are not sure how to interpret. This apparent drop in received level could be the result of bats flying further away or emitting more directional calls.

We introduced two automated analyses that can be performed on audio recordings of multiple CF-FM bats. Automated individual call analyses using the open-source itsfm package allows call component segmentation according to the rate of frequency modulation across the sound. The frequency-modulation based segmentation in our experience is also more robust to field recordings with fainter CF components, and thus performs better than filtering around the peak frequency as done in previous studies. To analyse audio with overlapping calls we measured acoustic parameters of short audio windows without assigning the measurements to individual calls. While coarser than the individual call analysis, the window based approach still provides complementary support to the individual call analyses by parametrising variables such as FM terminal frequency and dominant frequency range.

There are a set of parameters that we were not able to measure and thus excluded in our analyses. We did not measure call-sequence related parameters such as inter-call-intervals or duty-cycle. Bats in acoustically difficult situations are known to alter their call rate (Amichai, Blumrosen, and Yovel 2015; Jarvis, Jackson, and Smotherman 2013), and thus their duty cycle. Measuring inter-call-intervals is possible in single bat contexts, but extremely challenging in multi-bat recordings with overlaps and reverberation. The study of call-sequence related measures in multi-bat recordings is hindered by the difficulty in call assignment. In our individual call analyses we specifically avoided audio recordings with only overlapping calls, and this represents an unavoidable observational bias in our dataset. The use of a microphone array with at least four microphones to assign calls to the emitting bats is the next step in the study of CF-FM group echolocation.

What are the possible explanations for the absence of a strong echolocation response in groups? The main explanation we posit is that situations with 2-3 bats may not be very challenging echolocation-wise for multiple reasons. CF-FM bats rely on the tFM component to detect the distance of objects around them (Tian and Schnitzler 1997). The tFM components are short ($\\leq$ 3.4ms, 95 percentile value), and likely emitted every 40-50 ms (calculated using typical duty cycle values. Interval includes CF duration and inter-pulse interval), which is equivalent to a tFM duty cycle between 6.8-8.5%. For a pair of bats at these duty cycles, the probability of one tFM echo being overlapped by another bat’s tFM call component is relatively low at most between 1.6 - 2.1% (SI 9.0). Even if a single tFM echo is overlapped by another call, a bat may still be able to detect it if the signal-to-noise ratio is sufficient. Bats in small groups are unlikely to face major detriments to their echolocation (Beleyur and Goerlitz 2019), and thus not show specific alterations from solitary echolocation. Secondly, Fawcett et al. (2015) observed an increased tFM duration and bandwidth in *R. capensis* flying in pairs in a novel flight room setting. The combination of flight room characteristics (Surlykke, Boel Pedersen, and Jakobsen 2009) and species differences, may perhaps have led to the difference in results between their study and ours. Bats show long-term spatial memory (Barchi, Knowles, and Simmons 2013; Möhres and Oettingen-Spielberg 1949) and familiarity with the cave’s structure may have allowed them to easily recognise their location over time. Bats also use echoes across multiple calls and are thus resistant to occasional disruptions in echo arrival (Salles, Diebold, and Moss 2020). The combination of spatial memory and multi-echo integration may have allowed our bats to continue echolocating with conspecifics without altering their calls drastically.

Previous manipulative studies (Hage et al. 2013, 2014; Lu, Zhang, and Luo 2020) have revealed the exquisite control bats have over each call component. However, these call alterations are typically elicited in response to artifical stimuli with little resemblance to their natural auditory scenes. Our results suggest that bats may not regularly be employing strategies observed from playback and flightroom studies to enhance their echo detection while flying with conspecifics. We highlight the importance of observational studies in field settings to understand the frequency with which various sensory strategies are actually employed in ecological contexts.

## 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].

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## Author Contributions

Study design and conception: NMR, TB; Data collection: AK, NMR, TB; Audio and video annotation: AK, NMR; Audio-video synchronisation: TB; Analysis: HRG, NMR, TB; Interpretation of results: HRG, NMR, TB; Manuscript preparation: HRG, NMR, TB.

## References

Adams, Amanda M, Kaylee Davis, and Michael Smotherman. 2017. “Suppression of Emission Rates Improves Sonar Performance by Flying Bats.” *Scientific Reports* 7 (1): 1–9.

Amichai, Eran, Gaddi Blumrosen, and Yossi Yovel. 2015. “Calling Louder and Longer: How Bats Use Biosonar Under Severe Acoustic Interference from Other Bats.” *Proceedings of the Royal Society B: Biological Sciences* 282 (1821): 20152064.

Audacity-Team. 2019. “Audacity(R): Free Audio Editor and Recorder [Computer Application] Version 2.3.3.” <https://audacityteam.org/>.

Barchi, Jonathan R, Jeffrey M Knowles, and James A Simmons. 2013. “Spatial Memory and Stereotypy of Flight Paths by Big Brown Bats in Cluttered Surroundings.” *Journal of Experimental Biology* 216 (6): 1053–63.

Bechtold, Bastian, and Matthias Geier. 2019. *SoundFile* (version 0.10.3). <https://github.com/bastibe/SoundFile>.

Beleyur, Thejasvi. 2020. “Itsfm: Identify, Track and Segment Sounds by Frequency and Its Modulation, V 0.1.0.” <https://itsfm.readthedocs.io/en/latest/>.

Beleyur, Thejasvi, and Holger R. Goerlitz. 2019. “Modeling Active Sensing Reveals Echo Detection Even in Large Groups of Bats.” *Proceedings of the National Academy of Sciences* 116 (52): 26662–8. <https://doi.org/10.1073/pnas.1821722116>.

Chen, Y, Q Liu, YG Shao, LJ Tan, ZF Xiang, and LB Zhang. 2015. “Variation in Echolocation Calls of Hipposideros Amiger During Habituation to a Novel, Captive Environment.” *Behaviour* 152 (7-8): 1083–95.

Cvikel, Noam, Eran Levin, Edward Hurme, Ivailo Borissov, Arjan Boonman, Eran Amichai, and Yossi Yovel. 2015. “On-Board Recordings Reveal No Jamming Avoidance in Wild Bats.” *Proceedings of the Royal Society B: Biological Sciences* 282 (1798): 20142274.

Database, Mammal Diversity. 2020. “Mammal Diversity Database.” Zenodo. <https://doi.org/10.5281/zenodo.4139818>.

Dietz, Christian, and Andreas Kiefer. 2016. *Bats of Britain and Europe*. Bloomsbury Publishing.

Fawcett, Kayleigh, David S Jacobs, Annemarie Surlykke, and John M Ratcliffe. 2015. “Echolocation in the Bat, Rhinolophus Capensis: The Influence of Clutter, Conspecifics and Prey on Call Design and Intensity.” *Biology Open* 4 (6): 693–701.

Fawcett, Kayleigh, and John M Ratcliffe. 2015. “Clutter and Conspecifics: A Comparison of Their Influence on Echolocation and Flight Behaviour in Daubenton’s Bat, Myotis Daubentonii.” *Journal of Comparative Physiology A* 201 (3): 295–304.

Fenton, M Brock, Paul A Faure, and John M Ratcliffe. 2012. “Evolution of High Duty Cycle Echolocation in Bats.” *Journal of Experimental Biology* 215 (17): 2935–44.

Furusawa, Yuto, Shizuko Hiryu, Kohta I Kobayasi, and Hiroshi Riquimaroux. 2012. “Convergence of Reference Frequencies by Multiple Cf–Fm Bats (Rhinolophus Ferrumequinum Nippon) During Paired Flights Evaluated with Onboard Microphones.” *Journal of Comparative Physiology A* 198 (9): 683–93.

Gillam, Erin H., Nickolay I. Hristov, Thomas H. Kunz, and Gary F. McCracken. 2010. “Echolocation behavior of Brazilian free-tailed bats during dense emergence flights.” *Journal of Mammalogy* 91 (4): 967–75. <https://doi.org/10.1644/09-MAMM-A-302.1>.

Götze, Simone, Jens C Koblitz, Annette Denzinger, and Hans-Ulrich Schnitzler. 2016. “No Evidence for Spectral Jamming Avoidance in Echolocation Behavior of Foraging Pipistrelle Bats.” *Scientific Reports* 6 (1): 1–13.

Griffin, Donald R. 1958. “Listening in the Dark: The Acoustic Orientation of Bats and Men.”

Habersetzer, Joerg. 1981. “Adaptive Echolocation Sounds in the Batrhinopoma Hardwickei.” *Journal of Comparative Physiology* 144 (4): 559–66.

Hage, Steffen R, Tinglei Jiang, Sean W Berquist, Jiang Feng, and Walter Metzner. 2013. “Ambient Noise Induces Independent Shifts in Call Frequency and Amplitude Within the Lombard Effect in Echolocating Bats.” *Proceedings of the National Academy of Sciences* 110 (10): 4063–8.

———. 2014. “Ambient Noise Causes Independent Changes in Distinct Spectro-Temporal Features of Echolocation Calls in Horseshoe Bats.” *Journal of Experimental Biology* 217 (14): 2440–4.

Hase, Kazuma, Yukimi Kadoya, Yosuke Maitani, Takara Miyamoto, Kohta I Kobayasi, and Shizuko Hiryu. 2018. “Bats Enhance Their Call Identities to Solve the Cocktail Party Problem.” *Communications Biology* 1 (1): 1–8.

Ho, Joses, Tayfun Tumkaya, Sameer Aryal, Hyungwon Choi, and Adam Claridge-Chang. 2019. “Moving Beyond P Values: Data Analysis with Estimation Graphics.” *Nature Methods* 16 (7): 565–66.

Hunter, John D. 2007. “Matplotlib: A 2D Graphics Environment.” *Computing in Science & Engineering* 9 (3): 90–95.

Ivanova, Teodora. 2005. “Important Bat Underground Habitats (Ibuh) in Bulgaria.” *Acta Zool. Bulg* 57 (2): 197–206.

Izadi, Mohammad Rasool, Robert L Stevenson, and Laura Kloepper. 2019. “Segmentation of Overlapping Sources in Mixtures of Bat Echolocation Calls.” *The Journal of the Acoustical Society of America* 146 (4): 3026–6.

Jarvis, Jenna, William Jackson, and Michael Smotherman. 2013. “Groups of Bats Improve Sonar Efficiency Through Mutual Suppression of Pulse Emissions.” *Frontiers in Physiology* 4: 140.

Jones, G, M Morton, PM Hughes, and RM Budden. 1993. “Echolocation, Flight Morphology and Foraging Strategies of Some West African Hipposiderid Bats.” *Journal of Zoology* 230 (3): 385–400.

Jones, G, K Sripathi, and Dean A Waters. 1994. “Individual Variation in the Echolocation Calls of Three Sympatric Indian Hipposiderid Bats, and an Experimental Attempt to Jam Bat Echolocation.” *Folia Zoologica* 43: 347–62.

Kluyver, Thomas, Benjamin Ragan-Kelley, Fernando Pérez, Brian Granger, Matthias Bussonnier, Jonathan Frederic, Kyle Kelley, et al. 2016. “Jupyter Notebooks – a Publishing Format for Reproducible Computational Workflows.” Edited by F. Loizides and B. Schmidt. IOS Press.

Lin, Yuan, Nicole Abaid, and Rolf Müller. 2016. “Bats Adjust Their Pulse Emission Rates with Swarm Size in the Field.” *The Journal of the Acoustical Society of America* 140 (6): 4318–25.

Lu, Manman, Guimin Zhang, and Jinhong Luo. 2020. “Echolocating Bats Exhibit Differential Amplitude Compensation for Noise Interference at a Sub-Call Level.” *Journal of Experimental Biology* 223 (19).

McKinney, Wes, and others. 2010. “Data Structures for Statistical Computing in Python.” In *Proceedings of the 9th Python in Science Conference*, 445:51–56. Austin, TX.

Merten, Sophie von, and Björn M Siemers. 2020. “Shrew Twittering Call Rate Is High in Novel Environments—a Lab-Study.” *Mammal Research*, 1–11.

Möhres, FP, and Th Oettingen-Spielberg. 1949. “Versuche über Die Nahorientierung Und Das Heimfindevermögen Der Fledermäuse.” *Verhandlungen Der Deutschen Zoologen in Mainz*, 248–52.

Møhl, B., and A. Surlykke. 1989. “Detection of Sonar Signals in the Presence of Pulses of Masking Noise by the Echolocating Bat, Eptesicus Fuscus.” *J. Comp. Physiol. A* 165: 119–24.

Neuweiler, Gerhard (transl. Ellen Covey). 2000. “The Biology of Bats.” Oxford University Press.

Neuweiler, G, W Metzner, U Heilmann, R Rübsamen, M Eckrich, and HH Costa. 1987. “Foraging Behaviour and Echolocation in the Rufous Horseshoe Bat (Rhinolophus Rouxi) of Sri Lanka.” *Behavioral Ecology and Sociobiology* 20 (1): 53–67.

Oliphant, Travis E. 2006. *A Guide to Numpy*. Vol. 1. Trelgol Publishing USA.

Pye, JD. 1972. “Bimodal Distribution of Constant Frequencies in Some Hipposiderid Bats (Mammalia: Hipposideridae).” *Journal of Zoology* 166 (3): 323–35.

Ratcliffe, John M, Hannah M ter Hofstede, Rafa Avila-Flores, M Brock Fenton, Gary F McCracken, Stephania Biscardi, Jennifer Blasko, Erin Gillam, Jasmine Orprecio, and Genvieve Spanjer. 2004. “Conspecifics Influence Call Design in the Brazilian Free-Tailed Bat, Tadarida Brasiliensis.” *Canadian Journal of Zoology* 82 (6): 966–71.

Salles, Angeles, Clarice Anna Diebold, and Cynthia F. Moss. 2020. “Echolocating Bats Accumulate Information from Acoustic Snapshots to Predict Auditory Object Motion.” *Proceedings of the National Academy of Sciences*. <https://doi.org/10.1073/pnas.2011719117>.

Schnitzler, Hans-Ulrich. 1973. “Control of Doppler Shift Compensation in the Greater Horseshoe Bat, Rhinolophus Ferrumequinum.” *Journal of Comparative Physiology* 82 (1): 79–92.

Schnitzler, Hans-Ulrich, and Annette Denzinger. 2011. “Auditory Fovea and Doppler Shift Compensation: Adaptations for Flutter Detection in Echolocating Bats Using Cf-Fm Signals.” *Journal of Comparative Physiology A* 197 (5): 541–59.

Schnitzler, H-U, N Suga, and JA Simmons. 1976. “Peripheral Auditory Tuning for Fine Frequency Analysis by the Cf-Fm Bat, Rhinolophus Ferrumequinum.” *Journal of Comparative Physiology* 106 (1): 99–110.

Schoeppler, Diana, Hans-Ulrich Schnitzler, and Annette Denzinger. 2018. “Precise Doppler Shift Compensation in the Hipposiderid Bat, Hipposideros Armiger.” *Scientific Reports* 8 (1): 1–11.

Schuchmann, Maike, Sébastien J Puechmaille, and Björn M Siemers. 2012. “Horseshoe Bats Recognise the Sex of Conspecifics from Their Echolocation Calls.” *Acta Chiropterologica* 14 (1): 161–66.

Siemers, Björn M, Kristian Beedholm, Christian Dietz, Isabel Dietz, and Teodora Ivanova. 2005. “Is Species Identity, Sex, Age or Individual Quality Conveyed by Echolocation Call Frequency in European Horseshoe Bats?” *Acta Chiropterologica* 7 (2): 259–74.

Simmons, James A, Shelley A Kick, and Beatrice D Lawrence. 1984. “Echolocation and Hearing in the Mouse-Tailed Bat, Rhinopoma Hardwickei: Acoustic Evolution of Echolocation in Bats.” *Journal of Comparative Physiology A* 154 (3): 347–56.

Surlykke, Annemarie, Simon Boel Pedersen, and Lasse Jakobsen. 2009. “Echolocating Bats Emit a Highly Directional Sonar Sound Beam in the Field.” *Proceedings of the Royal Society B: Biological Sciences* 276 (1658): 853–60.

Tian, Biao, and Hans-Ulrich Schnitzler. 1997. “Echolocation Signals of the Greater Horseshoe Bat (Rhinolophus Ferrumequinum) in Transfer Flight and During Landing.” *The Journal of the Acoustical Society of America* 101 (4): 2347–64.

Ulanovsky, Nachum, M Brock Fenton, Asaf Tsoar, and Carmi Korine. 2004. “Dynamics of Jamming Avoidance in Echolocating Bats.” *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271 (1547): 1467–75.

Ulanovsky, Nachum, and Cynthia F Moss. 2008. “What the Bat’s Voice Tells the Bat’s Brain.” *Proceedings of the National Academy of Sciences* 105 (25): 8491–8.

Van Rossum, Guido, and Fred L Drake Jr. 1995. *Python Reference Manual*. Centrum voor Wiskunde en Informatica Amsterdam.

Virtanen, Pauli, Ralf Gommers, Travis E. Oliphant, Matt Haberland, Tyler Reddy, David Cournapeau, Evgeni Burovski, et al. 2020. “SciPy 1.0: Fundamental Algorithms for Scientific Computing in Python.” *Nature Methods* 17: 261–72. <https://doi.org/https://doi.org/10.1038/s41592-019-0686-2>.

Xie, Yihui, J. J. Allaire, and Garrett Grolemund. 2018. *R Markdown: The Definitive Guide*. Boca Raton, Florida: Chapman; Hall/CRC. <https://bookdown.org/yihui/rmarkdown>.

Yamada, Yasufumi, Yurina Mibe, Yuya Yamamoto, Kentaro Ito, Olga Heim, and Shizuko Hiryu. 2020. “Modulation of Acoustic Navigation Behaviour by Spatial Learning in the Echolocating Bat Rhinolophus Ferrumequinum Nippon.” *Scientific Reports* 10 (1): 1–15.